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THE DISTRIBUTION AND PHYTOGEOGRAPHIC RELATIONSHIPS OF THE WOODY PLANTS OF THE SOVIET FAR EAST

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ABSTRACT

The woody flora of the Soviet Far East is rich and diverse when compared to dendrofloras at similar latitudes of the world. The bulk of this region lies north of latitude 46 degrees. This area includes the northernmost stations in eastern Asia for many genera, e.g., *Abelia, Acer, Aralia, Carpinus, Corylus, Fraxinus, Hydrangea, Ilex, Juglans, Magnolia, Morus, Quercus, Phellodendron, Sasa, Schizophragma, Schisandra, Skimmia, Syringa, Tilia,* and *Ulmus.* The majority of the woody species native to the Soviet Far East do not occur elsewhere in the U.S.S.R. Many of the trees and shrubs are native to Japan, Korea, or China and extend into the Soviet Union, or are more closely related to temperate Asian taxa than to European or Siberian taxa. The woody species can be subdivided into seven major elements and from those elements four phytogeographic regions can be recognized in the Soviet Far East based upon the distribution of 311 species studied. The southern part of the region studied, along with most of Manchuria, serves as a refugium for taxa believed to have persisted from the Tertiary or to be at least derived from Tertiary ancestors.

Key words: Soviet Far East, dendroflora, phytogeography.

INTRODUCTION

The flora of the Soviet Far East contains approximately 3100 species of vascular plants (Voroshilov 1982). An interesting array of woody plants, including many broad-leaved, mesic taxa occur here even though 42% of the forested area of this region is covered by larch forest (Ageenko 1969). This study will focus on the distribution of the woody flora of the far eastern region and demonstrate the phytogeographic relationships of this dendroflora with other areas of the U.S.S.R., Manchuria, Korea, and Japan.

The eastern Soviet Union can be divided into three major geographic regions: Eastern Siberia, the Arctic, and the Far East (Fig. 1). The Far East includes virtually all of the Kamchatka Peninsula, the Kuril Islands, Sakhalin Island, the entire Amur-Primorsky region of the mainland, and the coastal regions adjacent to the Okhotsk Sea. Prior to World War II, Sakhalin and the Kuril Islands belonged to Japan. The Stanovoy Mountain Range forms an arc delimiting the northwestern boundary of the Far East (Fig. 2).

Physical Aspects

The physical aspects of the Soviet Far East are treated in the valuable work of Suslov (1961), on which the following summary is based.

The southern mainland of the Far East is often referred to as the Amur-Primorsky region and is characterized by its southerly location (between 42 and 55 degrees north latitude), pronounced monsoon type of climate, absence of glaciation

Fig. 1. Map showing three major geographic regions of the eastern Soviet Union.

in post-Tertiary times, and an interweaving of the northern landscapes of Eastern Siberia and Okhotsk taiga with southern landscapes of neighboring Manchuria and Korea.

Two major mountain ranges are separated by wide plains in the Amur-Primorsky region. The north-south running Sikhote-Alin range lies parallel to the Sea of Japan. The taller ridges of 4300 ft in the north gradually decrease to 3300 and 2300 ft in the south just northeast of Vladivostok. Forest vegetation ranges from oak to mixed broad-leaved/coniferous to coniferous forests at higher elevations.

The Yankan-Tukeringra-Dzhagdy range in western Amur-Primorsky extends basically east to west and lies north of the Amur River. These mountains are formed chiefly of metamorphic schists, massive conglomerates, calcareous sandstones, cherts, and crystalline limestone.

The Sea of Okhotsk, bounded on the northeast by the Kamchatka Peninsula, on the southeast by the Kuril Island chain, and to the south by Hokkaido, Japan, has a major influence on the vegetation of the coastal regions of the mainland. The low air temperature throughout the year, cold winters, and short cool summers with frequent fog reduce the water temperature.

The major mountain range of the northwestern coastal region of the Sea of Okhotsk is the Dzhugdzhur Mountain Range. In the southern part, this range arcs in a southwesterly direction, converging with the Stanovoy range. The major peaks of the Dzhugdzhur range reach about 7200 ft. Well-defined longitudinal valleys separate the Dzhugdzhur from the smaller Pribezhnaya mountains; the latter drop sharply off to the sea.

Sakhalin, a narrow island almost 600 mi long, lies parallel to the mainland coast and only 4 mi from it at the closest point. The two major mountain ranges are separated by a diagonal valley dividing the island into a southern and northern half. The highest peaks are 5500 to 6000 ft. The climate is relatively severe except in the southern part, where it is more typical of that experienced in Hokkaido.

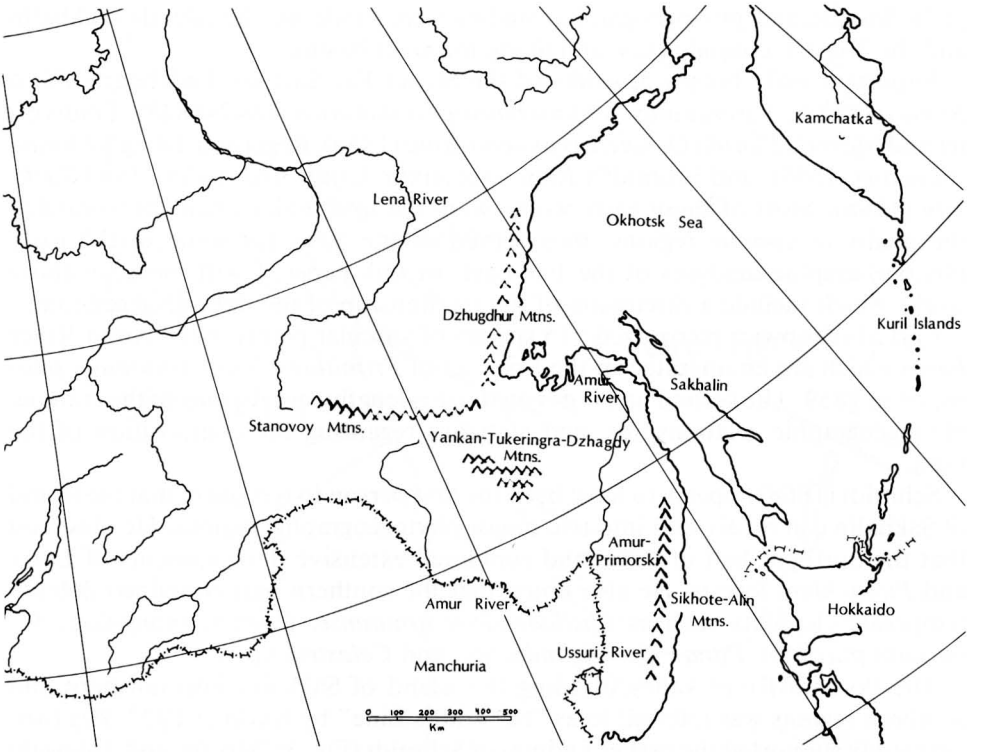

Fig. 2. Map of eastern U.S.S.R. showing major mountain ranges, rivers, regions, and islands.

Suslov (1961) cites −9.3 F (−23 C) as the average temperature for the coldest month in the northern part, whereas the southern tip has an average temperature of 17.5 F (−8 C).

The large peninsula of Kamchatka begins near 60 degrees north latitude and extends almost 720 mi southwards to 51 deg north latitude. Western, central, and eastern mountain chains are the main orographic features of this region. The highest peak, the extinct volcano Ichinskaya, is 11,834 ft. On the Kuril Islands active volcanos are present. The extremely severe climate is influenced by the cold seas and ocean currents; as a result, the vegetation is typically boreal to alpine tundra.

