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On the Distribution of Beech(*Fagus*, Fagaceae) and Beech-Dominated Forests in the Northern Hemisphere

Yim, Yang-Jai
(*Dept. of Biology, College of Liberal Arts and Science, Chung-ang University*)

北半球의 너도밤나무와 너도밤나무林의 分布에 關하여

任　良　宰
(中央大學校 生物學科)

ABSTRACT

The distribution of beech species (*Fagus*) and beech-dominated forests along climatic gradients in the Northern Hemisphere was studied by use of taxonomic and ecological literature. The genus *Fagus* as a whole occurs over the range of 4.5 to 20.0°C mean annual temperature and 600 to 1000 mm in lower limit, mean annual precipitation. At the higher end of the temperature range, beech occurs in zones with relatively high growing-season precipitation. Edaphically, beech species and beech-dominated forests tend to occur on mesic, moderately fertile sites.

Beech-dominated forests occur in a limited portion of the climatic range of the genus with sensitive responses to other environmental factors. The distributional range of beech-dominated forests on a global scale depends more on climatic factors and geological events than on soil conditions or other factors, summarizing the facts obtained by many researchers on beech dominated forests.

INTRODUCTION

In the Holarctic realm there are about 12 species (taxonomic treatment varies) in the genus *Fagus*. Beeches (*Fagus*) are important dominant species in mesic climax forests of the North Temperate Zone (Whittaker 1975, Vankat 1979, Wolfe 1979). However, there is no ecological study on a global scale of the various species, although many studies have been carried out in limited regions.

Many factors are responsible for determining plant distribution patterns. These factors may be inherent or geographic. Inherent factors include those related to the evolutionary history of taxa and to the disperse ability of individual plants. Geographic factors are of two major types: barrier factors and climatic factors. Barrier factors may be of greater significance to the distribution of the world's flora than climatic factors (Lawrence 1951). In this paper the relation of beech distribution patterns to climatic factors will be considered in depth.

To understand the behavior of related taxa in different regions, it is necessary to study their distributions including latitudinal and elevational distribution limits, relationships with climatic and edaphic conditions, role in plant communities, comparative competitive ability, and migration history.

The purpose of this paper is to summarize the ecology of *Fagus* species as reflected by their distribution in the Northern Hemisphere. This includes global-scale relationships to present-day climate and more local relationships to microclimate, topography, and substrate.

HISTORY AND TAXONOMY OF THE GENUS *FAGUS*

The center of origin of the family Fagaceae is ap-

Table 1. List of *Fagus* species

Name	Synonyms	Number of varieties	Distribution
F. grandifolia Ehrh.	*F. ferruginea* Ait. *F. americana* Sweet, *F. atropunica* Sudw.	3	eastern North America
F. sylvatica L.	(none)	many cultivars	Europe
F. orientalis Lipsky	*F. sylvatica* var. *macrophyllus* D.C., *F. macrophylla* Koidz., *F. winkleriana* Koidz.	(none)	middle Asia
F. engleriana Seemen & Deels	*F. sylvatica* var. *chinensis* Franch, *F. sylvatica* var. *bracteolis* Oliver, *F. sylvatica* Leville	(none)	central China
F. longipetiolata Seemen	*F. sinensis* Oliver, *F. longipes* Leville, *F. sylvatica* var. *longipes* Oliver	(none)	central, western China
F. lucida Rehd. & Wills	(none)	(none	western China
F. multinervis Nakai	(none)	(none)	southern Korea
F. crenata Blume	*F. sieboldii* Endl., *F. sylvatica* var. *asiatica* D.C.	(none)	Japan
F. japonica Maxim.	(none)	(none)	Japan
F. hayatae Palib.	(none)	(none)	Taiwan
F. tientaiensis Liou	(none)	(none)	southeastern China
F. chienii Cheng	(none)	(none)	Szechuan, China

parently in the highlands of southeastern Asia. There are several reasons to believe that this is so. All seven genera of the family today occur in this region, including the genus *Trigonobalanus,* which combines the characteristics of the two subfamilies within the family Fagaceae. The tropical montane flora of southeastern Asia is related to both temperate floras and lowland tropical floras by numerous phylogenetic connecting series (Daubenmire 1978, Pearson 1978) and may represent the center of origin of the genus *Fagus* or its immediate ancestors. *Nothofagus* may have followed a migration route from southeastern Asia through Antarctica to its present range at a time when Gondwanaland was not fragmented (Raven and Axelrod 1974).

