

Temperate summergreen forests of East Asia

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Abstract

The area of summergreen temperate forests lies in the eastern part of temperate zone, with- in cold and cool subzones of East Asia. The main vegetation type is mixed forests co-domi- nated by *Pinus koraiensis* and various broad-leaved tree species: *Tilia amurensis*, *T. mand- shurica*, *Fraxinus mandshurica*, *Quercus mongolica*, *Betula costata*, *Kalopanax septemlobus*, *Phellodendron amurense* and *Ulmus japonica*. Old-growth forests in the area were drastical- ly reduced in the 20th century as a result of forest exploitation and fires. However, they are still among the best preserved nemoral forest ecosystems in the world. This paper describes this vegetation in its basic types, with a focus on phytogeography, ecosystem structure and dynamics and developmental trends.

Keywords: East Asia, *Pinus koraiensis*, mixed forest, dynamics, diversity, nemoral zone, temperate vegetation

1. Introduction

The summergreen forests in East Asia are distributed within latitudinal range between 30 and 50°N. In these latitudinal limits climate drastically changes from ultracontinental in Mongolia, with desert as zonal vegetation type, to oceanic in Japan, with humid beech forests (Fig. 1).

Most western and driest summergreen forests first appear in the upper Amur basin and eastern spurs of Greater Xingan. They occupy northern slopes with more humid soils among steppes that represent major vegetation in landscapes. Interior summergreen forests are domi- nated by *Quercus mongolica*, forming pure stands or mixed with *Betula davurica*. The latter becomes dominant species in extreme northeastern part of the East Asian temperate zone. All components of the forest communities are drought tolerant and fire resistant. Fire is the most important factor influencing natural dynamics in the oak forests.

With the increasing humidity towards the east of continent, the dry interior oak forests change to humid, species rich, multi dominant summergreen forests mixed with temperate conifer species, such as *Pinus koraiensis* and *Abies holophylla*. The broadleaved–Korean pine forest is a zonal vegetation type in the maritime sector of the northern temperate subzone. It occurs in the Far East of Russia in the Sikhote Alin mountain range and in northeast China in the Changbai Shan, LaoYe and Lesser Hingan mountains. Relatively isolated areas of forests with *Pinus koraiensis* are found in northern (KOLBEK et al. 2003) and southern Korea (SONG 1988; KIM 1992), where they are associated with different vegetation types. The main vege- tation type is mixed forests co-dominated by *Pinus koraiensis* and various broad-leaved tree species: *Tilia amurensis*, *T. mandshurica*, *Fraxinus mandshurica*, *Quercus mongolica*, *Betu- la costata*, *Kalopanax septemlobus*, *Phellodendron amurense*, *Ulmus japonica* (KRESTOV 2003).

In the most humid conditions of East Asia in Japanese Archipelago the summergreen