The Kuril Islands form an arc which links Hokkaido, Japan to the Kamchatka Peninsula. This 750-mi archipelago consists of 56 islands along with numerous rocky islets. The southern Kurils including the major islands of Iturup and Kunashir, are separated from the more northerly islands by the Iturup Strait. Nearly all the Kurils are volcanic in origin, 35 to 40 of them currently active. Most volcanic cones are between 1650 and 4290 ft high, while a few exceed 6000 and 7000 ft. Long, cold winters and cool, wet, often foggy summers mark the climate of these islands.

Background

In the past, physical access to the far eastern region of the Soviet Union has been difficult and limited largely to the major river systems. Thus, much of the

early floristic and phytogeographic studies were made on the islands (Sakhalin and the Kurils), coastal areas, and along the river basins.

Important early botanical works of the Soviet Far East are Ledebour's *Flora Rossica* (1842), Turczaninow's *Flora baicalensi-dahurica* (1842–1845), Trautvetter and Meyer's *Florula Ochotensis phaenogama* (1856), Regel and Tiling's *Florula Ajanensis* (1859), and Schmidt's *Reisen im Amur-Lande und Auf der Insel Sachalin* (1868). Most of these early works were the first major attempts to catalog the plants of specific regions; they served as the basis for some of the early phytogeographic analyses of the Far East. In this paper, I will focus on those works which include a discussion of the relationship of the flora or vegetation.

Carl Maximowicz recognized 915 species of vascular plants in the Amur River Basin which are enumerated in the first half of *Primitiae Florae Amurensis* published in 1859. The second half is devoted to his lengthy discussions of the climate, phytogeographic relationships, and statistics regarding the composition of the flora.

Schmidt (1868) appears to have been the first person to recognize that the island of Sakhalin can be divided into two major phytogeographic regions. He observed that the northern half of the island contained extensive developments of *Larix* and *Picea/Abies* forests. He also noted that the southern part contained definite temperate elements such as *Phellodendron amurense, Quercus mongolica, Viburnum plicatum, Panax* sp., *Actinidia* sp., and *Celastrus* sp.

The Poronai River valley dividing the island of Sakhalin into northern and southern regions was referred to as "Schmidt's Line" by Kudo in 1927. His two-year study supported the earlier findings of Schmidt (Fig. 3). Miyabe and Tatewaki (1937) presented further evidence to support the recognition of this phytogeographic boundary.

Tatewaki (1958) outlined the characteristics of Schmidt's Line by the features which are present north of the line. These are an extensive development of *Larix kamtschatica,* the predominance of *Picea ajanensis* and *Abies sachalinensis,* the presence of arctic and subarctic plants, the absence of *Sasa* species, the lack of vines (except for *Clematis*), and the sharp decrease in temperate broad-leaved trees.

Miyabe (1890) and Engler (1899) discussed the role of Sakhalin and the Kuril Islands for the migration of plants. Later, Takeda (1913) supported Miyabe's and Engler's findings and stated that "in particular, the Kuriles served as an avenue for the movement of Arctic-alpine elements in the Kuriles and the higher elevations of Hokkaido."

The Kuril Island chain was the object of several botanical studies. In a 1922 paper, Professor Y. Kudo documented the major difference between the flora and vegetation of the southern and northern Kuril Islands. Tatewaki (1932) proposed that the boundary line between the two phytogeographic regions be called "Miyabe's Line" (Fig. 3).

Hulten (1933) studied the origin and distribution of the flora in the Kuril Islands and concluded that the large, southernmost islands of Kunashir and Eterofu are phytogeographically the same as Hokkaido. The remainder of the island archipelago, he concluded, was related to the flora of Kamchatka. In 1947, Tatewaki provided further support for the recognition of "Miyabe's Line" in a detailed statistical analysis of the Kuril flora.

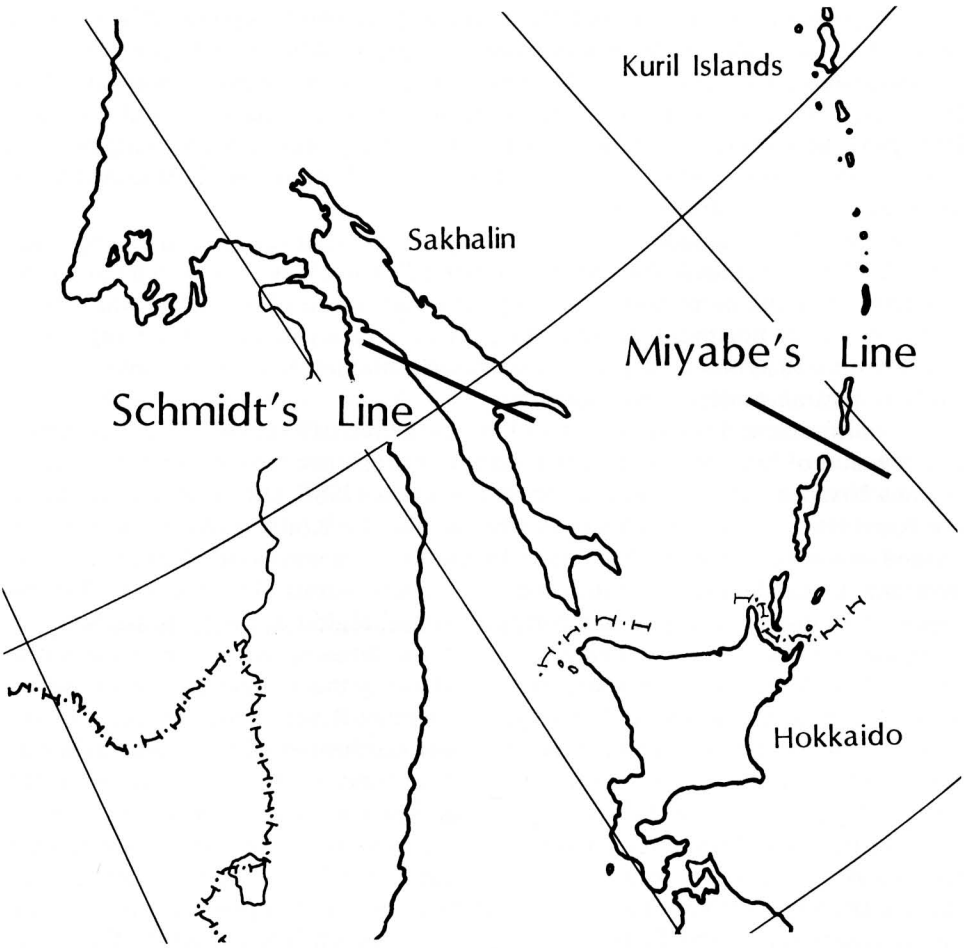

Fig. 3. Map showing position of Schmidt's Line on Sakhalin and Miyabe's Line in the Kuril Island chain, two important phytogeographic boundaries in the islands north of Japan.

Miyabe's Line is characterized by several features found north of the demarcation which are largely or totally absent south of it. These are the presence of spruce/fir and larch forests, the dominance of subarctic elements, the lack of broad-leaved forests belonging to temperate eastern Asia, the lack of climbing plants, and the sudden decrease in the number of Japanese, Chinese, and temperate eastern Asian elements (Fig. 3).

More recent works include a detailed study of the forest ecology of the islands of the North Pacific by Tatewaki (1958) and Ito (1980). Both papers support the recognition of these lines.

