Phytogeographical Problems in the Temperate Flora in Japan

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Abstract Studies of Japanese plants are reviewed from a phytogeographical point of view. The annual distribution of precipitation differs markedly between the Japan sea side and the Pacific side areas. This causes significant differentiation in the cool-temperate flora and vegetation between these two areas. Botanical and geological evidence suggests this differentiation proceeded since the latter part of the Riss-Wurm interglacial period and most of cool-temperate species were restricted to local refugia in both the Japan Sea and the Pacific side areas in the last glacial age when coniferous forest with *Abies* and *Tsuga* probably had wider range than at present under lowered temperature and decreased precipitation. Both the cool-temperate and the warm-temperate flora of Japan include many endemic and relictual species. The evolution of these species probably took place in the coastal regions of East Asia including the Japan Archipelago which have been at least locally under moderate climate throughout the Quaternary.

Introduction

The Japan Archipelago is composed of four main islands, Hokkaido, Honshu, Shikoku and Kyushu, and more than three thousand smaller islands. Its total area is 400,000 ㎢. In spite of its small area, the Japan Archipelago has a very rich vascular flora. According to Maekawa's estimation based on Ohwi's flora (Ohwi, 1972), about 1,110 genera comprising 3,900 species of seed plants are native in the Japan Archipelago excluding the Ryukyu and Bonin Islands (Maekawa, 1974, 1977). In the Ryukyu Islands, 1,400 species of seed plants are recorded by Hatusima (1971), of which 700 species do not occur on the four main islands and are not included in Ohwi's flora. The number of native seed plant species in the overall area of the Japan Archipelago is estimated to be about 5,000 species.

The Japan Archipelago has two characteristics concerning its climate that greatly affect the distribution of plants. Firstly, it is located between 24°N and 45.5°N and includes subtropical, warm-temperate, cool-temperate and subboreal regions. However, the larger part is in the temperate regions and the composition and historical development of the temperate flora is the major phytogeographycal subject in the Japan Archipelago. Secondly, the annual distribution of precipitation differs markedly between the Japan Sea side area and the Pacific side area. In the Japan Sea side area, there is much snowfall and the monthly precipitation during the winter months is from 150 to over 400 mm, but monthly precipitation in summer months is 100-200 mm. On the other hand, monthly precipitation during the summer months on the Pacific side is from 150 to over 400 mm and during winter months usually less than 100 mm. Accordingly, the cool-temperate flora and vegetation developed on the Japan Sea and Pacific sides are significantly different. The warm-temperate zone is mainly located on the Pacific side and there is no significant differentiation in the flora and vegetation between the Japan Sea and Pacific sides in this zone.

The patterns in plant distribution in the Japan Archipelago and their presumed historical development have already been comprehensively reviewed by Hara (1959), Yamazaki (1959, 1983), Maekawa (1974, 1977) and Hotta (1974). However, recent developments in systematic research on East Asian plants and also geological research on the Quaternary history have provided new evidence to apply to phytogeographical problems in the Japan Archipelago. The purpose of this paper is to briefly review our current phytogeographical understanding of the temperate Japanese flora.

Cool-temperate flora

Overall cool-temperate flora of Japan is closely related with the cool-temperate flora in the eastern part of the Asia continent and also with that of eastern and/or western North America. Disjunct distribution of related taxa between East Asia including Japan and eastern and/or western North America has been repeatedly documented since the time of Linnaeus (Graham, 1966, 1972b; Boufford & Spongberg, 1983). Review of this topic is beyond the scope of this paper. Recent knowledge on this subject are compiled in the Annals of the Missouri Botanical Garden vol. 70, nos. 3 and 4 published in 1983. From a systematic point of view, analytical studies on the affinities of disjunct taxa are needed. *Circaea* (Boufford, 1982; Averett and Boufford, 1985), *Diphylleia* (Ying et al., 1984), *Eupatorium* (reviewed by Watanabe, 1986), and *Trillium* (reviewed by Fukuda, 1983) are examples of genera critically studied in both East Asia and North America. Even for these genera, the phylogenetic relationships between Asian and American species are not well-documented. For *Acer*, not only the extant but also the fossil species are well-studied morphologically (see review by Wolfe and Tanai, 1987). However, few biosystematic studies have been carried out on extant species. Phylogenetic studies on *Acer* utilizing modern analytical methodologies are needful. Recently, Soltis and Bohm (1984) examined the karyology and flavonoid chemistry of the disjunct species of *Tiarella* in America and Asia. Affinities between 7 North American species and one East Asian species of *Agastache* sect. *Agastache* were analyzed using flavonoid chemistry (Vogelmann, 1984), crossability (Vogelmann, 1985) and allozyme variation (Vogelmann and Gastony, 1987). According to these studies, a single Asian representative *A. rugosa* differs from its North American congeners at only 2 of the 15 enzyme loci examined and has identical flavonoid compounds with western North American species. This suggests that the migration of *A. rugosa* to East Asia was a relatively recent event. Further studies like these will give us a better understanding and deeper insight into the historical development of disjunct distribution between eastern Asia and temperate North America.