Fossil records of the Fagaceae are known from the upper Cretaceous, and the genus *Fagus* is found first in Eocene deposits (Pearson 1978). *Fagus* was part of the so-called Arcto-Tertiary Geoflora and was widely distributed at high latitudes in the Northern Hemisphere during the Tertiary. According to Tanai (1974), the modern infrageneric species groups of beech appear to have originated during the mid-Tertiary. The *F. grandifolia* group first appeared during Oligocene time on both the eastern and western sides of the Pacific. The genus disappeared from western North America by the end of the Miocene, probably due to increasing aridity. In east Asia the genus has survived until the present. The *F. sylvatica* species group did not appear in the geological record until late Miocene time. During the Tertiary many species had wider distributions than they do now. European deposits from this period contain *F. crenata* and *F. japonica,* now restricted to eastern Asia, along with *F. sylvatica,* the only modern European species (Tralau 1962). Fossils similar to the American *F. grandifolia* are known in Europe from Miocene to Pliocene or Quaternary time. During the Oligocene and Miocene several species of beech reached higher latitudes in eastern Asia than they do now. The overall history of the genus thus involves a possible origin in southeastern Asia in the Cretaceous, invasion of the Northern Temperate Zone during the Tertiary, and very wide, in some cases nearly circumpolar, distribution of several species as components of the Arcto-Tertiary Geoflora. The present restricted ranges of *Fagus* species can apparently in many cases be attributed to climatic change and fragmentation of the region occupied by the Arcto-Tertiary Geoflora during the late Tertiary and the Quaternary.

The taxonomic treatment of modern species used in this paper is based on Lawrence (1951), Rehder (1956) and Benson (1979). Twelve species are currently recognized in the genus (Table 1). Among the characters used to separate species are leaf size and shape, bark color, and branching patterns.

Some of the twelve species listed may be hybrids or varieties of others; e.g. *F. multinervis* (Lee 1967) may be a variety of *F. japonica*. According to Lee (1973) *F. chienii* may be a hybrid of *F. longipetiolata* and *F. lucida*. Such relationships should be investigated for other species pairs, for example *F. chienii* and *F. tientaiensis*.

Intraspecific variation is well developed in several species. For example, Camp (1951) described three varieties of *F. grandifolia*. The "gray" variety tends to grow in sites with severe climates, the "red" in intermediate situations, and the "white" in milder climates. *F. sylvatica* contains many genotypes that have been sometimes recognized as varieties and have been propagated by horticulturalists for drooping branches, red leaves, or other unusual characteristics (Rehder 1956).

MATERIALS AND METHODS

The characteristics and distribution of beech species and beech-dominated forests were compared by use of vegetation maps, species distribution maps and other references. Three major distributional areas were recognized: northeastern America, Europe-Orient and northeastern Asia. Range areas of species were estimated using 1° latitude by 1° longitude cells on distribution maps. Areas were standardized to the 69–70° N cell. In many regions the natural vegetation has been destroyed by human activities, and actual vegetation and species distribution patterns do not clearly reflect the influence of climate and other environmental variables. Climax vegetation and natural ranges at present day were identified using local floras and potential natural vegetation maps of various authors. The most useful sources were U.S. Government (1960), Ganssen and Hädrich (1965), Little (1971), Rowe (1972), Geelan and Twichett (1974), Collins (1975, 1978), Miyawaki et al. (1975), Schmithusen (1976), Tsukada (1967a, b), Budyko (1977), Fukui (1977), Lawrence (1977), National Oceanic and Atmospheric Administration (1977), Ruffner and Bair (1977), Espenshade (1979), and Wolfe (1979).

Climatological and edaphic data on beech species and beech-dominated forest types were obtained from published data and estimated from maps. Annual mean temperature and mean annual precipitation are the major climatic variables used. Relative density or relative basal area of *Fagus* spp. in certain stand is used as a measure of response to environmental factors. Climatic data vary between regions. Climatological evaluations of latitudinal and elevational changes of climate were, however, standardized so far as possible for comparative study of the different regions. Soils and topographic relief were evaluated and compared using soil and topographic maps.

To compare elevational ranges, it is necessary to know the relationship of air temperature to elevation where temperature data are not directly obtainable. A temperature lapse rate of 5°C per 1000 m of elevation change is used throughout.

This value is typical of montane temperate regions. Temperature lapse rates in the southern Appalachian Mountains, USA, are in the range of 4.1 to 5.8°C per 1000 m (Hicks 1979). The lapse rate calculated from observations of the Central Meteorological Observatory, Pohang, Korea, is 5 to 6°C per 1000 m (Yim and Kira 1975). Wolfe (1979) also used a lapse rate of 5°C per 1000 m in eastern Asia, except for 20 to 30°N latitude in central China.