Modern Soviet floristic works used in this study include *Woody Flora of the Far East* by Ageenko, Vasilyev, and Globa-Mikhaylenko (1982), *Flora and Vegetation of the Ussuri Nature Preserve* by Kharkevich (1978), *Manual of Vascular Plants of the Kamchatka Oblast* by Kharkevich and Cherepanov (1981), *Flora of the Magadan Oblast* by Khokhryakov (1985), *Manual of Vascular Plants in the Vicinity of Vladivostok* by Vorobiev (1982), *Manual of Plants of the Soviet Far*

East by Voroshilov (1982), and the recently published *Vascular Plants of the Soviet Far East,* Part I, by Kharkevich. (1985). *A Manual of Higher Plants of Sakhalin and the Kuril Islands* edited by A. I. Tolmachev was published in 1974; however, I have not seen this volume. In addition, this paper would not have been possible without the detailed distribution maps presented in *Areas of Trees and Shrubs of the USSR,* Volume I (1977) and Volume II (1980), edited by Sokolov, Svyazeva, and Kubly.

The flora of Kamchatka Oblast was studied by Kharkevich and Cherepanov (1981). They concluded that the Kamchatka Peninsula is strictly related to the Far East while the more northerly nonpeninsular region of the oblast was related to the Arctic or northeastern Siberian provinces. They described the vegetation of the peninsula as boreal taiga and subdivided it into five floristic regions (western, middle, central, eastern, and southern).

The only current flora of the Soviet Far East is that of Voroshilov (1982), which is a revision of his 1966 flora of that region. Voroshilov recognized nine floristic regions based largely on those given in the Flora USSR (1933–1960). Sakhalin, the Kuril Islands, the Kamchatka Peninsula, and the Komandor Islands are each treated as a floristic region. The Amur-Primorsky area was divided into Primorye, Western Amur, Southern Amur, and the Eastern Amur. The Okhotsk floristic region is confined mainly to the northern coastal region of the Okhotsk Sea.

Ageenko et al. (1982) delineated four floristic areas each with their particular flora. Their Manchurian floristic area, containing the richest and most varied flora, occurs in the southern Primorye, the Ussuri River basin, the coast of the Sea of Japan, the Middle Amur river basin, and northeastern China. The Okhotsk-Kamchatka floristic area is less diverse and is found on the lower reaches of the Amur river, Sakhalin, and the Kuril Islands. The Chulitkan (Beringian), floristic area, the most northern of the floristic areas, occupies the Anadyr and the Penzhina rivers and the Chukotka peninsula. The fourth major floristic area recognized was the Eastern Siberian (Yakutsk) flora, which extends into the upper Zeya and central Amur rivers across the Stanovoy range from eastern Trans-Baikal. They also recognized other vegetation complexes of the steppe Mongolian-Dahurian floras, the ante-"subtropical" North Korean flora, and the forested "subtropics" of northern Japan common to southern Sakhalin and the southern Kuril Islands.

The most recent floristic work for this region is the publication of the first of a multi-volume treatment, *Vascular Plants of the Soviet Far East,* Part I, by Kharkevich (1985). The boundaries of this work are defined by political considerations rather than the phytogeographic ones recognized by Voroshilov. The work in progress includes the Primorye and Khabarovsk districts and the Amur, Magadan, Kamchatka, and Sakhalin oblasts. Kharkevich (1985) divided the Soviet Far East into 20 floristic regions.

The boundaries of the Soviet Far East used in this paper are in agreement with those used by Voroshilov (1982) rather than those of Kharkevich (1985).

It is clear that Soviet workers have not been in agreement on floristic subdivisions of the far eastern region of their country. Also, it is interesting to note that the recent Soviet works mentioned in this paper do not acknowledge Schmidt's Line or Miyabe's Line, nor do they cite most of the important floristic and phytogeographic papers of Japanese botanists.

There is a wealth of books and published papers relating to the flora and

vegetation of the Soviet Far East. Readers are referred to the valuable reference *Flora, Vegetation and Plant Resources of the Far East* by Gorovoy, Kochmareva, and Samoylenko (1973). This bibliography covers the period from 1928 through 1969. A second volume listing references from 1970 to the present is in preparation. Another useful reference is *Literary Sources on the Flora of The U.S.S.R.* by Lipschitz (1975).

Two major floristic treatments of regions adjacent to the Soviet Far East which are important to this study are Kitagawa (1979) and Ohwi (1984).

MATERIALS AND METHODS

Background information and data presented here are the result of a combination of field work in the Soviet Union, Japan, and the People's Republic of China; the study of Soviet and Japanese literature; and the examination of numerous herbarium specimens. I was fortunate to be able to examine and study specimens at the Komarov Botanical Institute in Leningrad, the Main Botanical Garden in Moscow, the Central Siberian Botanical Garden in Novosibirsk (U.S.S.R.), the Botanical Institute in Beijing, and the universities in Tokyo, Kyoto, and Sapporo, Japan. The Herbaria of the Rancho Santa Ana Botanic Garden and the New York Botanical Garden were used extensively in this study as they have the largest holdings of specimens from the U.S.S.R. in the U.S.A. I have received numerous herbarium specimens from the Far East from several Soviet institutions and have assembled a large library of modern Soviet botanical works relating to this region. Many of these are cited in this paper.

RESULTS

The majority of the woody species present in the Far East are not represented in other regions of the Soviet Union but are either endemic or have ranges which extend into Manchuria, Korea, and Japan. The "Siberian Shield" formed largely by the Stanovoy Mountains forms a natural boundary between southeastern Siberia and the Far East. This is also the northernmost limit of the range of many species of trees and shrubs.

A study of the distributions of woody plants of the region reveals that several distinct elements contribute to the composition of the dendroflora of the Far East. These are the:

COSMOPOLITAN ELEMENT.—Wide-ranging species extending from the European Soviet Union across Siberia to the Far East.

EASTERN SIBERIAN ELEMENT.—Species having most of their range in Siberia but extending slightly or moderately into the Far East.

WIDESPREAD FAR EASTERN USSR ELEMENT.—Species largely or totally confined to the region east of Siberia and also present throughout most of the Far East. Some of these also extend into northern China or Korea.

MANCHURIAN ELEMENT.—Species of the Amur and Ussuri River valleys and the Primorsky region but also present in Manchuria. These are largely Manchurian species which have the northern or northeastern part of their range in the U.S.S.R.

EASTERN MANCHURIAN ELEMENT.—Manchurian species restricted in the U.S.S.R.

to the Ussuri River Valley or the southern part of the Primorsky. Most, if not all, of these species have their major distribution in China and Korea.

OKHOTSK-KAMCHATKA ELEMENT.—Species largely confined to the broad mainland coastal regions of the Okhotsk Sea, the Kamchatka Peninsula, the northern half of Sakhalin, and most of the Kuril Islands. Some are found only on Kamchatka while others occur only on the mainland.

SAKHALIN-HOKKAIDO ELEMENT.—Species found in the southern half of Sakhalin, the two large southernmost Kuril Islands and also Hokkaido, the northernmost major island of Japan.

Cosmopolitan Element (3.9%)

A limited number of woody plants are widely distributed across the vast expanse of the U.S.S.R., ranging from Europe to the Far East. They have relatively little importance in this study because they occur in a wide range of floristic regions and represent a very small proportion of the total dendroflora. Their ranges are likely the result of successful dispersal mechanisms, physiological tolerance to a broad range of climatic and edaphic factors, and their ability to readily colonize areas, particularly disturbed sites. They are listed here since they are an element, albeit forming a small percentage, of the dendroflora of the Far East.

Betula fruticosa Pall.
Betula pendula Roth
Cotoneaster melanocarpus Fisch. ex Blytt
Pinus sylvestris L.
Populus tremula L.
Potentilla fruticosa L.
Prunus (*Padus*) *avium* Mill.
Ribes spicatum Robson
Rosa acicularis Lindl.
Salix caprea L.
Salix myrtilloides L.
Salix triandra L.