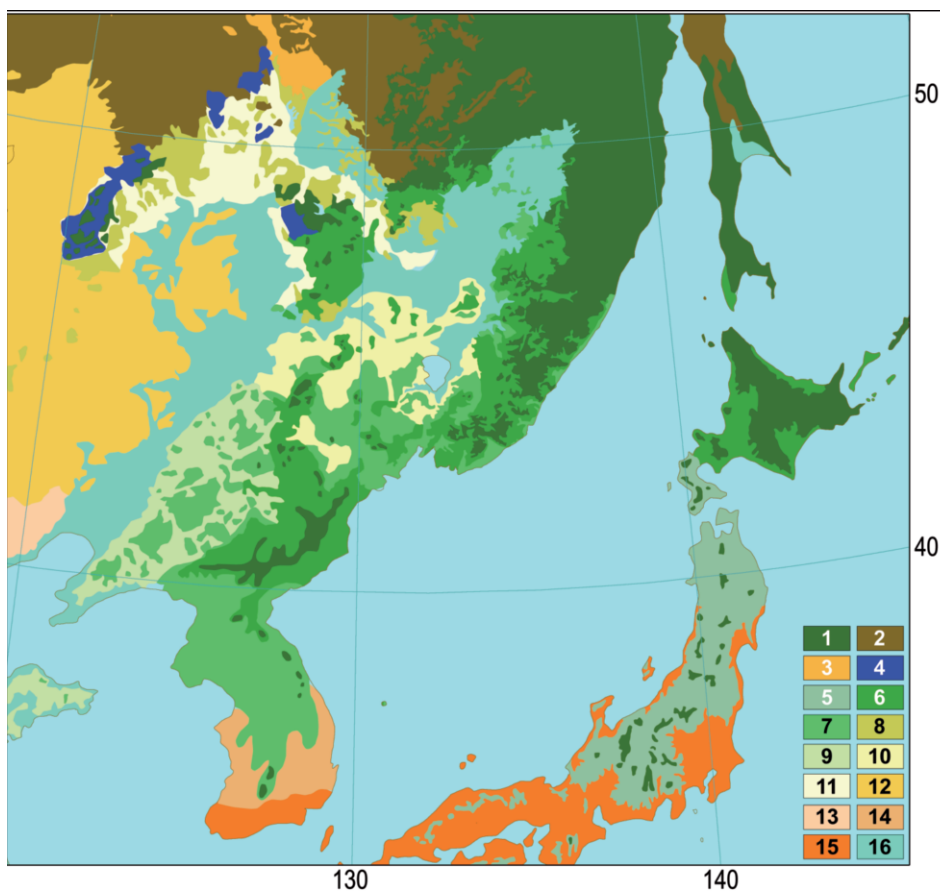


Fig. 1. Scheme of distribution of main vegetation types in the Asian mainland based on vegetation maps of YIM & KIRA (1975), SOCHAVA (1969 a) and ANONYMOUS (1982).

1. Boreal *Abieti-Piceetalia* (KRESTOV & NAKAMURA 2002) forests; 2. Boreal *Larix cajanderi* forests; 3. Boreal *Pinus sylvestris* forests; 4. Boreal *Betula platyphylla* forest; 5. Temperate *Fagetalia crenatae* forests; 6. Temperate mixed broadleaved-coniferous forests; 7. Temperate *Lespedezo-Quercetalia* forests; 8. Temperate *Querco-Betuletalia davuricae* (ERMAKOV 2003) forests; 9-11. Secondary shrubs on places of temperate forests; 12. Steppe and desert; derivative shrubs; 13. Derivative shrubs; 14. Temperate *Aceri-Quercetalia* forests with evergreen broadleaved trees; 15. Warm temperate *Camellitea japonicae* forests; 16. Wetlands.

forests; Wetlands are represented by series of *Quercus crispula*, *Fagus crenata* and *Fagus japonica* forests that occupy low mountain belt in Hokkaido and northern part of Honshu. These areas receive more than 1500 mm precipitation and are characterized by deep snow cover in winter time. Summergreen forests of Japan were treated as temperate rain forests by NAKAMURA et al. (2011).

This paper intends to overview the major regularities in distribution, stand structure and the major focal areas of the recent studies on history, diversity, ecology, dynamics and anthropogenic loss of the summergreen forests of East Asia.

2. Results and discussion

2.1 Distribution, climatic conditions and history of formation

The rather wide distribution of this forest type from the seacoast inland, where there is a sharp transition from an oceanic monsoon to a continental climate, have led to marked heterogeneity of vegetation within the zone. It is reflected in phytogeographical units (Table 1) and vegetation maps (KOLESNIKOV 1956 a, 1963, SOCHAVA 1969 a, b). The area remained unglaciated during the Pleistocene (GRICHUK 1984), although at present it borders with permafrost areas in the north. The present climatic contrasts, marine transgressions, and the long period of uninterrupted development of vegetation cause a great mixture of northern and southern as well as maritime and steppe elements in the flora and vegetation of the region.

The occurrence of this vegetation type between clearly distinguishable boreal and temperate zones is a subject of disagreement among phytogeographers. However, the dilemma of whether it should be regarded as boreal or temperate, has in recent decades been settled in favor of temperate. TATEWAKI (1958) related it to a special Pan Mixed forest zone, temperate in its nature, which includes also climatically and physiognomically similar vegetation of central Europe and in the eastern part of North America including the northern Appalachian mountains and the surroundings of the Great Lakes, though interrupted towards the interior of the continent by steppes or deserts. HÄMET-AHTI et al. (1974) treated this vegetation as the northern subzone of the temperate zone; SOCHAVA (1969 b) and KOLESNIKOV (1963) treated it as belonging to the nemoral and temperate zones, respectively.

At altitudes of 800–900 m in Sikhote-Alin and 500–600m on the southern spurs of the Tukuringra-Dzhagdy and Badzhal'skiy ranges, broadleaved–Korean pine forests gradually give way in the altitude range from 500–1200 to 1500–2000 m to evergreen conifer *Abies nephrolepis*–*Picea jezoensis* forests representing the oroboreal belt.