The differentiation of the Japanese cool-temperate flora between the Japan Sea and Pacific sides of Japan is evidently a more recent event than the origin of the disjunct distribution between eastern Asia and eastern and/or western North America. Recent geological studies have demonstrated that there was much less snowfall on the Japan Sea side during the maximum last glacial age (ca. 18,000 years B.P.). However, both the Japan Sea side and the Pacific side floras include endemic relictual genera and species, and the differentiation of these two floras undoubtedly preceded the last glacial age. Before going further into this problem, I will briefly summarize the difference in climate and flora between the Japan Sea and Pacific sides of Japan. The difference in vegetation is documented by Sasaki (1972) and Fujita (1986). The eco-physiological effect of deep snow on plant life on the Japan Sea area is comprehensively reviewed by Sakai (1976).

In phytogeographical literature, taxa endemic to the Japan Sea side area and those to the Pacific side area are designated as the Japan Sea elements and the Pacific elements respectively (Yamazaki, 1959). The Pacific side area as defined here includes the area comprising Kyushu, Shikoku, the Kii Peninsula and the Pacific side of the Chubu district (called the Tokai district). It is the area influenced by the warm, humid monsoon wind from the Pacific in summer and by the warm Kuroshio current flowing along the Pacific coast from south to north, and is characterized by a warm and humid climate in summer and relatively low precipitation in winter. The Pacific side of the Tohoku district and Hokkaido are less influenced by the monsoon wind from the Pacific and the Kuroshio current but more so by the cold Oyashio current flowing southward from the Kuril Islands. Those areas are relatively cooler and less humid in summer and have more snowfall than the Pacific side region in the strict sense. Therefore, the flora of the Pacific side of Tohoku and Hokkaido includes many species common to the Japan Sea region. *Glaucidium palmatum* of the monotypic family Glaucidiaceae is an example.

On the Pacific side, in the strict sense as defined above, Kyushu, Shikoku and the Kii Peninsula are collectively called the Sohayaki region. In this region, there are many relictual species comprising the Sohayaki elements (Koidzumi, 1931; Maekawa, 1974, 1977; Murata and Koyama, 1976, 1980). Among them are *Hydrangea shikokiana*, *Kirengeshoma palmata*, *Peltoboykinia watanabei*, *Platycrater arguta* and *Tanakaea radicans* (Saxifragaceae), *Stewartia monadelpha* and *S. serrata* (Theaceae), *Impatiens hypophylla* (Balsaminaceae), *Hypericum sikokumontanum* (Guttiferae), *Angelica shikokiana* and *A. ubatakensis* (Umbelliferae), *Cacalia tebakoensis* and *Myricacalia makineana* (Compositae), *Perillula reptans* (Labiatae), *Alectorurus yedoensis*, *Hosta kikutii* and *Tricyrtis nana* (Liliaceae), and others. However, some of these species occur beyond the Sohayaki region. It is difficult to define the Sohayaki elements in a different category from the Pacific elements (Yamazaki, 1959; Hotta, 1962). The Pacific side region includes four isolated districts: Kyushu, Shikoku, the Kii Peninsula and the Tokai district, and floristic differences among these four districts are recognizable. In contrast with the Japan Sea side region, geographical speciation within the Pacific side region is known in many genera such as *Astilbe*, *Mitella*, *Angelica*, *Cacalia*, *Cirsium*, *Saussurea*, *Arisaema*, *Hosta* and *Tricyrtis*.

In the region facing the Japan Sea, there are also notable local differences in the amount of snowfall in winter. The major factors that cause large amounts of snowfall in the Japan Sea side region are the cold winter monsoon wind from Siberia, the high evaporation rate of the Japan Sea caused by the inflow of the Tsushima warm current, and the existence of high mountains facing the Japan Sea. Combinations of these factors are most evident on the Japan Sea side in the Chubu district (Ishikawa, Toyama, Niigata Prefectures and adjacent areas). The mean annual maximum snow cover exceeds 3 m in these regions. Several plant species such as *Alnus fauriei* (Fukuoka, 1966), *Ranzania japonica* (Hara and Kanai, 1959), *Camellia japonica* var. *lusticana* (Ishizawa, 1978), and *Pedicularis nipponica* (Yamazaki, 1983) are restricted to this area. Other Japan Sea elements have wider ranges (Fukuoka, 1966). The isometric line of 50 cm mean annual maximum snow cover encloses the Japan Sea side of the Chugoku, Chubu and Tohoku districts, and almost all of Hokkaido. This line coincides with the distribution limit of several Japan Sea elements such as *Ilex leucoclada*, *Daphniphyllum macropodium* var. *humile* (Yamazaki, 1959) and *Sasa nipponica* (Suzuki, 1961). The line is located on the Pacific side of the Tohoku district.

Many of the Japan Sea elements occur on the Pacific side of the Tohoku district (Fukuoka, 1966; Yamazaki, 1983).