Eastern Siberian Element (7.7%)

The dendroflora of Siberia was recently studied by Koropachinsky (1983). Siberia has 375 species of trees, shrubs, and perennials representing 122 genera and 40 families. Siberian species are defined here as those in which the greatest part of their range is in Siberia. It is surprising that only a limited number of true Siberian woody plants extend into the Far East. Some extend well into the Far East, while others such as *Pinus sibirica* and *Abies sibirica* (Fig. 4) barely reach it. Others extend much further eastward, especially in the more northern areas, e.g., *Picea obovata* and *Larix gmelinii* (Fig. 4). The Siberian element present in the Far East includes:

Abies sibirica Ledeb.
Alnus manshurica (Call.) Hand.-Mazz.
Alnus sibirica (Spach) Turcz. ex Kom.
Berberis sphaerocarpa Kar. et Kir
Betula exilis Sukacz.
Clematis aethusifolia Turcz.
Juniperus sibirica Burgsd.
Larix gmelinii (Rupr.) Rupr.
Picea obovata Ledeb.
Pinus sibirica Du Tour
Rhododendron adamsii Rehd.
Rhododendron dauricum L.
Ribes pauciflorum Turcz. ex Pojark.
Salix abscondita Laksch.
Salix bebbiana Sarg.
Salix berberifolia Pall.
Salix taraikensis Kimura
Sorbaria pallasii (G. Don fil.) Pojark.
Sorbaria sorbifolia (L.) R. Br.
Sorbus sibirica Hedl.
Spiraea betulifolia Pall.
Spiraea media Fr. Schmidt
Spiraea salicifolia L.

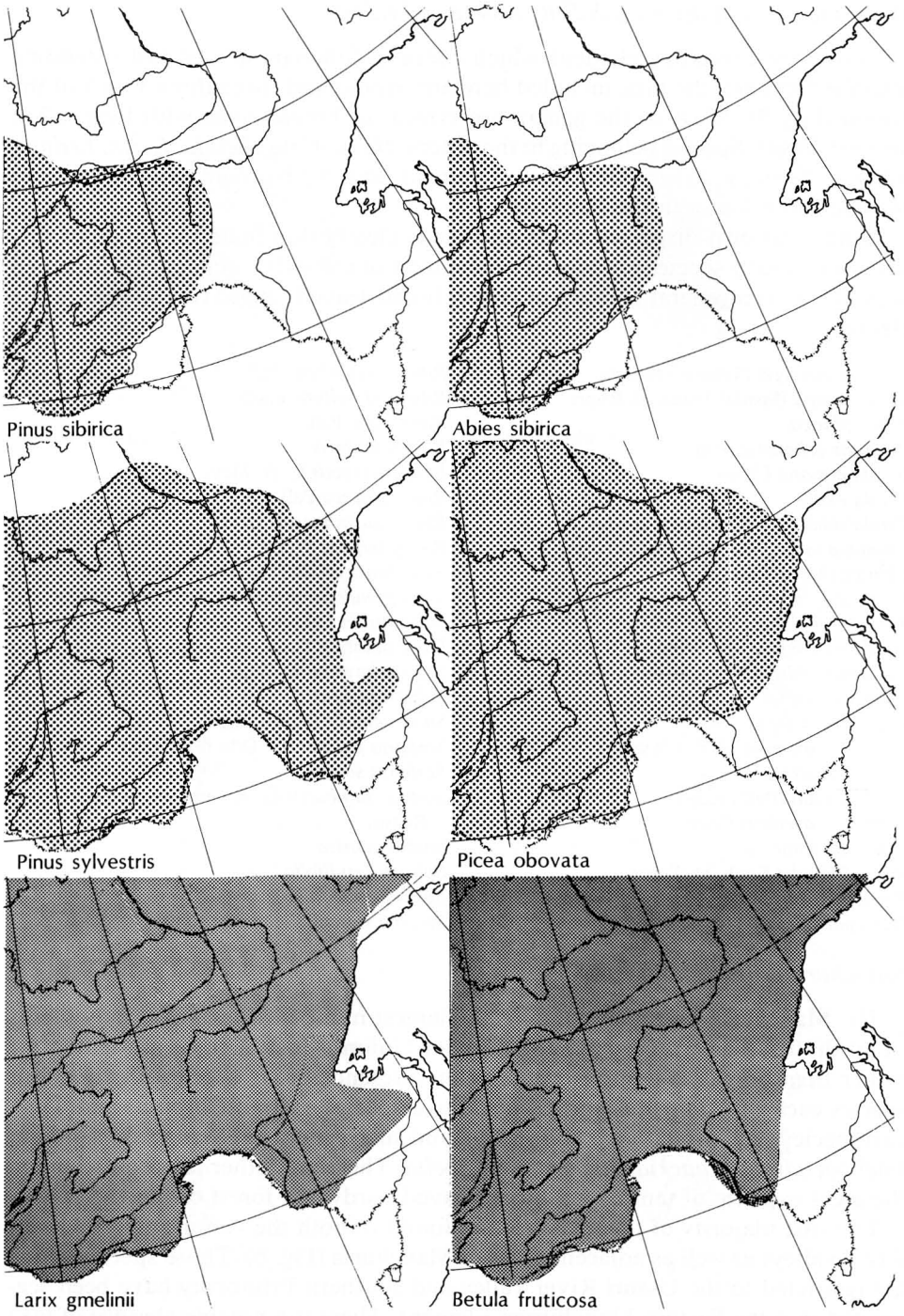

Fig. 4. Distribution of six species typical of the Cosmopolitan Element *(Pinus sylvestris* and *Betula fruticosa)* and the Eastern Siberian Element *(Pinus sibirica, Abies sibirica, Picea obovata,* and *Larix gmelinii).* Adapted from Sokolov et al. (1977).

Widespread Far Eastern U.S.S.R. Element (14.5%)

Unlike the preceding element which contains Siberian species just extending into the Far East, the taxa included here are widespread throughout much of the region (Fig. 5). Most of the genera are typical of boreal areas with long, often severe winters. Species belonging to the genera *Abies, Alnus, Betula, Larix, Ledum, Myrica, Populus, Ribes, Rosa, Salix, Spiraea,* and *Sorbus* comprise the bulk of the widespread taxa in the Far East.

Wind- and bird-dispersed fruits and seeds clearly dominate the mode of dispersal and many species are effective colonizers of natural or man-made disturbed sites. There is a general absence of larger, broad-leaved, mesic tree species in the element.

Abies nephrolepis (Trautv.) Maxim.
Alnus hirsuta (Spach) Turcz. ex Rupr.
Alnus sibirica
Atragene ochotensis Pall.
Betula ermanii Cham.
Betula exilis
Betula middendorffii Trauvt. et Mey.
Chosenia arbutifolia (Pall.) A. Skvorts.
Clematis fusca Turcz.
Crataegus dahurica Koehne ex Schneid.
Juniperus davurica Pall.
Juniperus foetidissima Willd.
Juniperus sibirica
Larix gmelinii
Ledum palustre L.
Myrica tomentosa (DC.) Aschers. et Graebn. (coastal area only)
Pinus pumila (Pall.) Regel
Populus suaveolens Fisch.
Potentilla fruticosa
Ribes dikuscha Fisch. ex Turcz.
Ribes fragrans Pall.
Ribes pauciflorum
Ribes procumbens Pall.
Ribes pulchellum Turcz.
Ribes triste Pall.
Rosa acicularis
Rosa amblyotis C. A. Mey.
Rosa davurica Pall.
Rubus sachalinensis Levl.
Rubus serpens Weihe ex Lej. et Court.
Salix brachypoda (Trautv. et Mey.) Kom.
Salix pseudopentandra (B. Floder) B. Floder
Salix rorida Laksch.
Salix saxatilis Turcz. ex Ledeb.
Salix schwerinii E. Wolf
Salix taraikensis
Salix udensis Trautv. et Mey.
Sorbaria pallasii (G. Don fil.) Pojark.
Sorbaria sorbifolia
Sorbus sambucifolia (Cham. et Schlecht.) M. Roem.
Sorbus sibirica
Spiraea betulifolia
Spiraea salicifolia
Spiraea stevenii (Schneid.) Rydb.