The climatic features of the broadleaved–Korean pine forest area are determined by the monsoon circulation of air masses. In winter the territory is under the influence of cold and dry air masses, formed in the region where the powerful Asian anticyclone develops. With the summer monsoon, southeastern winds carry cool and moist marine air during the first half of the summer, and very moist warm air in the second half. The coldest month is January; minimum temperature varies from -22°C to -26°C in the more continental part on the western slopes of Sikhote Alin, and from -17°C to -21°C on the eastern slope, exposed to the sea. The average summer temperature is $+15$ – 17.5°C on the coast up to $+18.5$ – 20°C in continental regions. The warmest month in the continental regions is July, in coastal regions August. The day degree temperature sums $[T_{\max}(0, T_i - 10)]$, where T_i is the mean temperature in $^{\circ}\text{C}$ of the i th day] in continental regions range from 2400° to 2600° in the southernmost part of the Russian Far East and from 1600° to 1800° in the northern part of the subzone. Kira's warmth index ranges from 45 in the north to 60 in the south of the lower belt (NAKAMURA et al. 2007) and from 25 to 45 in the oroboreal belt.

Many authors explain the species richness and high diversity of broadleaved–Korean pine forests by the fact that these areas have been unaffected by glaciation throughout the Pleistocene, or indeed since the high temperatures reached during the Pliocene optimum. Most of the present species constituting the broadleaved–Korean pine communities had ancestor taxa in the Tertiary palaeofloras of the Late Miocene and Pliocene. During the Pleistocene Ice Age the rich mesophytic flora in this area lost most of its mesothermic species. The vegetation of the maximum stage during the last glacial period consisted of drought-tolerant meadows and larch woodlands on the plains and dark-conifer taiga in the lower mountain belts. During the following warming, broadleaved temperate species invaded this territory from warmer and

Table 1. Distribution of dominant species, major phytosociological and phytogeographical units of East Asian temperate summergreen forests in the scheme of vegetation zones and continentality sectors (KRESTOV & NAKAMURA 2002; KRESTOV et al. 2006, NAKAMURA et al. 2007)

Subzone	Continentality sector				
	ultracontinental	continental	maritime	suboceanic	oceanic
Northern (cold) temperate	dominant species	Betula davurica, Ulmus macrocarpa, Pinus sylvestris	Quercus mongolica, Q. liaotungensis, Betula davurica	Pinus koraiensis, Fraxinus spp., Tilia spp., Quercus mongolica	Quercus crispula, Abies sachalinensis, Kalopanax septemlobus
	phytogeographical province	Daurian forest-steppe	Manchurian summergreen forest	Manchurian summergreen forest	Sakhalin-Hokkaido mixed forest
	alliance	Kitagawio terebinthaceae-Betulion davuricae	Dictamnno dasycarpic-Quercion mongolicae	Abieti nephrolepidis-Pinion koraiensis (north), Phrymon-Pinion koraiensis (middle), Jeffersonio-Quercion mongolicae (south)	Carpino-Quercion grosseserratae
Middle (cool) temperate	dominant species	Caragana microphylla	Caragana microphylla, Ostryopsis davidiana, Quercus mongolica, Ulmus macrocarpa	Abies holophylla, Pinus koraiensis, Quercus mongolica, Fraxinus spp., Tilia spp.,	Fagus crenata, F. japonica, Quercus serrata
	phytogeographical province	Mongolian steppe	Manchurian summergreen forest	Manchurian summergreen forest	Japanese summergreen forest
	alliance	unknown	unknown	Pino koraiensis-Quercion mongolicae (north), Lindero-Quercion (south)	Sasamorpha-Fagion crenatae sieboldii

wetter regions in the south. However, some of them had survived in refugia in the montane belt, and spread out widely with the warming. This is indirectly proved by the great number of endemic species in the Manchurian nemoral vegetation (QIAN et al. 2003).

According to the traditional, dominant-based, concept, the broadleaved–Korean pine forests are subdivided into southern, middle and northern units.