RESULTS AND DISCUSSION

Global distribution ranges of beech species

Global beech distribution ranges on a latitude-longitude grid between 19° and 61°N and between 100° and 360° longitude are shown in Fig. 1. The frequency

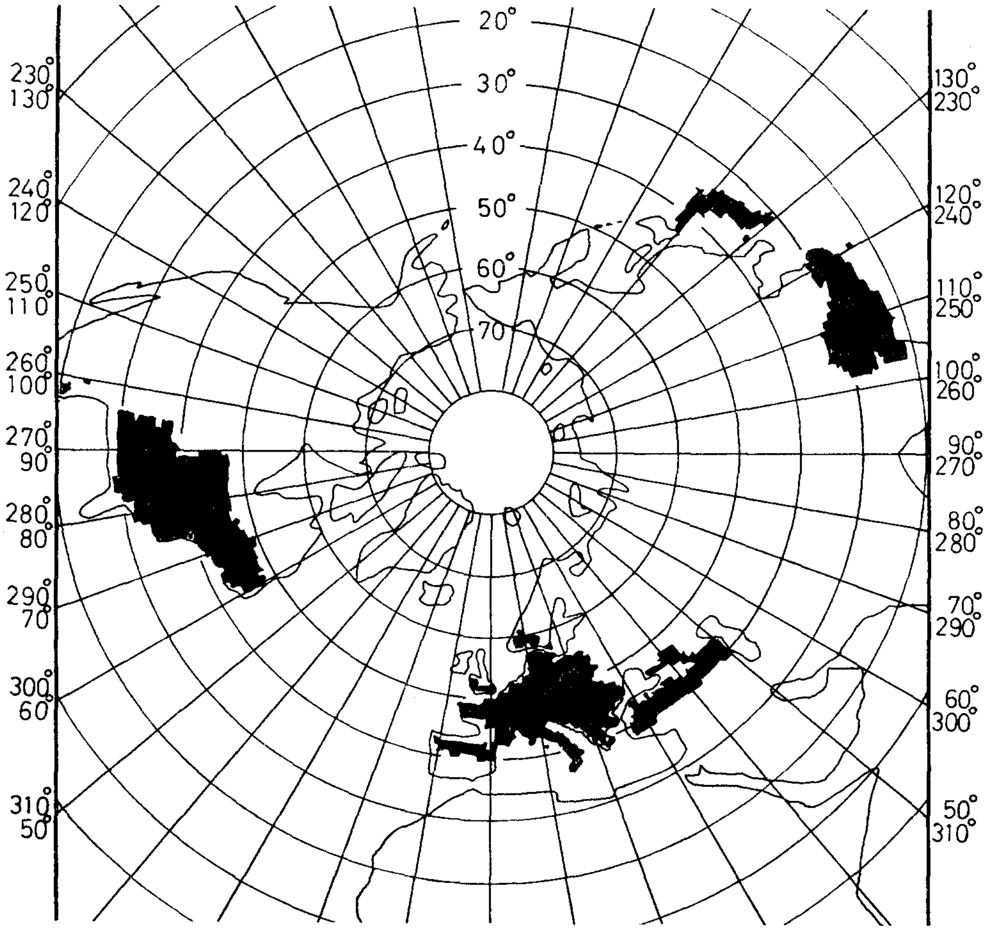

Fig. 1. Distribution of the genus *Fagus* in the Northern Hemisphere. Distributions are projected on a polar coordinate system with the North Pole at the center. Each 1° latitude × 1° longitude cell containing one or more *Fagus* species is blackened.

distribution curve of the genus against latitude appears almost bell-shaped, with a peak at 40°N. The curves for individual species were almost similar in shape to that for the genus, although each species has a distinctive latitudinal range (Fig. 2 and 3). The bulge in the genus curve at latitude 45°N (Fig. 3) is attributed to a "lake effect" due to climatic modification by the Great Lakes in North America and the Black Sea in the Europe-Orient region. The Great Lakes region of North America is rather less continental in temperature regime than areas immediately to the west. There is also a slight increase in precipitation near the Lakes (Trewartha 1961).

Climates at a given latitude differ considerably. To compare actual environments occupied by beech species, the ranges of the species were plotted in a climatic space using mean annual temperature and mean annual precipitation as axes (Fig. 4). Species of widely separated geographic areas are quite similar in distribution within the climatic space.

An example of an elevational distribution pattern is shown for *F. sylvatica* (Fig. 5). There is a negative correlation between the upper elevational limit and north latitude for this species in Europe. This suggests that the upper elevational limit parallels temperature conditions.

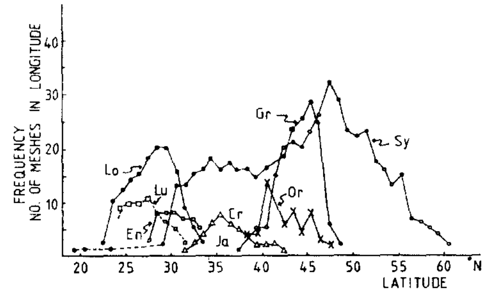

Fig. 2. Latitudinal distribution of *Fagus* species in the Northern Hemisphere. Each point represents the area occupied by a species in a latitudinal band 1° wide. The area was estimated by counting the number of 1° × 1° cells occupied and standardizing so that the 69° N to 70° N cell = 1.0. Symbols: Gr or G = *F. grandifolia,* Sy or S = *F. sylvatica,* Or or O = *F. orientalis,* Cr or C = *F. crenata,* Ja or J = *F. japonica,* Lo = *F. longipetiolata,* En or E = *F. engleriana,* Lu = *F. lucida,* H = *F. hayatae.*