Manchurian Element (33.1%)

The Manchurian element contains the largest number of taxa of woody plants in all the Far Eastern Region of the Soviet Union. Most of these are temperate rather than boreal as demonstrated by the presence of six species of *Acer,* four species each of *Euonymus* and *Ulmus,* three species each of *Carpinus* and *Tilia,* two species each of *Actinidia* and *Aralia,* and such genera as *Syringa, Schisandra, Phellodendron, Maackia, Juglans,* and *Abelia.* These and other taxa contribute to the great expanse of temperate, broad-leaved hardwood forest of the U.S.S.R.

The vast majority of these species are found in both the Amur and the Ussuri River valleys as well as adjacent areas of Manchuria (Fig. 6). Those species which are restricted to the Ussuri River valley and southern Primorsky have been segregated into the Eastern Manchurian Element. There is a notable absence of taxa restricted solely to the western Amur River valley and Manchuria with the exception of *Atragene macropetala.* The southern Ussuri River valley and southern Primorsky have climates tempered by the ocean while that of western Amur is more continental in nature. About 12% of the Manchurian element also occurs

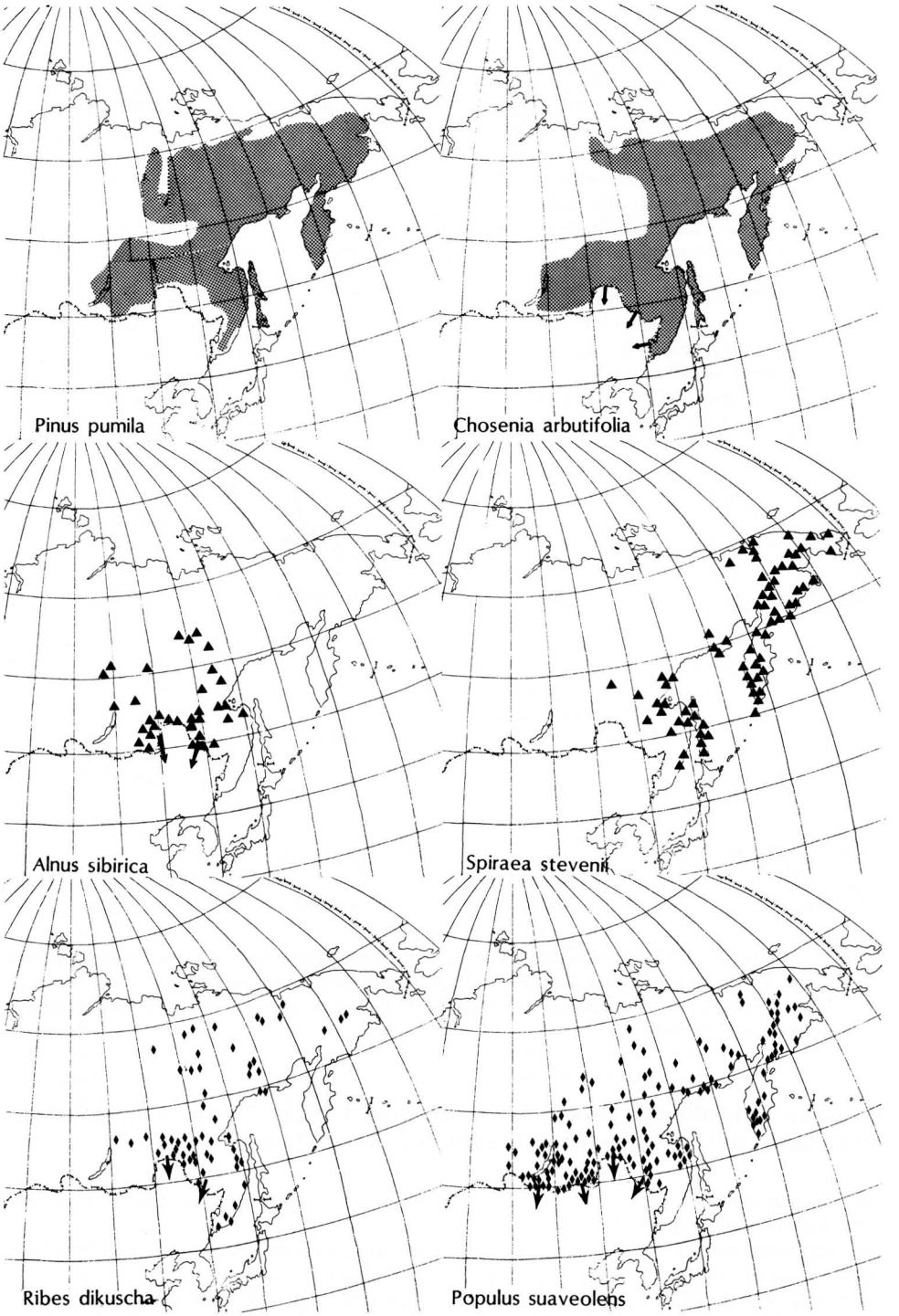

Fig. 5. Distribution of six species typical of the Widespread Far Eastern U.S.S.R. Element. Adapted from Sokolov et al. (1977, 1980).