Several relictual taxa are included among the Japan Sea elements. *Glaucidium palmatum*, belonging to a monotypic family, *Ranzania japonica* belonging to a monotypic genus, and *Viola rostrata*, with a disjunct distribution in eastern North America and the Japan Sea side region are representatives of them. However, most of the Japan Sea elements are regarded as having originated rather recently. Many examples of closely related vicarious taxa differentiated between the Japan Sea and Pacific sides have been reported. The following two generalizations can be made from these examples (Yahara, 1986): (1) differentiation between vicariants is infraspecific, with a few exceptions of rather recently differentiated species pairs; (2) taxa on the Japan Sea side are derived from Pacific side ancestors. These suggest that the vicariance was caused by rather recent climatic changes in the Japan Sea side region.

Recent geological research has revealed that the amount of snowfall in the Japan Sea region during the last glacial maximum (ca. 18,000 years B.P.) was much less than that at present. There has been a prevaling view that a land bridge was formed during the last glacial maximum between the Korean Peninsula and mainland Japan due to a lowering of the sea level by more than 120 m. The inflow of the Tsushima Current to the Japan Sea was prevented by this land bridge. If this is true, one of major factors causing large amounts of snowfall in the Japan Sea region did not exist at the height of the last glacial age. Oshima (1982) strongly disagreed with a 120 m depression in sea level. He re-examined various facts used as evidence and concluded that a land bridge never formed in the Korean strait during the last glacial age. Additional comprehensive reviews and critical papers on sea level changes and related problems can be found in the journal the Quaternary Reserch (Japan) vol. 21 no. 3 (1982).

Although the sea level during the last glacial maximum is controversial, it is doubtless that the amount of snowfall in the Japan Sea region was much less through the later part of the last glacial age. Based on glacial landforms in the northern Japan Alps, Ono (1982) estimated that the amount of snowfall in the Japan Sea region at about 25,000 years B.P. was 50-70 % less than at present. Evidence from pollen analysis demonstrates that there was no marked difference in vegetation between the Japan Sea and Pacific sides at that time (Yasuda, 1982; Nakabori, 1986). On the other hand, the occurrence of relictual species, *Ranzania japonica* and *Glaucidum palmatum*, which are specialized to grow in habitats with snow cover even into late spring suggests that abundant snowfall, which ensures survival of these species, occured during the last glacial age somewhere in the Japan Sea region, or possibly in more southerly regions of Honshu.

It is uncertain that some of the vicarious taxa between the Japan Sea and Pacific areas have differentiated during the 20,000 years since the last glacial maximum. Here, I refer to recent studies on some of these vicarious taxa. *Boehmeria sylvestrii* occurs throughout the mainland of Japan and in the northern part of China, but its diploid race is restricted to the Japan Sea area. This species is distinguished from *B. gracilis* by slight morphological differences and the two have been treated as varieties or subspecies. *Boehmeria. gracilis* occurs on the mainland of Japan, on the Korean Peninsula, and in the eastern part of China. Its diploid race is restricted to Shikoku and the Pacific side of the Chubu and Kanto districts in Japan to Mt. Huangshan in Anhui, China. *Boehmeria sylvestrii* is regarded as having originated from *B. gracilis* in the Japan Sea side area (Yahara, 1986). *Boehmeria sylvestrii* includes sexual diploid and agamospermous polyploid races. The comparison between the ranges of the ancestral diploid and the derivative polyploid provides a clue for understanding the historical development of present distribution patterns. In *B. sylvestrii*, the following scenario is suggested : the diploid race originated in the Japan Sea region, and then the polyploid race originated within or at the edge of the range of the diploid race and migrated to northern China. The agamospermous polyploid race has a high colonizing ability. Its migration to northern China might have occurred along with rapid vegetational changes during the last glacial age. However, the origin of the diploid *B. sylvestrii* undoubtedly preceded the last glacial age.

Eupatorium chinense s. lat. is also an amphi-agamic complex composed of sexual diploid and agamospermous polyploid races. From a series of recent cytogeographical studies (Watanabe et al., 1982; Watanabe and Yahara, 1984; Watanabe, 1986), two diploid races differing in geographical range have been recognized. Each has characteristic morphological traits and esterase isozyme phenotypes and they are regarded as different species, *Eupatorium chinense* var. *oppositifolium* and *E. glehni* (Kawahara et al., 1989). The diploid race of the former species is restricted to the Pacific side; that of the latter species occurs on the Japan Sea sides of the Chugoku and Kinki districts, and in the Chubu, northern Kanto and Tohoku districts and Hokkaido. In *E. chinense* var. *opposotifolium*, some agamospermous polyploid races have much wider ranges than the diploid race and occur throughout mainland Japan, on the Korean Peninsula and in northern and central China. It is suggested that some of the agamospermous polyploid races originated in Japan and migrated to the continental part of Asia. The differentiation of two species at the diploid level is considered to have preceded the last glacial age.

In the *Hypericum pseudopetiolatum* complex, differentiation of the Japan Sea and Pacific side races at the species level has been confirmed through precise analysis of morphological and allozyme variation (Kato, 1985, 1987 and pers. com.) In northern Kyushu, a hybrid zone between two species has been found. Two additional races are locally differentiated from the Pacific side species on Yakushima Island and on Mts. Fuji and Hakone. It seems unlikely that the differentiation of the Japan Sea and Pacific side species and the subsequent local differentiation on the Pacific side have occurred during at most 20,000 years since the last glacial age.