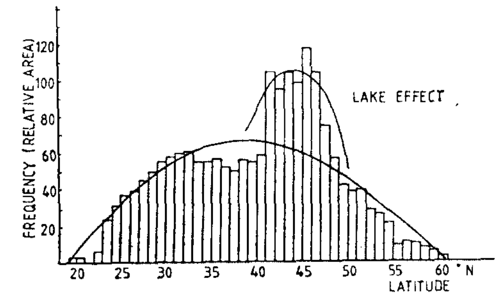

Fig. 3. Latitudinal distribution of the genus *Fagus* in the Northern Hemisphere. Each bar represents the area of cells occupied by *Fagus* species in a 1° latitudinal band, standardized as in Figure 2.

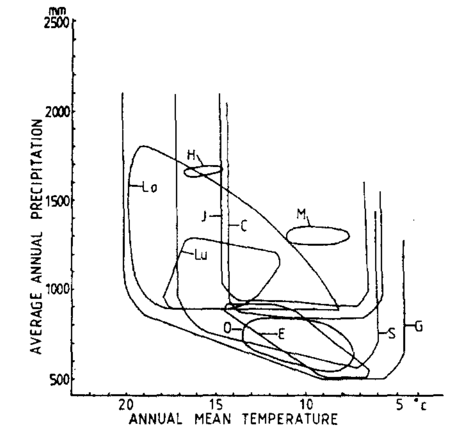

Fig. 4. Distribution of *Fagus* species in a two-dimensional climate space. Each polygon or oval outlines climatic conditions suitable for a single species. Symbols as given for Figure 2.

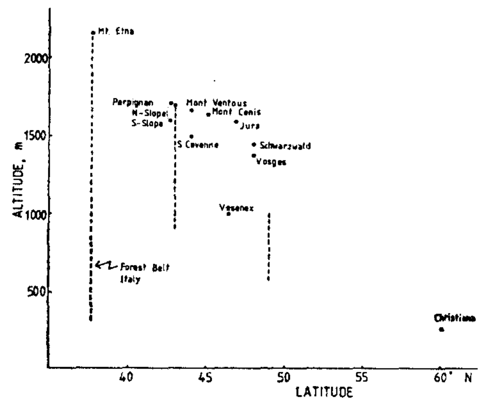

Fig. 5. Elevational distribution of *F. sylvatica* in Europe. Each point represents the upper elevational limit of the species in a particular region. The solid line was fit by eye to indicate the trend of these points. The dotted lines indicate the elevational range of deciduous forest at certain latitudes.

Such a phenomenon has also been reported for beech species in other regions (Horikawa 1972, 1976).

The distribution of climate types in the Northern and Southern Hemispheres is overall rather similar, as shown by plots of weather station data within the climate space used to analyze species distributions (Fig. 6). Areas in the Southern Hemisphere lie within the range of climatic tolerance of beeches in the Northern Hemisphere. This suggests that *Fagus* does not now grow in the Southern Hemisphere because of historical causes rather than because of a lack of suitable environments.

Influence of nonclimatic factors on local distribution

Thus far, the distribution of the genus *Fagus* and of individual species in relation to global climate has been discussed. Analysis of the relationship of beech species to topographic and edaphic factors is necessary to interpret the distribution of beech and beech-dominated forests on local scales. A beech-dominated forest is defined as a vegetation type in which beech species compose ≥ 40% of total stems or of stand basal area.

In North America beech(*F. grandifolia*) is an important or potentially dominant species in five of the vegetation

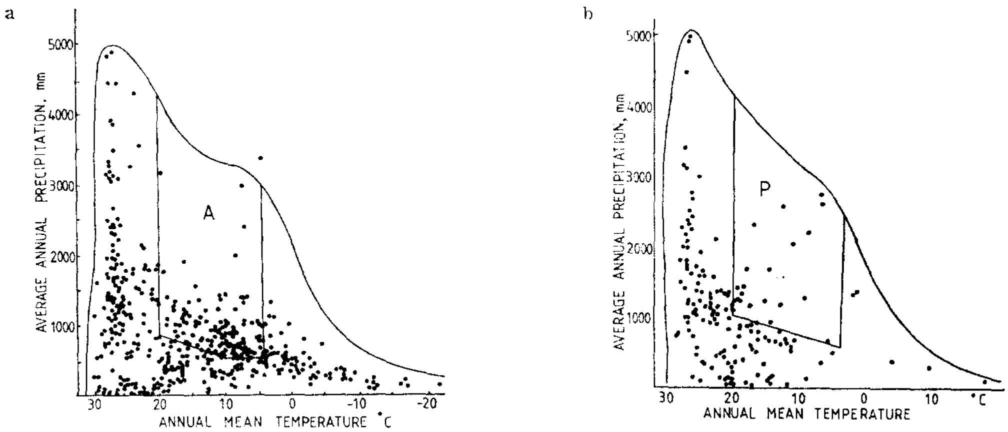

Fig. 6. Distribution of existing climates in a two dimensional climate space. Each point represents climatic data for one station. In both cases the outer line was drawn by eye to enclose these points. The climatic range of the genus *Fagus* is shown by the inner line.

a. Northern Hemisphere. The inner line and the symbol A indicate the actual climatic range of *Fagus.*

b. Southern Hemisphere.