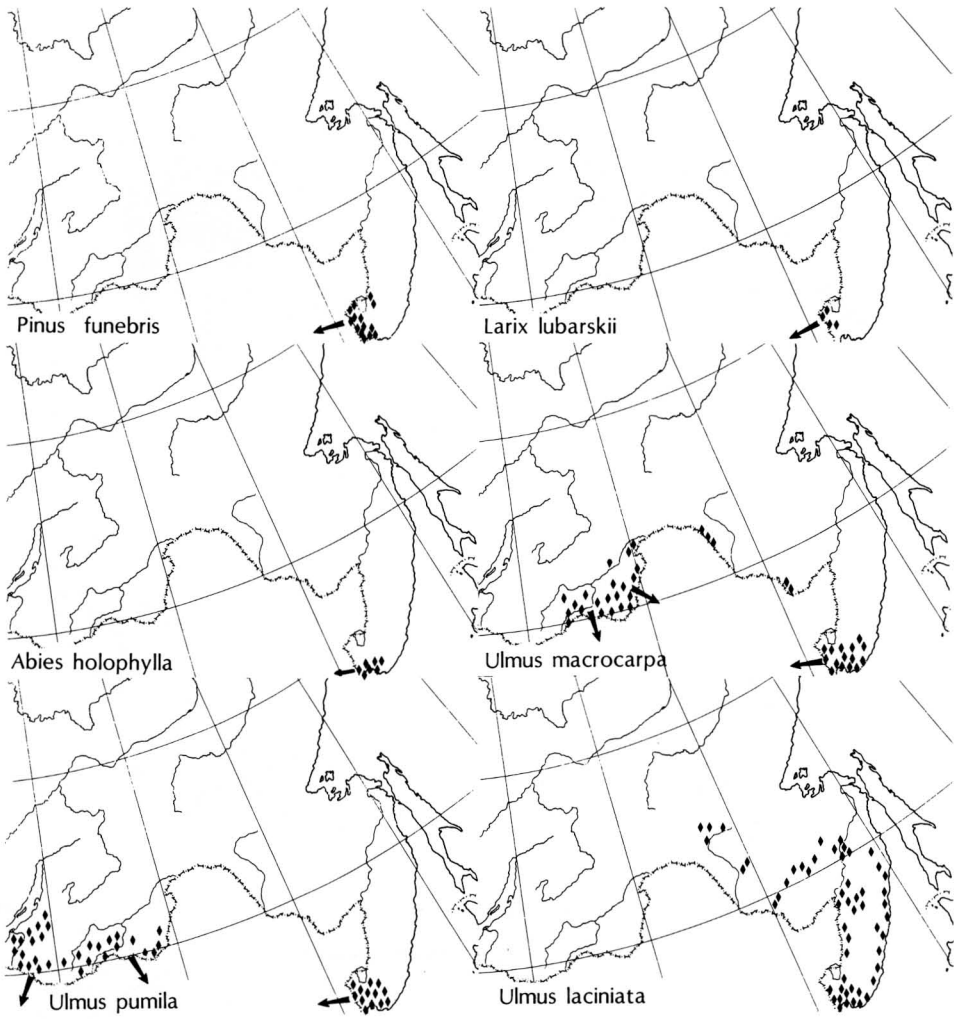

Fig. 6. Distribution of six species typical of the Manchurian Element (*Ulmus macrocarpa, Ulmus pumila* and *Ulmus laciniata*) and the Eastern Manchurian Element (*Pinus funebris, Larix lubarskii* and *Abies holophylla*). Arrows indicate continued distribution in adjacent countries. Adapted from Sokolov et al. (1977, 1980).

on Japan, Sakhalin and usually the lower Kuril Islands. These are noted in parentheses in the following list of Manchurian woody taxa.

Abelia coreana Nakai
Abies nephrolepis—E. Amur
Acer barbinerve Maxim.
Acer ginnala Maxim.
Acer mandshuricum Maxim.
Acer mono Maxim.
Acer tegmentosum Maxim.
Acer ukurunduense Trautv. et Mey.
Actinidia kolomikta (Maxim.) Maxim. (Jap, Sak, Kur)
Actinidia polygama (Siebold et Zucc.) Mig. (Jap, Sak, Kur)
Alnus japonica (Thunb.) Steud.
Alnus manshurica
Ampelopsis brevipedunculata (Maxim.) Trautv. (Jap, Sak, Kur)

Aralia continentalis Kitag.
Aralia elata (Miq.) Seem. (Jap, Sak, Kur)
Armeniaca (*Prunus*) *mandshurica* (Maxim.) Skvorts.
Armeniaca (*Prunus*) *sibirica* (L.) Lam.
Atragene macropetala (Ledeb.) Ledeb.
Betula costata Trautv.
Betula davurica Pall.
Betula ovalifolia Rupr.
Berberis amurensis Rupr.
Caragana fruticosa (Pall.) Bess.
Caragana ussuriensis (Regel) Pojark.
Carpinus cordata Blume
Celastrus flagellaris Rupr. (Jap)
Clematis brevicaudata DC.
Clematis fusca (Kam)
Clematis manshurica Rupr.
Corylus heterophylla Fisch. ex Trautv.
Corylus mandshurica Maxim.
Crataegus dahurica
Crataegus maximowiczii Schneid.
Crataegus pinnatifida Bunge
Deutzia amurensis (Regel) Airy Shaw
Euonymus maackii Rupr.
Euonymus macropterus Rupr. (Jap, Sak, Kur, Korea)
Euonymus pauciflora Maxim.
Euonymus sacrosancta Koidz.
Fraxinus mandshurica Rupr.
Fraxinus rhynchopylla Hance
Grossularia burejensis (Fr. Schmidt) Berger
Ilex rugosa Fr. Schmidt
Juglans mandshurica Maxim.
Juniperus davurica
Larix amurensis Beissn.
Maackia amurensis Rupr. et Maxim. (Kur)
Malus baccata (L.) Borkh.
Malus mandshurica (Maxim.) Kom.
Malus pallasiana Juz. (E. Sib)
Padus (*Prunus*) *maackii* (Rupr.) Kom.
Padus (*Prunus*) *maximowiczii* (Rupr.) Sokolov (Sak, Kur, Jap)
Padus (*Prunus*) *serrulata* (Jap, Sak, Kur)
Phellodendron amurense Rupr. (Jap)
Philadelphus schrenkii Rupr. et Maxim.
Philadelphus tenuifolius Rupr. et Maxim.
Physocarpus amurensis (Maxim.) Maxim.
Pinus koraiensis Siebold et Zucc.
Populus amurensis Kom.
Populus koreana Rehd.
Populus maximowiczii A. Henry (Jap, Kur)
Pyrus ussuriensis Maxim.
Quercus dentata Thunb.
Quercus mongolica Fisch. ex Ledeb.
Rhamnus davurica Pall.
Rhamnus diamantiaca Nakai
Rhamnus ussuriensis Vassil. (Jap)
Rhododendron mucronulatum Turcz.
Rhododendron schlippenbachii Maxim.
Ribes mandshuricum (Maxim.) Kom.
Ribes maximoviczianum Kom.
Ribes palczewskii (Jancz.) Pojark.
Rosa amblyotis (Och, Kam)
Rosa davurica (E. Sib)
Rosa rugosa Thunb.
Rosa ussuriensis Juz.
Rubus crataegifolius Bunge
Rubus komarovii Nakai (Sak)
Salix cardiophylla Trautv. et Mey.
Salix gracilistyla Miq.
Salix miyabeana Seemen
Sambucus coreana (Nakai) Kom. et Aliss.
Schisandra chinensis (Turcz.) Baill.
Sorbus alnifolia (Siebold et Zucc.) C. Koch
Sorbus amurensis Koehne
Spiraea elegans Pojark.
Spiraea humilis Pojark.
Spiraea pubescens Turcz.
Spiraea sericea Turcz.
Spiraea ussuriensis Pojark.
Syringa amurensis Rupr.
Tilia amurensis Rupr.
Tilia mandshurica Rupr.
Tilia taquetii Schneid.
Ulmus japonica (Rehd.) Sarg.
Ulmus laciniata (Trautv.) Mayr
Ulmus macrocarpa Hance
Ulmus pumila L.
Viburnum burejaeticum Regel et Herd.
Viburnum sargentii Koehne
Vitis amurensis Rupr.

Eastern Manchurian Element (12.9%)

The eastern Manchurian element comprises species of the Ussuri River valley and adjacent areas of Manchuria, Korean species which extend just into the U.S.S.R., and species extending to Japan (Fig. 6). Typical Ussuri River valley taxa include *Berberis amurensis, Dasiphora mandshurica, Microbiota decussata, Populus amurensis, Prunus ussuriensis,* and *Rosa ussuriensis. Microbiota* is the only endemic genus of conifer in the U.S.S.R. Among those considered typically

Korean taxa are *Populus koreana, Rosa gracilipes, Rosa maximowicziana,* and *Salix kangensis.* Those species which also occur in Japan are indicated in the following list of species.

Abies holophylla Maxim.
Acer komarovii Pojark.
Acer pseudosieboldianum (Pax) Kom.
Alnus japonica
Alnus maximowiczii Call.
Aristolochia contorta Bunge
Armeniaca (*Prunus*) *vulgaris* Lam.
Berberis amurensis
Betula schmidtii Regel
Carpinus cordata
Celastrus orbiculata Thunb.
Cerasus (*Prunus*) *glandulosa* (Thunb.) Loisel.
Clematis brevicaudata
Clematis serratifolia Rehd.
Dasiphora mandshurica (Maxim.) Juz.
Deutzia amurensis
Deutzia glabrata Kom.
Hocquartia manshuriensis (Kom.) Nakai
Juniperus rigida Siebold et Zucc.
Larix lubarskii Sukacz.
Malus mandshurica
Microbiota decussata Kom.
Philadelphus schrenkii Rupr. et Maxim.
Pinus funebris Kom.-P.
Populus amurensis
Populus koreana
Prinsepia sinensis (Oliv.) Bean
Prunus ussuriensis Koval. et Kostina
Ribes horridum Rupr.
Ribes komarovii Pojark.
Ribes maximoviczianum
Rosa gracilipes Chrshan.
Rosa maximowicziana Regel
Rosa ussuriensis
Salix kangensis Nakai
Schizophragma hydrangeoides Siebold et Zucc.
Sorbaria rhoifolia Kom.
Sorbus (*Micromeles*) *alnifolia*
Spiraea flexuosa Fisch. ex Cambess.
Syringa wolfii Schneid.