The examples cited above suggest differentiation of the Japan Sea side taxa before the last glacial age. On the other hand, the vicarious species cited above are closely related and differ relatively slightly from each other in comparison with differences between them and their other relatives. Thus the vicariance is regarded as being of recent origin. To estimate the age of the vicariance, I briefly summarize our current knowledge of relevant climatic and vegetational changes since the Pleistocene. According to Oshima (1982), the inflow of the Tsushima Current into the Japan Sea began in the early Shimosueyoshi transgression in the Riss-Wurm interglacial period, 120,000-130,000 years B.P.(Ohta and Naruse, 1977). From about 60,000-40,000 years B. P., the mountain glaciers in the Japan Alps and the high mountains of Hokkaido conspicuously advanced (Ono, 1982). This suggests that there was an active flow of the Tsushima Current into the Japan Sea and abundant snow fell on to these mountains. According to results of pollen analysis in Osaka Bay (Tsukada, 1974), in the pollen zone I-3 which includes the marine sediment Ma 9 dated at 300,000 years B.P. and regarded as corresponding to the Riss-Wurm interglacial period, *Tsuga* and *Sciadopitys* increased in the earlier past of the period and then *Fagus* became predominant. This suggests that central Japan was under a humid cool-temperate climate during the Riss-Wurm interglacial period. The fossil flora in the vicinity of Osaka Bay from this interglacial period, called as *Sapium* bed, includes warm-temperate tree genera such as

Sapium, *Melia*, *Lagerstroemia*, *Vernicia*, *Hemiptelea* and others (Nasu, 1972).

Based on this evidence, the following scenario is suggested. In the later part of the Riss-Wurm interglacial period when *Fagus* was predominant in central Japan, the inflow of the Tsushima Current into the Japan Sea caused the onset of abundant snowfall in the Japan Sea region. Since that time, differentiation of the cool-temperate flora into Japan Sea and Pacific elements proceeded. The origin of relictual species in the Japan Sea area preceded this event. In the earlier part of the last glacial age when the mountain glaciers conspicuously advanced, the increase in snowfall in the Japan Sea region caused an acceleration in the differentiation of vicarious taxa. When the air temperature reached its lowest point in the later part of the last glacial age, the amount of snowfall in the Japan Sea region decreased to less than 50-70 % of the present amount and the Japan Sea side races adapted to an environment with rich snowfall became restricted to local refugia. In this period, agamospermous polyploids of *Boehmeria sylvestrii* and *Eupatorium chinense* var. *oppositifolium* colonized new habitats with lowered temperature and decreased snowfall and migrated to continental Asia. Even if mainland Japan and the Korean Peninsula were not connected by a land bridge, *Boehmeria* and *Eupatorium*, bearing abundunt small achenes could probably easily migrate to the Korean Peninsula across the narrowed strait. It is difficult to thoroughly document this scenario. However, further accumulation of geological evidence and analytical studies on the vicarious taxa like those on *Eupatorium* and *Hypericum* will enable us to test the validity of this scenario.

While most of the Japan Sea elements are regarded as relatively recently derived, the Pacific elements include many relictual genera. Among 21 angiospermous genera endemic to Japan or to Japan and adjacent restricted areas, 13 genera (62 %) occur mainly in the Pacific area (Hotta, 1974). These include seven monotypic genera endemic to Japan : *Anemonopsis* (Ranunculaceae), *Ancistocarya* (Boraginaceae), *Perillula* (Labiatae), *Diaspananthus* and *Miricacalia* (Compositae), *Alectorurus* (Liliaceae), and *Hakonechloa* (Graminae); *Peltoboykinia* (Saxifragaceae) with two species endemic to Japan; and five oligotypic saxifragaceous genera endemic to Japan and a few localities in adjacent regions : *Cardiandra* (2 spp.), *Deinanthe* (2 spp.), *Kirengeshoma* (monotypic), *Platycrater* (monotypic) and *Tanakaea* (2 spp.). These five semi-endemic genera of Saxifragaceae occur disjunctly in Japan and in a few localities in central and southern China. This has been regarded as evidence for floristic affinity between the Pacific side of Japan and central and southern China. The distribution of these genera in China provides a clue to the origin of the temperate flora on the Pacific side of Japan. Among the five genera, *Platycrater* and *Cardiandra* occur mainly in the warm-temperate region. *Tanakaea radicans* occurs on cliffs in the warm- and cool-temperate zones. The other two genera are restricted to the cool-temperate zone in Japan.

Tanakaea occurs disjunctly in a small area around Mt. Omei in Sichuan, China (*T. omeiensis*), and in a few localities in Shikoku and central Honshu, Japan (*T. radicans*). Recently Mt. Omei has attracted the attention of Japanese taxonomists as a locality with many species related to the temperate flora in Japan. However, the cool-temperate deciduous forest associated with *Fagus* as found in Japan is not found in Mt. Omei. According to Ying (1983), the deciduous broad-leaved forests have disappeared in western Sichuan. On Mt. Tashueshan located west of Mt. Omei, deciduous broad-leaved trees are mixed with evergreen broad-leaved trees in a narrow transitional zone between the evergreen broad-leaved forest zone and the coniferous forest zone.