The southern broadleaved–Korean pine forests occur from the southernmost points of the Russian Far East at 42°40′N, northwards to a latitude of 44°N. In the southern spurs of the Sikhote Alin mountain range and on the Borisovskoye plateau they occupy gentle slopes of low mountains or hills within the altitude range from 50 to 600 m. These forests have a very rich species composition and a complex structure. They are usually dominated by two species of nemoral conifers *Abies holophylla* and *Pinus koraiensis*, which reach 45 m in height, as well as by nemoral broadleaved trees. *Carpinus cordata* always forms the lower tree layer on mesic sites. The shrub layer includes nemoral shrubs with southern and typical Manchurian ranges. The herb layer consists mostly of nemoral mesic herbs, ferns and sedges. Less significant are xeromesic herbs and sedges. Their ecological range is from xeromesic to hygromesic, and nutritionally from medium to very rich. Overall, the species composition of southern mixed forests includes 565 species of vascular plants. The species with Manchurian distribution have an affinity to geoelements in the Korean–South Manchurian and the Japanese–South Manchurian areas.

Typical or middle broadleaved–Korean pine forests usually form the lowest altitudinal vegetation zone in southern and middle Sikhote Alin range. *Pinus koraiensis* and broadleaved nemoral trees with typical Manchurian and Japanese-Manchurian distribution form the dominant layer. These forests accommodate more than 500 vascular plant species, mainly of the Manchurian geo-element, but with more Okhotsk-Manchurian species than the southern forests. The ecological range of the forests is xeromesic to mesic, and nutritionally medium to very rich. The typical broadleaved–Korean pine forests were considerably disturbed by clear-cutting in the past 80 years. Most of the conserved stands of these forests lie on the west slope of the Sikhote Alin range, along the big rivers (water-protective belts), and in the Bikin and Bolshaya Ussurka river basins. In addition to clear-cutting, the frequent fires cause great damage to the forests. About 30% of the distribution area is today occupied by stable secondary oak forests of low productivity with *Quercus mongolica* replacing the typical broadleaved–Korean pine forests.

Northern broadleaved–Korean pine forests occur in all parts of the distribution area of *Pinus koraiensis*. In the southern Sikhote Alin they occupy the upper part of the broadleaved–Korean pine zone, while in the north they dominate completely. The flora of this forest type includes 394 species of vascular plants. The role of Manchurian nemoral species in the phytocoenoses decreases in comparison to the other vegetation classes discussed. The role of taiga and deciduous boreal forest species increases. The canopy is dominated by both nemoral and taiga species. The ecological range differs from typical broadleaved–Korean pine forests in that the main phytocoenoses are concentrated on mesic medium sites. On poor sites mosses and small herb types of the taiga occur. At present, the northern broadleaved–Korean pine forests are strongly affected by clear-cutting and by subsequent fires, and have been changed into persistent derivative *Betula platyphylla* and *Larix cajanderi* forests.

Pure *Pinus koraiensis* forests have a narrow range on the eastern slopes of the Sikhote Alin range. The canopy is absolutely dominated by *Pinus koraiensis* reaching its maximum size in pure pine forests: 40–45 m high and about 1.2 m in diameter. The sub-tree layers are not clearly expressed. The shrub layer usually consists of *Lespedeza bicolor*, *Rhododendron mucronu-*

latum, *Ribes horridum* and *R. maximoviczianum*. In the herb layer single individuals or small groups of oligomesotrophic, xeromesic and mesic herbs and dwarf shrubs may be present. The ecological range of this class is xeromesic to mesic, growing on poor to medium brown forest soils and podzols. The present distribution of this forest is very local because of a unique climatic condition on the eastern marine slope with low temperatures and high humidity on the one hand, and a strong disturbance regime, mainly clearcutting, on the other hand.

According to our recent phytosociological study the East Asian summergreen forests (KRESTOV et al. 2006) were related to the class *Quercetea mongolicae* Song ex Krestov et al. 2006 that includes the following orders and alliances with constant participation of Korean pine:

Class

Order

Alliance

Quercu mongolicae-Betuletea davuricae Ermakov et Petelin 1997 (QUE-BET)

Quercu mongolicae-Betuletalia davuricae Ermakov 1997 (Que-Bet)

Kitagawio terebinthaceae-Betulion davuricae Ermakov 1997

Lespedezo bicoloris-Quercetalia mongolicae Krestov et al. 2006 (Les-Que)

Corylo heterophyllae-Quercion mongolicae Krestov et al. 2006

Quercetea mongolicae Song ex Krestov et al. 2006 (QUE)

Tilio amurensis-Pinetalia koraiensis Kim ex Krestov et al. 2006 (Til-Pin)