Okhotsk-Kamchatka Element (12.5%)

There are a limited number of woody taxa which occur solely in this element. Many of the species included here are largely boreal or arctic taxa which extend into the region, sometimes at a higher elevation (Fig. 7). Willows, primarily arctic taxa, predominate. Conifers present include *Abies, Picea,* and *Larix.* Shrubs are abundant and include *Rhododendron, Myrica, Daphne, Cornus,* and *Caragana.* There are no significant broad-leaved trees in this element.

Abies gracilis Kom.
Alnus kamtschatica (Regel) Kom.
Caragana jubata (Pall.) Poir.
Cornus alba L.
Crataegus chlorosarca Maxim.
Daphne kamtschatica Maxim.
Larix kamtschatica (Rupr.) Carr.
Larix ochotensis Kolesn.
Myrica tomentosa (DC.) Aschers. et Graebn.
Picea ajanensis (Lindl. et Gord.) Fisch. ex Carr.
Rhododendron aureum Georgi
Rhododendron camtschaticum Pall.
Rhododendron parvifolium Adam
Rhododendron redowskianum Maxim.
Salix alaxensis Cov.
Salix arctica Pall.
Salix argyracea E. Wolf
Salix chamissonis Anderss.
Salix dshugdshurica A. Skvorts.
Salix erythrocarpa Kom.
Salix fuscescens Anderss.
Salix glauca L.
Salix hastata L.[1,2]
Salix khokhriakovii A. Skvorts.
Salix krylovii E. Wolf[1,2]
Salix lanata L.[1]
Salix nummularia Anderss.[1]
Salix polaris Wahlenb.[1]
Salix pulchra Cham.[1]
Salix recurvigemmis A. Skvorts.[1]
Salix reptans Rupr.[1]
Salix reticulata L.[1]
Salix saxatilis[1,2]
Salix sphenophylla A. Skvorts.
Salix tschuktschorum A. Skvorts. subspecies *kamtschatica* A. Skvorts.
Sorbus kamtschatcensis Kom.
Sorbus sambucifolia

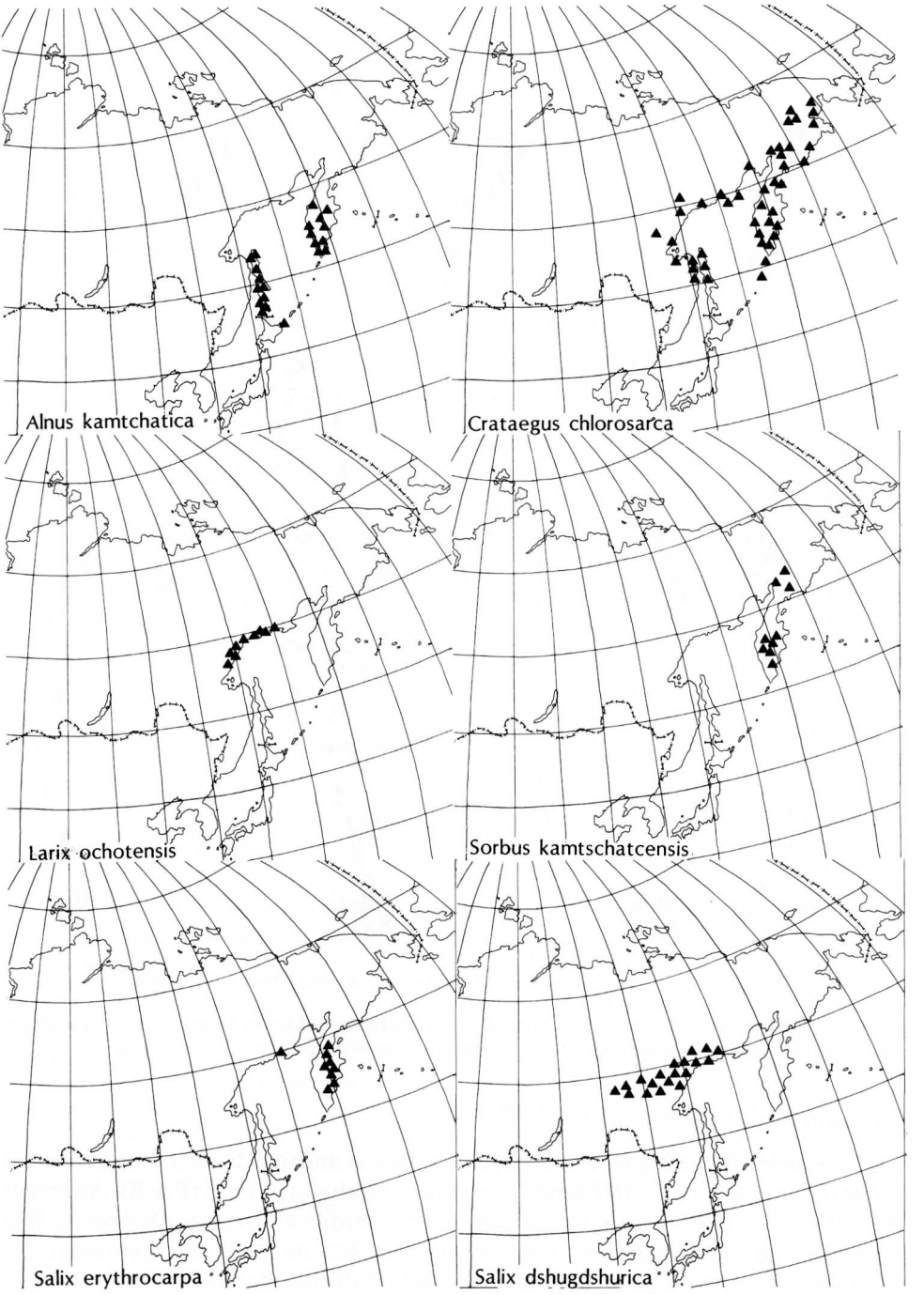

Fig. 7. Distribution of six species typical of the Okhotsk-Kamchatka Element. Adapted from Sokolov et al. (1977, 1980).