Deinanthe occurs in western Hubei, China, (*D. caerulea*) and on the Pacific side of Japan (*D. bifida*). In the northern part of western Hubei, the temperate deciduous broad-leaved forests are found (Hou, 1976, 1983), and in Shennongjia in western Hubei the temperate deciduous forests occur between 1,700 and 2,200 m (Ying et al., 1979).

Kirengeshoma palmata occurs on Mt. Huangshan in Anhui, on Mt. Tiangmushan in Zhejiang, China, at few localities in South Korea and in some localities on Kyushu and Shikoku, in the Chugoku district and on the Kii Peninsula. The vegetation of Mt. Huangshan has been studied in detail by Chow (1965). In the cool-temperate zone on this mountain, a deciduous broad-leaved forest, including *Fagus*, is found. The species composition of this forest is very similar to that of the temperate deciduous forest on the Pacific side of Japan. *Stewartia* and *Sasamorpha*, which characterize the temperate deciduous forest on the Pacific side of Japan, are found in the temperate deciduous forest of Mt. Huangshan. Many other species associated with the temperate deciduous forest of Huangshan are common to the temperate deciduous forest of the Pacific side of Japan. Among those are *Acer mono*, *Cornus controversa*, *Hydrangea paniculata*, *Ilex macropoda*, and *Sapium japonicum*. The following examples are notable. The sexual race of *Boehmeria gracilis*, which is restricted to the Pacific side of Japan, is found on this mountain (Yahara, 1986). *Magnolia sieboldii* subsp. *japonica* distributed in the temperate zone of western Japan, including the Pacific side, occurs disjunctly on Mt. Huangshan and in Chuen Yuen of Gwangxi (Ueda, 1980). The temperate deciduous forest of Huangshan is undoubtedly closely related to that of the Pacific side of Japan.

It is notable that the temperate deciduous forest occupies relatively narrow areas in China. According to Hou (1983), it is found in sporadic montane regions in the transitional subtropics. The transitional subtropics occupy a narrow zone along the northern margin of the Yantsushen River crossing southern Anhui, southern Henan, northern Hubei, southern Shaanxi and eastern Sichuan. The temperate decidous forests in these regions usually lack *Fagus* and are dominated by such xerophytic oak species as *Quercus variabilis* because of the influence of a continental dry climate. Several species of *Fagus* occur in the mixed broad-leaved deciduous and evergreen montane forests in the subtropics south to the Yantsushen River. These forests are characterized by a mixture of such warm-temperate or subtropical evergreen components as *Cyclobalanopsis* and *Castanopsis* and many relictual deciduous species of Tertiary origin such as *Cercidiphyllum japonicum* var. *sinensis*, *Davidia involucrata*, *Camptotheca acuminata*, *Nyssa sinensis*, *Aesculus chinensis*, *A. wilsonii*, *Liriodendron chinense*, and *Emmenopteris henryi*. Thus *Fagus* is not always characteristic of the temperate deciduous forest in China

In conclusion, the temperate deciduous forest associated with *Fagus* occupies wide area in Japan but is very restricted in China. Narrow range of the temperate deciduous forest with *Fagus* may be partly due to destruction by man. Palynological evidence for vegetation changes in central China is needed. In the Japan Archipelago, it is well-documented that *Fagus* was restricted to coastal refugia during the last glacial period due to low temperature and low precipitation and began to expand northward and to higher elevations ca. 12,000 years ago (Tsukada, 1982b, c). As Hou (1983) pointed out, *Fagus* is a moisture-loving group of tree species. Because of drastic climatic changes during the Quaternary period, beech forests are considered to have been restricted to two humid regions in East Asia; the coastal refugia in the Japan Archipelago and the montane area in the eastern part of central China.

The hypothesis that the temperate flora of Japan formed through migration of a continental flora has prevailed among Japanese taxonomists and phytogeographers. However, the cool-temperate flora on the Pacific side of Japan includes many endemic and relictual species. The evolution of these endemic and relictual species probably took place in the coastal regions of East Asia, including the Japan Archipelago.

Before ending the discussion on the cool-temperate flora, I refer to problems related to the temperate coniferous species. In the cool-temperate zone of Japan, many coniferous species occur. These are *Abies firma*, *A. homolepis*, *Tsuga sieboldii*, *Pseudotsuga japonica*, *Picea polita*, *Sciadopitys verticillata*, *Cryptomeria japonica*, *Thuja standishii*, *Thujopsis dolabrata*, *Chamaecyparis obtusa*, *C. pisifera*, *Torreya nucifera*, *Taxus cuspidata* and *Cephalotaxus harringtonia*. These are endemic to Japan, except for *Cephalotaxus harringtonia*, which also occurs in Korea. *Sciadopitys* and *Thujopsis* are monotypic. The following genera are oligotypic and relictual : *Cryptomeria* (2 spp.; 1 in China), *Pseudotsuga* (4 spp. in East Asia and western North America), *Thuja* (6 spp. in East Asia and western and eastern North America), *Chamaecyparis* (7 spp. in Japan, Taiwan and western and eastern North America), *Cephalotaxus* (6 spp. in East Asia), *Torreya* (8 spp. in East Asia and eastern and western North America), and *Tsuga* (10 spp. in East Asia and western and eastern North America). The present ranges of these genera coincide with the well-known bicontinental disjunction of the Arcto-tertiary elements. Fossil evidence shows that these genera were already in existence by the Palaeo-tertiary (Hotta, 1974). The occurrence of these endemic and relictual coniferous genera is a notable characteristic of the cool-temperate flora in Japan.