Phrymo asiaticae-Pinion koraiensis Krestov et al. 2006

Jeffersonio dubiae-Quercion mongolicae Kim ex Krestov et al. 2006

Aceri-Quercetalia mongolicae Song ex Takeda et al. 1994 (Ace-Que)

Rhododendro-Quercion mongolicae Song ex Takeda et al. 1994

Lindero obtusilobae-Quercion mongolicae Kim 1990

Fagetea crenatae Miyawaki, Ohba et Murase 1964 (FAG)

Saso-Fagetalia crenatae Suzuki-Tokio 1966 (Sas-Fag)

Saso-Fagion crenatae Miyawaki, Ohba et Murase 1964

Sasamorpho-Fagion crenatae Miyawaki, Ohba et Murase 1964

Quercetalia serrato-grosseserratae Miyawaki et al. 1971 (Que-Que)

Carpino-Quercion grosseserratae Takeda, Uematsu et Nakanishi 1983

2.2 Stand structure

The dominants of broadleaved–conifer forest ecosystems differ in growth forms and life strategies. Up to 12 tree species growing together can be found in the upper layer of one forest stand. The main species forming the dominant layer are *Abies holophylla*, *Betula costata*, *Fraxinus mandshurica*, *F. rhynchophylla*, *Juglans mandshurica*, *Kalopanax septemlobus*, *Phellodendron amurense*, *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, *T. mandshurica* and *Ulmus japonica*. Their usual height is 25–35 m, but on rich sites *Abies holophylla* and *Pinus koraiensis* may reach a height of 45 m, exceeding the height of other tree species and forming a sparse layer above the canopy. Uneven age structure is a characteristic feature of oldgrowth broadleaved–Korean pine forest.

Lower sublayers normally occur in all communities of mixed forests. The main species in the second sublayer are *Acer mandshuricum*, *A. mono*, *Maackia amurensis*, *Micromeles alniifolia*, *Padus maximowiczii*, *Sorbus amurensis*, *Taxus cuspidata* and *Ulmus laciniata*. Their crowns occupy a space from 12 to 20 m above the ground, without a visible boundary separating them from the crowns of the upper layer. In almost all undisturbed phytocoenoses a

third layer is clearly expressed. *Acer pseudosieboldianum*, *A. ukurunduense*, *Carpinus cordata* and *Ligustrina amurensis* form a sublayer 6–10 m in height. They are all shade-tolerant species, but they differ in ecology and growth form.

The shrubs in the broadleaved–Korean pine forests are diverse and abundant. Commonly the shrub layer is sparse under the canopy and sometimes very dense in the gaps. It may include some sublayers, because of differences in the height of the shrubs. Whereas *Berberis amurensis*, *Lonicera chrysantha* and *Ribes maximoviczianum* normally do not exceed 1 m in height, *Acer barbinerve* and *Corylus mandshurica* may reach 6–7 m. A special feature of this kind of forest is the presence of woody vines. The most common are *Actinidia arguta*, *A. kolomikta*, *A. polygama*, *Celastrus flagellaris*, *C. orbiculatus*, *Parthenocissus tricuspidata*, *Pueraria lobata*, *Schisandra chinensis* and *Vitis amurensis*.

The herb layer is usually very well developed and characteristic in broadleaved–Korean pine forests; however, the driest sites on steep slopes and ridges may be free of herbs. Usually herbs of different species are grouped in patches of different size occupying certain ecological niches. Because of light deficit, almost all herbs are shade-tolerant, with intensive vegetative reproduction. The herbs differ very greatly in growth forms and life strategies. The nemoral wideleaved forbs – herbs with wide leaves oriented in the same horizontal plane – are more competitive. The average number of plants for one phytocoenosis may vary between 20 and 100 species.

A moss and lichen layer is not characteristic of the nemoral vegetation. However, the quantity of mosses may increase in the northern part of the range of Korean pine forests. A moss layer is often formed of common boreal species such as *Hylocomium splendens*, *Pleurozium schreberi* and *Ptilium crista-castrensis*. As small patches, the nemoral mosses *Climacium dendroides*, *Pleuroziopsis ruthenica* and *Rhytidiadelphus triquetrus* also can be found.

2.3 Disturbance regime and dynamics

Having many potential strong competitors, a broadleaved–Korean pine phytocoenosis is characterized by complex dynamics even during the lifespan of one generation of Korean pine. This is controlled by different ecological factors, and by the disturbance regime. In a phytocoenosis oriented approach a scheme of nemoral forest dynamics was elaborated by IVASHKEVICH (1933), and later added to and improved by KOLESNIKOV (1956 b). Since that time no new ideas or special research concerning phytocoenosis dynamics have been proposed. Some significant researches on stand dynamics have been accomplished with no success on the way to confirm or reject the Kolesnikov's hypothesis on the forest dynamics.