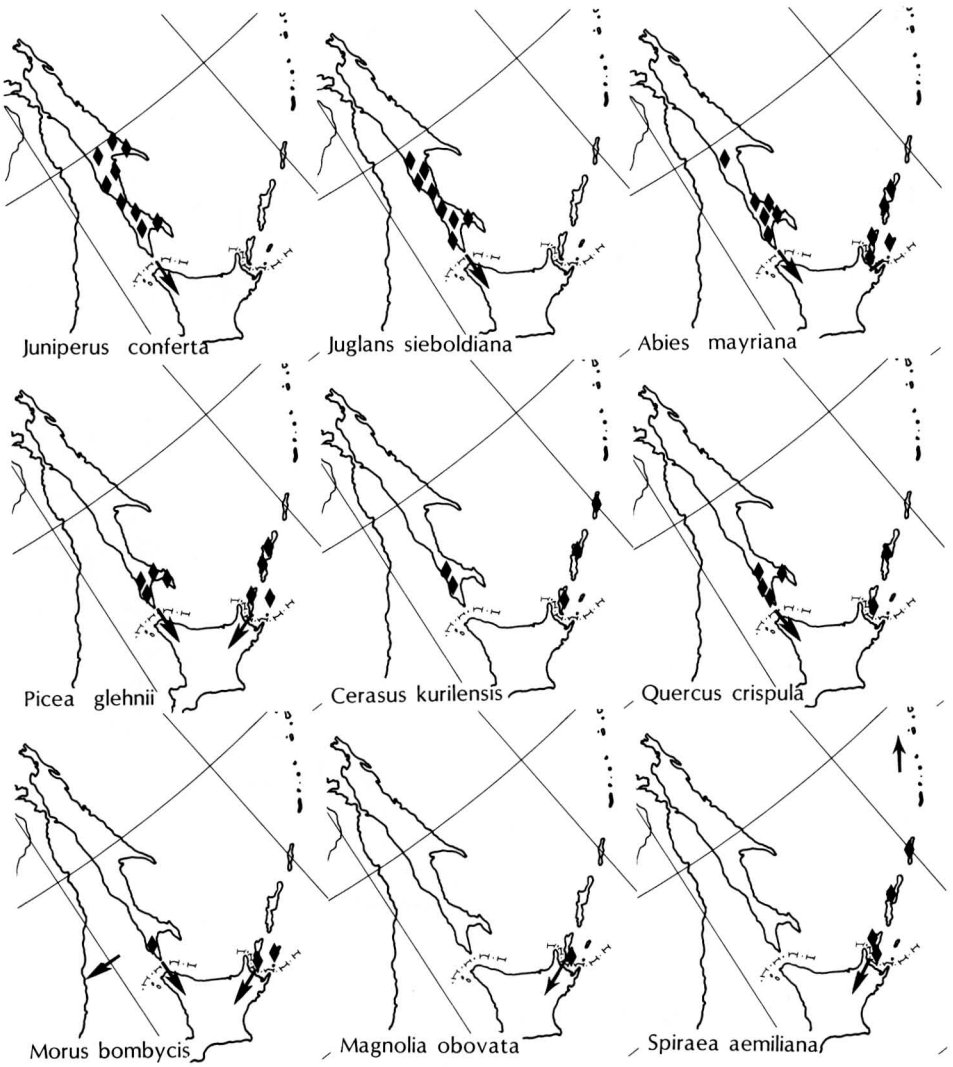

Fig. 8. Distribution of nine species typical of the Sakhalin-Hokkaido Element. Arrows indicate continued distribution in adjacent countries. Adapted from Sokolov et al. (1977, 1980).

Sakhalin-Hokkaido Element (15.4%)

The species included here are largely Japanese and reach their northernmost range in the southern Kuril Islands or southern Sakhalin or both (Fig. 8). Although Ageenko et al. (1982) refer to the forested "subtropical" representatives in this region, I find no examples of subtropical taxa, but rather typical temperate or even warm-temperate genera. Clearly, this area is the northernmost limit for many genera and species in eastern Asia. Some of the taxa occur also on the Chinese mainland but they are absent from the Soviet mainland. Examples of such temperate genera are *Magnolia, Morus, Acer, Hydrangea, Skimmia,* and *Tilia.* Southern Sakhalin and the lower Kuril Islands are the only areas of the U.S.S.R. where three species of bamboo (*Sasa*) occur.

Fig. 9. Map showing four major phytogeographic regions of the Soviet Far East based upon the distribution of the woody taxa.

The ranges of these taxa clearly support the recognition of both Schmidt's and Miyabe's lines. The species found in this region are:

Abies mayriana (Miyabe et Kudo) Miyabe et Kudo
Abies sachalinensis Fr. Schmidt
Acer japonicum Thunb.
Acer pictum Thunb.
Acer tschonoskii (*A. komarovii*) Maxim.
Alnus maximowiczii
Betula maximowicziana Regel.
Cerasus kurilensis (Miyabe) Czer.
Hydrangea paniculata Siebold
Hydrangea petiolaris Siebold et Zucc.
Fraxinus sieboldiana Blume
Ilex crenata Thunb.
Ilex rugosa
Ilex sugerokii Maxim.
Juglans ailanthifolia Carr.
Juglans sieboldiana Maxim.
Juniperus conferta Parl.
Juniperus sargentii (A. Henry) Takeda ex Koidz.
Ligustrum tschonoskii Decne.
Magnolia obovata Thunb.
Morus bombycis Koidz.
Padus (*Prunus*) *ssiori* (Fr. Schmidt) Schneid.
Picea glehnii (Fr. Schmidt) Mast.
Prunus (*Cerasus*) *kurilensis* Miyabe
Quercus crispula Blume
Quercus dentata
Rhododendron tschonoskii Maxim.
Rhus ambigua Lav. ex Dipp.
Rhus trichocarpa (Miq.) O. Kuntze
Ribes latifolium Jancz.
Ribes sachalinense (Fr. Schmidt) Nakai
Salix gilgiana Seemen
Salix kurilensis Koidz.
Salix reinii Franch. et Savat. ex Seemen
Salix vulpina Anderss.
Sambucus sieboldiana (Miq.) Schwer.
Sasa kurilensis (Rupr.) Makino et Shibata
Sasa senanensis (Franch. et Savat.) Rehd.

Sasa spiculosa (Fr. Schmidt) Makino
Schizophragma hydrangeoides
Skimmia repens Nakai
Smilax kurilensis Koidz.
Sorbus commixta Hedl.
Spiraea aemiliana Schneid.
Spiraea beauverdiana Schneid.
Syringa reticulata (Blume) Hara
Tilia maximowicziana Shirasawa
Viburnum wrightii Miq.
Vitis coignetiae Pulliat ex Planch.

CONCLUSIONS

Four major phytogeographic regions based upon the distribution of the woody taxa (Fig. 9) are recognized in this study. These are the Eastern Siberian, the Okhotsk-Kamchatka, the Manchurian (subdivided in northern and eastern components), and the Sakhalin-Hokkaido. The cosmopolitan and wide-ranging species are ignored as they do not contribute significantly to the recognition of phytogeographic subdivisions of the Far East.

It is clear that the vast majority of woody plants of the Soviet Far East do not occur elsewhere in the Soviet Union. Only 26.1% of the species are present in Siberia or are cosmopolitan or widespread in the Eastern region of the U.S.S.R. Most of the species are temperate east Asiatic and also distributed in Japan, Korea, or northeastern China. The following table summarizes the distribution of woody species by major geographic ranges.

Cosmopolitan	3.9%
Eastern Siberian	7.7%
Widespread Far Eastern	14.5%
Manchurian	33.1%
Eastern Manchurian	12.9%
Okhotsk-Kamchatka	12.5%
Sakhalin-Hokkaido	15.4%
	100.00%

The northern limit in eastern Asia of many broad-leaved, deciduous hardwood species is reached just inside the present boundary of the Soviet Union. This extension of Chinese (mainly Manchurian), Korean, and Japanese species into the U.S.S.R. accounts for the majority of its hardwood species.

The distribution of woody species supports the recognition of Miyabe's Line in the southern Kuril Islands and also Schmidt's Line dividing Sakhalin Island.

Finally, the region under study contains numerous genera which extend back geologically to the Tertiary and earlier. This is particularly true for the Amur-Primorsky region where an absence of glaciation since the Tertiary has allowed many relicts or their direct descendants to survive. Among them are genera such as *Abelia, Actinidia, Alnus, Aralia, Betula, Carpinus, Corylus, Crataegus, Euonymus, Fraxinus, Ilex, Juglans, Populus, Prunus, Quercus, Rhamnus, Salix, Spiraea, Sorbus, Tilia,* and *Ulmus.* Thus, Manchuria and the adjacent Amur-Primorsky region have served as the most important of the northern refugia in eastern Asia for Tertiary relicts.

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FOOTNOTES

[1] Arctic species.
[2] Also occurs in Eastern Siberia.