Among the species listed above, *Abies firma*, *A. homolepis*, *Tsuga sieboldii*, and *Cryptomeria japonica* are often predominant components of the cool-temperate forest in Japan. *Abies firma* and *Tsuga sieboldii* sometimes form dense stands in the lower part of the cool-temperate zone. This *Abies firma-Tsuga sieboldii* forest is mainly found on the Pacific side. Some Japanese ecologists designated this forest as an intermediate temperate forest, but it can be regarded as a kind of cool-temperate coniferous forest (Yamazaki, 1983). According to palynological evidence, the cool-temperate zone of the Pacific side lacked *Fagus crenata*, except in coastal refugia, during the last glacial maximum (Tsukada, 1982a, b, c). The cool-temperate coniferous forest with *Abies* and *Tsuga* probably had a wider range than at present.

Abies homolepis is frequently associated with *Fagus crenata* and other temperate deciduous trees in the upper part of the cool-temperate zone. In this zone occur several characteristic species showing disjunction between eastern Asia and North America. Representatives are *Clintonia udensis* and *Tiarella polyphylla*. These two species occur in the coniferous forests in China and in the eastern Himalaya (Kanai, 1963). *Clintonia* and *Tiarella* are associated with coniferous and coriferous-mixed broad-leaved deciduous forests in North America. These genera are regarded as members of the cool-temperate coniferous forest.

Cryptomeria japonica is differentiated into a Japan Sea side and a Pacific side race. The Japan Sea side race is frequently found intermixed with *Fagus crenata* and other temperate deciduous broad-leaved trees on the Japan Sea side. The Pacific side race is almost extinct due to logging except in the cool-temperate zone of Yakushima Island where it forms a dense forest intermixed with *Tsuga shieboldii*, *Abies firma* and *Trochodendron aralioides*. Migration of this species since the last glacial maximum is reviewed in detail by Tsukada (1982a). At the last glacial maximum, this species was restricted to a small area around Wakasa Bay on the Japan sea side and to Yakushima Island and probably to some other coastal refugia in the Pacific side region. The shrinkage in the range during the last glacial age is similar to that in *Fagus crenata*. *Cryptomeria japonica* is also a moisture-loving species, as is *Fagus*. According to the palynological record from Osaka Bay, *Cryptomeria* appeared in the Japan Archipelago about 1,000,000 years ago, after the first glacial period (Tsukada, 1974). Fossil records agree with this estimation (Nasu, 1972). Until that time, many tertiary relics as *Metasequoia*, *Cunninghamia*, *Liquidamber*, *Eucommia* and *Nyssa* dissapeared from the Japan Archipelago. The prototype of the present cool-temperate forest flora in Japan was probably shaped at that time.

Warm-temperate flora

In the lowlands of southwestern Japan, evergreen broad-leaved forests occur. These forests include evergreen oaks (*Castanopsis*, *Cyclobalanopsis* and *Lithocarpus*) as predominant members and microphyllous evergreen trees such as Lauraceae, Theaceae, Myrsinaceae, Symplocaceae and others. These are frequently designated as the lucidiphyll forests in Japan. These forests are physiognomically and floristically similar to the montane microphyllous forests in the subtropical and tropical regions of East and Southeast Asia. Relatively less phytogeographical attentions have been paid to the warm-temperate flora of mainland Japan than to the cool-temperate flora. However, several emdemic or semi-endemic genera are found mainly in this zone or from this zone to the lower part of the cool-temperate zone of mainland Japan. They are *Pseudopyxis* (2 spp. endemic to Japan), *Perillula* (1 sp. endemic to Japan), *Cardiandra* (2 spp. in Japan, Taiwan and southern China), *Platycrater* (1 sp. in Japan and east central China) and *Alectorurus* (1 sp. endemic to Japan). In addition, many endemic species are found in this zone. Four genera, excluding *Cardiandra*, are almost restricted to the Pacific side and are sometimes referred to as examples of the Pacific or Sohayaki elements.

Cardiandra was recently revised by Ohba (1985). According to him, the Chinese taxon of this genus is a subspecies of the Japanese one (*C. alternifolia* subsp. *moellendorffii*) and occurs in lower montane regions between 600 and 1,200m in Guizhou, Hubei, Jiangxi, Zhejiang, Anhui, Fujian, and Jiangsu. It probably grows in evergreen montane forests or in gallery forests within the *Pinus* forest zone at lower altitudes. It occurs disjunctly in evergreen forests at the southernmost margin of the Ryukyu Islands in Japan on Iriomote Island. A variety *binata* is endemic to evergreen montane forests between 1,000 and 1,500 m in Taiwan. Another species with ancestral features (*C. amamiohsimensis*) is endemic to Amami-oshima Island located at the northern end of the Ryukyu Islands in Japan. This genus is a good example suggesting floristic affinity among isolated evergreen broad-leaved forests in the southwestern part of the Japan mainland, the Ryukyu Islands, Taiwan, and the southeastern part of continental China.