The outer line and the symbol P represent climatic conditions under which *Fagus* occurs in the Northern Hemisphere, and thus represent the potential range of the genus in the Southern Hemisphere.

types recognized by Küchler (1964): Beech-Maple forest, Mixed Mesophytic forest, Northern Hardwoods forest, Northern Hardwoods-spruce forest, and Southern Mixed forest. The relationship of these vegetation types is shown in a climatic space diagram (Fig. 7). Two important features should be noted: First, beech-dominated forests do not occur over the entire climatic range of *F. grandifolia*; rather, they occur only in the central part of the range. Second, beech-dominated forests do not cover the entire landscape within areas mapped as one of the types named above. Local features of soil and topography restrict the dominance of beech. Examples of such restrictions will be discussed for North American, European-Oriental, and East Asian beech-dominated forests.

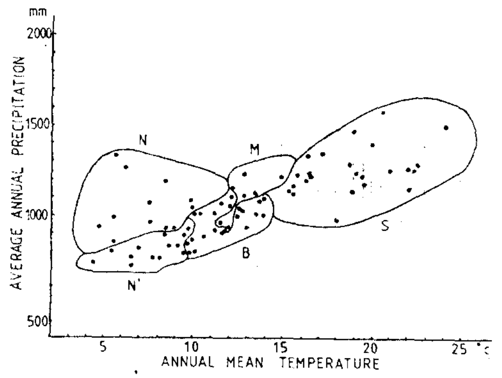

Fig. 7. Distribution of five North American vegetation types in which *Fagus grandifolia* is potentially dominant, shown in a two-dimensional climatic space. Symbols: N′ = Northern Hardwoods forest, N = Northern Hardwoods-Spruce forest, B = Beech-Maple forest, M = Mixed Mesophytic forest, S = Southern Mixed forest. Note that some forest types, particularly the Southern Mixed, extend beyond the climatic range of beech. Not all sites within the range of each type are beech-dominated.

North American beech-dominated forests tend to occur in mesic situations, on somewhat acid soils of moderate to high fertility, and in a variety of topographic situations.

In Ohio, USA, an area representative of the northern part of the range of *F. grandifolia*, several types of beech-dominated forest occur. Gordon (1969) recognized five: beech-sugar maple, wet beech, hemlock-beech, beech-maple-tulip tree, and beech-white oak. Beech-maple, the geographically most extensive type, is found only north of the glacial limit (Braun 1947), perhaps reflecting a large-scale influence of substrate. Beech is not usually dominant in sites that are flooded for long periods or that are exposed to intense solar radiation (Gordon 1969). The beech-dominated forest types of Ohio occur commonly on middle and lower slopes, usually north-facing, and on streamside flats (Gordon 1969). However, where the wet beech type occurs on streamside flats, the trees are raised above flood level on mounds and experience at most a brief period of flooding (Braun 1916). In the Neotoma Valley in south-central Ohio beech occurs in the cove and on lower northeast-facing slopes, sites that have moist soil and moderate temperatures through most of the year (Wolfe *et al.* 1949). The studies of Braun (1916) in the beech-maple region near Cincinnati indicate that beech is most abundant near the midpoint of a gradient between permanently wet soil in the lowest part of depressions and dry sites at the rim. Gordon (1969: p.92) indicates that beech-dominated forests occur on soil types ranging from "poorly drained" (wet beech) to "moderately well drained" (most of the other types). As noted above, beech trees in the wet beech type may avoid flooding, and so actually experience better drainage conditions than Gordon's drainage category indicates. Beech-dominated forests do not occur on "well drained" or "droughty" soils in Ohio.

Whittaker (1956) has provided information on the distribution of *F. grandifolia* in the Great Smoky Mountains of Tennessee and North Carolina. The relationships of relative density of beech to estimated mean annual temperature and soil moisture gradients (Fig. 8) show how the effect of these factors influence beech distribution in mountainous terrain. The relative