According to the scheme of Ivashkevich and Kolesnikov the normal development of a mixed phytocoenoses goes through a sequence of eight stages replacing one another. The first stage starts when the new surviving generation of Korean pine is appearing under the canopy of the mother generation (Table 2). Then the development of Korean pine normally encounters two periods of suppression as a minimum – the first in the youngest years (Stage 1), and the second when it starts forming a canopy (Stage 3). These periods are indicated by analysis of growth patterns. At 160–200 years (Stage 5) the Korean pine generation reaches maturity.

Stand age structure normally shows clusters of *Pinus koraiensis* trees regenerated at the same time. The existence of these clusters is caused by the propensity of Korean pine to intensive regeneration every 35–40 years – the so-called explosions of regeneration mentioned by IVASHKEVICH (1933) and SOLOVYOV (1958) – and by a complex patch structure of a phytocoenosis that reflects the gap character of regeneration. Gap formation in broadleaved–Korean pine forests depends mainly on natural death of old trees, and rarely, but over large areas, on natural disturbances such as winds and storms. The size of gaps ranges

Table 2. KOLESNIKOV's (1956 b) hypothesis on the development of stands of Korean pine (*Pinus koraiensis*) in the middle part of its range during the life cycle of one generation

Stage	Duration (year)	The state of main phytocenotic components
1(6)	1-40	Appearance and early development of a new Korean pine generation, with the preceding generation causing a deficit of light and nutrition.
2(7)	40-80	Development of Korean pine saplings within a subordinate layer
3(8)	80-120	Maximum increment in height and inclusion in the canopy. Canopy density is increasing. Role of broadleaved trees of older generations in canopy composition is important.
4	121-160	Fast increment in diameter of young Korean pines and dominance in the upper canopy. Old broadleaved trees and oldest trees of Korean pine die and fall. Density of young generation of Korean pine increases.
5	161-200	Mature canopy stage. Maximum proportion of Korean pine in canopy (up to 80-90%) while proportion of broadleaved trees is minimal. Increment rates of Korean pine are small. New pine seedlings die quickly. Lower layers are badly suppressed.
6(1)	201-240	Fast death of trees of older generation (older than 300 years). Canopy density and proportion of Korean pine decrease (to 50-60%). Appearance of new Korean pine generation (future dominant generation) as suppressed saplings. Shrub and herb layers grow up. Tree layer becomes susceptible to insects, droughts and wind impact.
7(2)	241-280	Over-mature stage. Almost all older Korean pines, and most broadleaved trees associated with the dominant generation of Korean pine have died. Minimum proportion of Korean pine in canopy (30-50%), minimum canopy density. Maximum development of lower layers, vines and saplings of broadleaved trees. No seedlings of Korean pine. Destruction of the canopy.
8(3)	>281	Place of older generation is occupied by young generation of Korean pine and broadleaved trees. Slow increase of young pine proportion in biomass and canopy density. Death of shade-intolerant shrubs and herbs.

Note: The numbers in parentheses indicate the stage of the preceding and following generations of Korean pine

from 20 m (crown diameter size) to 40–50 m in diameter. Usually crowns of broadleaved trees, which are sufficiently transparent to light for a new generation of Korean pine to develop, close the gaps formed by Korean pine. Korean pine increases in biomass as well as in basal area, but at the same time biomass and basal area for broadleaved species remain relatively stable. With increasing age there is a tendency for the number of stems to decrease. The basal area and total volume increase up to an age of 300 years, and then decrease.

In recent studies of ontogeny of trees, shrubs and herbaceous species, disturbance history and disturbance regimes, natural regeneration patterns of tree and shrub species; structure of population mosaics of different tree species and factors influencing structure of the mosaics and stand canopy structure (by terrestrial laser scanning) based on large (1-10 hectare) permanent plots, we received information that clarify the pattern of natural dynamics of old-growth mixed forest (UKHVATKINA et al. 2011)

Immature plants (small saplings) of the dominant species can survive for a long time without height increment under stand canopy. Age of immature plants of conifers (*Pinus koraiensis*, *Picea jezoensis*, *Abies nephrolepis*) can reach 100 and more years. These plants are very important for the natural stand dynamics, since after light conditions improvement (formation of a canopy gap) they sharply increase growth and occupy the gap.