According to a recent study by Hara (1986), *Platycrater arguta* includes two varieties, var. *arguta* on the Pacific side of the mainland of Japan and var. *sinensis* in a few localities in low montane regions along the border between Zhejiang and Fujian where the montane evergreen forests occur (Hou, 1983). The range of Chinese taxon is very restricted. Var. *arguta* occurs in very humid places in Japan. Probably this species is limited to its present range in the coastal area due to its demand for abundant rainfall in summer supplied by the monsoon wind from the Pacific Ocean.

Not only these relictual species but also the major component species of the lucidiphyll forest should be considered in understanding the affinity of the warm-temperate forest flora of the mainland Japan. The ranges of major component tree species of the lucidiphyll forests in Japan have not been reviewed in detail. For Fagaceae, *Lithocarpus edulis* and *Cyclobalanopsis sessilifolia* are endemic to Japan. *Cyclobalanopsis acuta*, *C. gilva*, *C. salicina*, and *Lithocarpus glabra* are restricted to the coastal regions of southeastern China, Taiwan, the southernmost part of Korea and southwestern Japan. *Cyclobalanopsis glauca* and *C. myrsinaefolia* have wide ranges covering central and southern China, northern Indo-China and eastern Himalaya. The taxonomy of *Castanopsis sieboldii* remains unclear. In its strict sense, it is restricted to the southwestern mainland of Japan, the southwest Islands, Taiwan and the coastal region of central and southern China, although it may be conspecific with *C. carlesii* in inland China. For Lauraceae, *Neolitsea aciculata*, *Litsea japonica* and *Machilus japonica* are endemic to Japan and the southernmost part of Korea. *Cinnamomum japonicum* and *Machilus thunbergii* are restricted to Japan, southern Korea, Taiwan and eastern China facing the East China Sea. In Theaceae, *Eurya japonica* is restricted to Japan, southern Korea, Taiwan and Zhejiang. Thus major component tree species of the lucidiphyll forest include many examples of local species restricted to the coastal region facing the East China Sea and/or the Pacific Ocean. In continental China, the montane flora of Zhejiang and Fujian seems to be especially closely related to the lucidiphyll forest flora of Japan.

In the southwest Islands between Kyushu and Taiwan, evergreen broad-leaved forests are well developed. The southwest Islands are composed of six groups of islands : the Osumi Islands south of Kyushu, the Tokara Islands, the Amami Islands, the Okinawa Islands, the Miyako Islands and the Yaeyama Islands east of Taiwan. Among them, the lucidiphyll forest flora of the Osumi Islands is rather similar to that of southwestern Japan, whereas that of the Amami, Okinawa, Miyako, and Yaeyama islands (collectively called the Ryukyu Islands) includes many endemic species and is notably different from the former.

The Osumi Islands include two main islands : Yakushima and Tanegashima. Tanegashima is a very flat island while Yakushima has high mountains including Mt. Miyanoura-dake with the peak of 1,935 m above the sea level. On Yakushima Island, which is only about 100 ㎞², 45 endemic species and 27 endemic subspecies or varieties are found (Yahara et al., 1987). Some endemic taxa suggest a floristic affinity between Yakushima and southern China. The follwing taxa are notable. *Hancockia japonica* is rarely found in humid understory of the lowland lucidiphyll forest on Yakushima. This genus includes two species; another species *H. uniflora* occurs in Yunnan and Northern Vietnam. *Elatostema yakushimense* is sporadically found on wet rocks along small streams in the lucidiphyll forest. It is somewhat rheophytic. Its relative is known from Guangxi. *Ainsliaea faurieana* is a common, typical rheophyte on stream margins below 1,400 m. A related rheophytic species occurs in Guangdong and Guangxi. *Callicarpa shikokiana* is endemic to Yakushima and a few localities in southwestern Japan. Its closest relative occurs in Sichuan and Yunnan. *Pinus armandii* var. *amamiana* occurs in small areas on Yakushima and Tanegashima in the lucidiphyll forest zone. Var. *armandii* is one of the major components of the subtropical pine forests in southern China. Another variety, var. *mastersiana* is endemic to the highlands of Taiwan. It is notable that fossils with an affinity to var. *amamiana* were reported from middle Pleistocene sediments in Kyoto City (Miki, 1957) and in Yokohama City (Minaki, 1983) in central Japan.

In the lucidiphyll forest on Yakushima, several species of ferns occurs disjunctly from montane forests in Yunnan and Sichuan. They are *Arachniodes cavalerii*, *Diplazium heterophlebium*, *Vittaria forrestiana* and *Lemmaphyllum pyriforme.*

The montane zone above 1,200 m on Yakushima is occupied by the cool-temperate coniferous forests with *Cryptomeria japonica* and *Tsuga shieboldii* as predominant components and also several predominant evergreen broad-leaved species such as *Trochodendron aralioides*, *Symplocos myrtacea*, *Daphniphyllum macropodium* and *Eurya yakushimensis*. *Eurya yakushimensis* is an endemic species with its closest relative found in Anhui, Hunan, Fujian, Guangdong and Guangxi. *Zanthoxylum yakumontanum*, which is common in secondary forests in the *Cryptomeria* zone has a related species in the montane areas of southern China and nothern Indochina. Several herbaceous species in the cool-temperate zone also have relatives in southern China (Yahara et al., 1987).