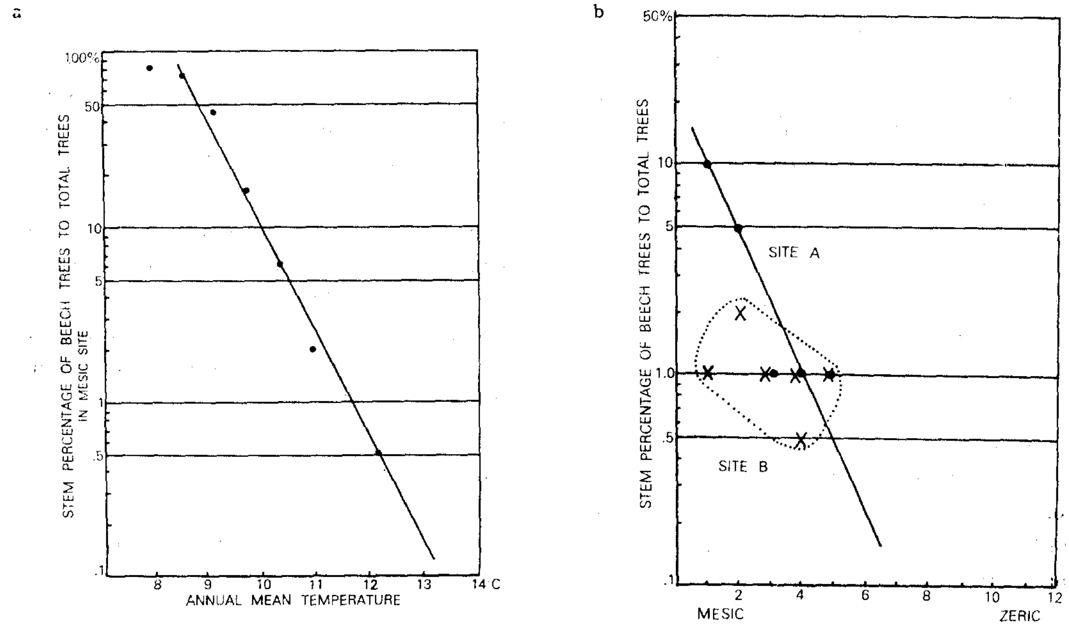

Fig. 8. Distribution of *F. grandifolia* along temperature and moisture gradients in the Great Smoky Mountains. Beech distribution data from Whittaker (1956).

a. Abundance of beech along a gradient of mean annual temperature in mesic sites. Temperature inferred from elevation using climatic data of Shanks (1954). The data are fit well by a straight line on a semilog plot.

b. Distribution of beech along a moisture gradient over two elevational ranges. Site A (solid line and filled points) includes the range 763 to 1068 m. These data approximate a straight line on a semilog plot. Site B covers the elevational range 1068 to 1373 m (dotted line, X's). These data are scattered and are not fit by a line.

density of beech is closely related to estimated mean annual temperature (Fig. 8a). At low elevations (763 to 1068 m) relative density is closely related to soil moisture status, but at high elevations (1068 to 1373 m) the relationship is poor (Fig. 8b). This suggests that the local range of beech is limited by temperature when soil moisture is suitable, i.e. in mesic sites, whereas soil moisture is a limiting factor when temperature is favorable.

The edaphic relationships of *F. grandifolia* appear to be consistent throughout its range. This is indicated by consideration of its distribution near the southern range limit, in the Coastal Plain of the southeastern US. In this region upland soils are sandy and leached and are thus xeric and nutrient-poor. Beech is absent from such sites, but is a dominant in topographic situations where soil conditions are ameliorated. Beech-dominated forests are found in narrow coves where soils are mesic and have higher nutrient content. Nesom and Treiber (1977) describe such a site in North Carolina and Thompson (1977) mentions a stand in northwestern Arkanasas, which is however in the Ozarks rather than the Coastal Plain. In the Gulf Coastal Plain of Florida, Louisiana and Texas, beech-dominated forests occur on floodplain terraces of small streams, in addition to protected lower slopes adjacent to stream floodplains. In such sites beech is usually of secondary importance to *Magnolia grandiflora*, *Quercus* spp. and other species, although it can dominate in some cases. Stands have been described by Nixon *et al.* (1980) and Delcourt (1977). Similar forests occur in the Coastal Plain of South Carolina (Barry 1980). See Quarterman and Keever (1962) for considerations of role of beech in the Southeastern Mixed Forest as a whole. These stands occur on floodplain terraces that are infrequently flooded, but are mesic and of relatively high fertility compared to surrounding sandy or loess-derived soils. Again, beech is restricted in local distribution by edaphic, topographic and probably microclimatic factors.

The same sorts of restrictions on local distribution also seem to characterize European and Asian beech-dominated forests. *Fagus sylvatica* forests are found on mesic sites with soil pH of 4.0 to 6.5 (sometimes as high as 7.5) in Denmark (Nielsen 1978), Sweden (Nilsson 1978; Nihlgård 1970, 1971; Nihlgård and Lindren 1977), England (Anderson 1973), and Italy (de Santo *et al.* 1976). Asian forests are similar in environmental relationships, but are often richer in both beech and non-beech species than are European and American stands. Studies have been carried out in Japan (Nakane 1978; Yoshioka and Kaneko 1962; Tohoyama 1965; Sasaki 1973; Nomoto 1956), China (Tsin *et al.* 1975), and Korea (Cha *et al.* 1975, Yim *et al.* 1980). The European and Asian studies are similar to the American ones in indicating that beech species occur most frequently and are most likely to dominate on mesic, somewhat acid, moderately fertile soils in topographic situations with a moderate microclimate. They are not often found on extremely wet and extremely dry sites with soils of low fertility(Table 2).