Disturbance history of broadleaved-Korean pine stands shows, that in absence of fires and human impacts, low and moderate disturbances are prevalent (Fig. 2). Stand-replacing disturbances are not characteristic. Moderate disturbance seems to be associated with strong winds, some peaks of growth release coincide with the time when typhoons comes. This disturbance regime promotes coexistence of different tree species.

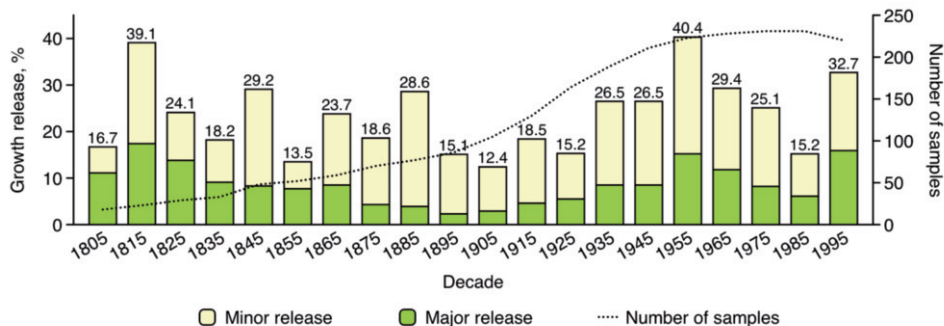


Fig. 2. 200-years disturbance history of an old-growth Korean pine dominated forest (3 ha sample plot, Verkhneussurijsky research station FEB RAS).

Pre-generative plants of dominant species with normal vitality were found only in canopy gaps or on their periphery. This suggests that development of shade-tolerant species (for example, *P. jezoensis* and *A. nephrolepis*) as well as light-demanding plants (for example, *Betula costata*) requires a significant improvement of light conditions. Low and moderate intensity disturbances lead to forming of small gaps so for most plans multiple releases is necessary to reach the stand canopy.

The dynamics of population mosaics of different dominant species is similar. Immature plants form dense groups (accumulation of small saplings), spatial distribution of virginal plants is more homogenous and finally distribution of generative plants is substantially homogenous, regardless of factors determined by topography.

The study of age structure in old growth Korean pine forest led to confirmation of the cyclic pattern of development and to its connection with natural patch structure (ISHIKAWA et al. 1999). Growth releases on increment cores suggested peak periods of growth releases indicating partial canopy disturbances have repeatedly occurred over the past 230 year at intervals of about 80 years. Under the natural disturbance, *Pinus koraiensis* has maintained its populations through its dependence on canopy gaps for establishment. Age distribution and gap dependence of *Picea jezoensis*, *Abies nephrolepis* and *Acer mono* suggested continuous establishment of these species under a closed canopy, whereas occasional establishment of *Tilia amurensis* was derived largely from vegetative reproduction. Restricted establishment of *Abies holophylla* and *Betula costata* suggested a variety in kinds of disturbance throughout the histories.

The most important disturbance factors determining the pathway of recovery in the broadleaved-Korean pine forests are wood harvesting and human-initiated fires. The pattern of community development after cutting is similar to that of natural dynamics. Most nemoral species continue to be present in the ecosystem but decrease sharply in biomass because of the appearance of seral gap-dependent species (*Actinidia kolomikta*, *Aralia elata*, *Betula platyphylla*, *Padus maackii*). During the first years of succession the diversity of nemoral species decreases only slightly, as a result of strong competition from gap-dependent species

for nutrients and space. Following this invasion, the number of species in the community reaches a maximum at this time. With the formation of a forest environment the recovery of the former diversity may take 20-30 years. The recovery of community structure requires a longer time, equal to the life span of the dominant trees.

Wildfires are rare events in the nemoral forest zone because the decomposition of debris is relatively fast and no great amount of flammable material accumulates. However, a wild fire occasionally takes place in the driest years. Post-fire succession may continue for some hundreds of years, and may never reach the climatic climax stage because of the formation of stable secondary phytocoenoses dominated by self-regenerated long-lived species such as *Larix cajanderi* in the northern parts of the Korean pine forest range.