The overall flora of Yakushima is closely related to the montane flora of southern China. Three patterns can be recognizable. Two rheophytic or riparian species have relatives in the coastal regions of Guangxi and Guangdong, some others (especially ferns) have relatives or occur disjunctly in the humid montane regions of Yunnan and Sichuan, and the third group of species has relatives ranging widely in southern China.

As already stated, during the last glacial maximum (ca. 18,000 years ago), the coastal regions of southwestern Japan were refugia of beeches. Yakushima and Tanegashima are considered to have been refugia for the lucidiphyll forests. The fact that the lucidiphyll forest flora includes endemic species related to species in montane regions of southern China supports this idea. On the other hand, the lucidiphyll forests in southwestern Japan include several tree species not found in the southwest Islands including Yakushima, but which occur disjunctly in southern China. They are *Ilex goshiensis*, *I. latifolia*, *I. purpurea*, *Symplocos laurina*, *Photinia glabra*, *Prunus spinulosa*, *Lithocarpus glaber* and *Cyclobalanopsis gilva*. In addition, the lucidiphyll forests in the southwestern Japan include many endemic fern species and also many fern species disjunctly distributed in southern China. Endemic species are *Arachniodes cantilenae*, *A. hekiana*, *A. hiugana*, *A. tomitae*, *A. tsutsuiana*, *A. yasu-inouei*, *Cyrtomium microindusium*, *Polystichum otomasui*, *Deparia minamitanii*, *D. otomasui* and others. Disjunct species are *Arachniodes assamica*, *A. yaoshanensis*, *Cyrtomium hookeriana*, *Dryopteris hangchowensis*, *D. lunanensis*, *Polystichum kiusiuense*, *Diplazium pinfaense*, and others. *Platycrater* and *Cardiandra* do not occur on Yakushima and Tanegashima. It is uncertain that these species inhabited the Osumi Islands during last glacial maximum and then expanded northward in the late-glacial age and eventually disappeared from the Osumi Islands. The lucidiphyll forests probably survived in the coastal regions on the Pacific side of Japan at least locally through the lastglacial maximum.

In the lucidiphyll forest on Yakushima, two endemic pioneer tree species, *Acer morifolium* and *Lagerstroemia subcostata* var. *fauriei* commonly occur. These species have considerable ability for dispersal and colonization. If Yakushima had been connected with Kyushu during the last glacial maximum, they could have migrated to the mainland. The maximum depth of Osumi Strait between Kyushu and the Osumi Islands is 118 m; the depth of the stait between Tanegashima and Yakushima is 84 m. If the sea level during the last glacial maximum was 80 ± 5m as postulated by Oshima (1982), Yakushima was then isolated from Kyushu during the last glacial period. Evidence from present day plant distributions supports Oshima's estimation.

There is no doubt that the lucidiphyll forest flora of southwestern Japan and Yakushima originated through northward migration of the subtropical montane flora of southern China. The age of such an event is, however, uncertain. The fossil "Uegahara flora" or "*Sysigium* bed" from the middle Pleistocene includes many extant species of evergreen broad-leaved trees (Nasu, 1972). The pollen zone I-2 at Osaka Bay dated at 350,000-400,000 years B. P. (Tsukada, 1974) are probably from the same age as this fossil flora. Since that age, the lucidiphyll forests could have survived in local refugia in southwestern Japan and Yakushima through two glacial periods. Before that age, there is no record of a lucidiphyll forest in Japan. In the Ryukyu Islands, which have probably been under the influence of a warm-temperate or subtropical climate throughout the Quaternary, the lucidiphyll forest might have developped earlier.

The lucidiphyll forests in the Ryukyu Islands include many endemic species and are largely different from those on Yakushima and mainland Japan. Among the major components of the lucidiphyll forests, the following species are endemic to the Ryukyu Islands : *Castanopsis sieboldii* var. *lutchuensis*, *Cyclobalanopsis miyagii*, *Ilex liukiuensis*, *I. maximowicziana* var. *mutchagara*, *I. warburgii*, *Euonymus lutchuensis*, *Camellia lutchuensis*, *Eurya osimensis*, and *Symplocos microcalyx*. The Ryukyu islands are considered to have been isolated from the mainland Japan, continental China and Taiwan since about 1,000,000 years ago. The high endemism is recognized not only for plants but also for animals, including vertebrates. However, the geological and vegetational changes in the Ryukyu islands during the Quarternary are poorly understood at present. Also, our systematic knowledge of plant species endemic to the Ryukyu islands is still at the alpha level in many cases. The origin of the lucidiphyll forests in the Ryukyu islands therefore remains an open question. Further geological and systematic evidence is needed even to speculate on a probable scenario.

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