CONCLUSIONS

This paper has attempted to relate the present-day patterns of distribution of species of the genus *Fagus* to present-day distribution of climate types, and to local edaphic and topographic factors.

The modern species of beech occur over climatic zones with ranges of mean annual temperature of 4.5 to 20.0°C (Fig. 9) and a range of mean annual precipitation of 600 to 1000 mm in lower limit with no pronounced dry season. Along a northern hemisphere latitudinal gradient

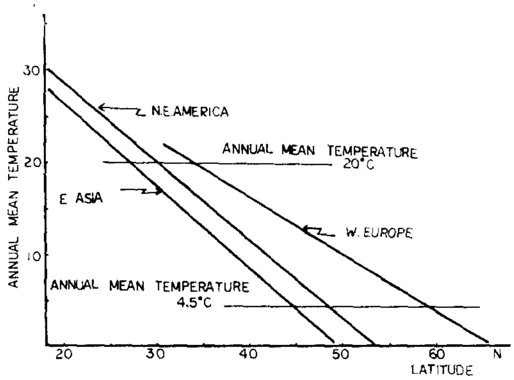

Fig. 9. Comparison of thermal environment between the continents. Three oblique lines were obtained, plotting the climatic data from the references cited.

the genus *Fagus* displays an approximately bell-shaped distribution curve. Individual species also show such curves, and are similar in dispersion within a two-dimensional climate space. Forests dominated by beech occur only in the optimal part of the temperature range (6 to 12°C mean annual temperature) if precipitation enough. On local scales beech species and beech-dominated forests occur most frequently in mesic sites of moderate fertility with short or no period of flooding. Such sites tend to occur in areas with well developed topography, with mature stream valleys (Fig. 10).

This summary of the environmental relationships of beech species and beech-dominated forests provides a background for tracing the past migrations and evolution of beech species in relation to pale environmental conditions.

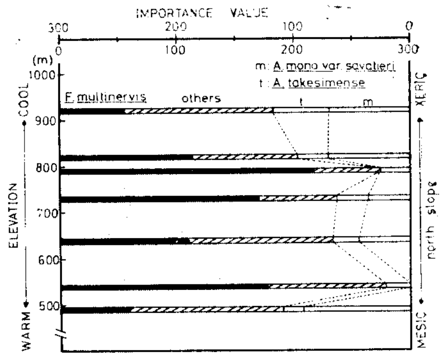

Fig. 10. Structure of beech-maple forest on the northern slope of Seongin-bong, Ulreung-do, S. Korea.
At Dodong (221m), Ulreung-do;
- mean annual precipitation: 1,485 mm
- Kira's warmth index: 94.2
- Thornthwaite's moisture index: 110.9

Table 2. Selected beech forests and their environments in North Hemisphere.

Character of stand	Locality	Climate AMT (°C) AAP(mm)	Ground and other conditions	Source
Beech gap *F. grandifolia* 50–80% of total stems ≧ 2.5cm class	Great smoky Mts. (1586–1708^{m}) 35°30′N 83°30′W	7–9°C 1,250mm	mesic, rich in humus	Whittaker, 1956
Beech-maple *F. grandifolia* 50%, *A. saccharum* 12% basal area	Warren Woods, Michigan 42°N 86°30′W	9.9 1,020	till plain lake district 25 seasons, wind throw of trees ≧ 25.4cm dbh. 0.2 trees/ha/yr.	Cain, 1935 Brewer & Meritt, 1978 Woods, 1979
Mesophytic forest *F. grandifolia* 50% of tree growth	Cincinati region, Ohio 39°N 84°30′W	9.5 1,208	till plain, shallow depression, Illinolan drift pre-erosion climax	Braun, 1916
Oak-beech *F. grandifolia* 24.2%, *Q. alba* 41.0% in relative density	near Washington D.C. 38°51′N 77°03′W	14.1 1.029	10–25% slope undisturbed for 67 yr. granite	Dix, 1957
Maple-beech *F. grandifolia* *A. saccharum*	Allegany state Park, New York 42°N 79°W	7.8 1,103		Gordon, 1937
Beech-maple *F. grandifolia* *A. saccharum* 61% cover (2 species)	Ontario lowland W. New York 43°N 78–79°W area	8.4 8.51	lowland drift lime stone dolomites	Miller, 1973
Beech-maple *F. grandifolia* S. group seeding frequency 1.4% central stand 9.4%	Wisconsin beech border, Wisconsin 19 stands total 23 stands		pH: northern 5.5 southern 6.5 soil chemical (C. Mg. K. P.) no correlation with seedling no. to water remaining	Ward, 1961