Ground fires are very common in nemoral ecosystems. They do not affect significantly species diversity, because most nemoral species are relatively fire-tolerant. Spring ground fires initiate seed germination of some gap-dependent species (*Betula platyphylla*, *Chamaenerion angustifolium*, *Chelidonium majus* var. *asiaticum*), which can take prominent positions in early post-fire succession (KOMAROVA 1992). If cover by the tree canopy remains the same, the nemoral species may quickly recover. However, the conifer seedlings are seriously damaged and usually die. If ground fires are repeated regularly every one to three years, the species of the nemoral ecosystems gradually give place to fire-tolerant forms. The nemoral species, in the first instant the nemoral trees, decrease in abundance and diversity. Fire-tolerant species of all growth forms become more competitive in the community and take the leading position in all layers. Repeating ground fires bring *Acer mono* to the dominance that may considerably inhibit regeneration of shade-intolerant mesic species, including Korean pine.

2.4. Associated animals

Korean pine and Mongolian oak are the basis for the major food chains in this vegetation zone. The longest food chains from seeds and acorns include several species of small rodents (*Sciurus vulgaris mantschuricus*, *Clethrionomys rufocanus irkutensis*, *Eutamias sibiricus*), wild boar (*Sus scrofa continentalis*) and black bear (*Ursus tibetanus*), and continue in predators, which include abundant representatives of the mink family (*Martes zibellina schantari-cus*, *Mustela sibirica*) specializing in small rodents, and big cats [the Amur leopard (*Panthera pardus orientalis*) and Amur tiger (*P. tigris altaica*)] specializing in big artiodactyls. Also closely connected with the ecosystem are a number of deer [*Cervus elaphus xanthopygus*, *C. nippon*, roe deer (*Capreolus capreolus*) etc.]. The population of wolves (*Canis lupus*) is controlled mainly by tigers, because the ecological niches of these species are very similar. The forest avifauna is rich. The birds include *Eurystomus orientalis*, *Falci pennis falcipennis* (a rare species) and *Tetrastes bonasia sibiricus*. *Nucifraga caryocatactes macrorhynchos* specializes in the seeds of Korean pine, but it is not as abundant as in ecosystems with *Pinus pumila* or *P. sibirica*. Some birds: Eurasian nutcracker, Eurasian nuthatch (*Sitta europaea*), Japanese grosbeaks (*Eophona personata*), hawfinch (*Coccothraustes coccothraustes*), Eurasian jay (*Garrulus glandarius*), azure-wing magpie (*Cyanopica cyana*) and animals: squirrel, Siberian chipmunk, and other rodents play the important role in Korean pine dissemination that described comprehensively by various authors (KOSTENKO 1966; HUTCHINS et al. 1995; OMELKO et al. 2007).

2.5 Change in forest area

Over seventeen years, changes in forest cover (103 ha) in Primorskiy Krai (ANONYMOUS 1990) were:

	1966	1983	change (%)
scrub	25.1	38.1	+51.8
oak forests	2301.2	3126.8	+35.8
other broadleaved forests	2123.6	1733.4	-18.4
larch forests	1090.1	1136.7	+4.3
broadleaved Korean-pine forests	2439.4	2181.9	-10.6
total forest area	0 778.0	11 146.1	+3.4

The maps of potential vegetation (KOLESNIKOV 1956 a, 1961) and bioclimatic indices (KRESTOV & NAKAMURA 2007) assume a wide distribution of broadleaved–Korean pine forests on edaphically suitable sites in the subarctic sector of the northern temperate zone. However, the area of this vegetation type has considerably decreased in the Russian Far East. In the beginning of the 19th century the basin of the Ussuri river was settled by Russians. The first forest records appeared in the second half of that century (BUDISHCHEV 1898), but more extensive forest records from China and Russia date from the time when local and international forest companies started to operate at the beginning of the 20th century. According to records from the 1890s, the broadleaved–Korean pine forests on Sikhote Alin covered an area of about 65000 km². Nowadays the areas have decreased by 33000 km² (PETROPAVLOVSKIY et al. 1985). The major reasons for the decrease of forest area are extensive logging and fires. The area formerly covered with broadleaved–Korean pine forests is now occupied by secondary *Betula platyphylla* and *Larix cajanderi* forests (3500 km²) formed mainly after logging and/or single fires, secondary *Quercus mongolica* forests (12000 km²) formed after logging and regularly repeated fires, especially around settlements, and by agricultural land and meadows (about 15000 km²). Decrease in forest area, however, does not reflect the decline of the quality of forests as a consequence of the disturbance regimes and the features of post disturbance succession in different vegetation types.

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