N. group 55.4% *A. saccharum*			capacity (A. horizon)	
Beech-maple *F. grandifolia* *A. saccharum* importance 80.2 11.3 70.4 13.5 54.7 23.5	Allenberg Bog area, New York near Little Valley 42°15′N 78°55′W 42°30′N 78°40′W 42°35′N 78°30′W	 7.1 1,240 7.9 1,049 7.9 1,049	presettlement Survey data	Miller, 1973
Beech-maple *F. grandifolia* 7 stands (70 trees) test,	Northern half of Indiana	17.8–26.7 (June) 0–25.4 (June)	beech growth, width of growing ring correlate with precipitation (June)	Diller, 1935
Beech forest *F. sylvatica*, age 90yr. 3ha, pure beech, LAI 5.0 ~ 6.9 Leaf Production 247.5 ~ 316.2g m /yr.	near Rönde E. Jutland Denmark		defoliation by Dasychira pudibunda 3ha of pure beech tree height < 20m DBH > 4 cm	Nielsen, 1978
Beech stand *F. sylvatica* 90yr. tree cover 85% tree height 18–20m Beech-fir stand, 70–yr. *F. sylvatica* *A. alba* tree cover 90% tree height 30m	Monte Taburno (1394m) Italy 41°0′N, 12°27′E	7.9 (80yr. average) 2,166 (40yr. average)	Mesozoic Calcareous block slope 25° pH 5.9(A_1) soil respiration 0.50(Nov.)-0.56 mgco2/100gdw. slope 18–20° pH 6.3(A_1) soil respiration 0.23 (Dec.)-0.55 (Nov.) co2/100gdw	De Santo *et al*, 1976
Beech forest *F. sylvatica*, 90yr. height 25.0–30.1m treebiomass 322–375ton/ha basal area 24.0–31.4m^2/ha	Archaean ridge, Söderasen, S, Sweden 55°59′N 13°10′E	6–7 800	Cambrian Shales, sandstone, acid brown soil pH 4.2(A_1) S-slope influence of D. Pudibunda	Nilsson, 1978
Beech and spruce forest *F. sylvatica*, 100yr. 240trees/ha 39cm dbh. *Picea alba* 55yr. 880 trees/ha 28cm dbh.	Kongalund, Scania S. Sweden, 55°59′N 13°10′E 115–120m alt.	6–7 800	composition of rainfall, a: through 70% (PH5.7), stem flow 11%, interception 19% b: through, 58% (PH4.5), stem f. 3%, interception 19%	Nihlgård, 1970
Beech forest uninfluenced by underground water suffer most damage from podcalization when planted with spruce	Kongland, Schm'a S. Sweden	6–7 800	soils of moderately good mineral composition.	Nihlgård, 1971
Beech forest *F. sylvatica* Mercuralis type, 80–100yr. height 28, Basal area 31.1m^2/ha Lamium type, 45–130yr. height 25m.	S. Sweden 55°42′N 13°38′E 60m alt. 55°59′N 13°10′E 120m alt	 7 650 7 700–800	Silurian shales, silt clay pH 6.0–7.5 Cambrian shales and sandstone all grainsizes	Nihlgård & Lindgreu, 1977

Basal area 31.4m²/ha				pH 4.0–4.5	
Deschampsia type, 80–120yr. height 22m, basal area 29.7m²/ha	55°45′N 13°55′E 150m alt.	6	800	Cambrian sandstone stone-sand pH 4.0–4.5	
Beech forest *F. sylvatica*, coppicing 15yr. intervals canopy stem/ha (10.0dbh) 1307 little fall 4.67 ton/ha	Blean Woods National Reserve in Kent, 84malt SE. England		746	alluvial sand weakly podolized humus moderate pH (4.1 Castanea site 4.5 Fagus site) London clay	Anderson, 1973
Beech-fir forest *F. crenata* 63.7% in basal area (dbh ≧ 4.5cm) 216 trees/ha *A. hololepis* 12.4% in basal area (dbh ≧ 4.5cm) 244 trees/ha 140ton c/ha	Mt. Odaigahara 1490m alt C. Japan 34°11′N 136°05′E	6.2	4,773	Sandstone mesic pH 4.0–5.0	Nakane, 1978
Beech forest	Mt. Fanshing Shan				Tsin *et al.* 1975
F. engleriana	C. China	8.4– 9.2		Eastern N. slope	
Sinamindinaria chungii	1850–2000m				
F. lucida	1700–1900m	8.9– 9.9		Western N. slope	
S. chungii	1600–1850m	9.2–10.4		Eastern N. slope	
F. lucida	1600–1900m	8.9–10.4		Eastern S. slope	
S. chungii					
F. longipetiolata	1300–1600m	10.4–11.9		Eastern N. slope	
S. chungii	1500–1700m	8.9–10.9		Western N. slope	
F. longipetiolata	1200–1600m	10.4–12.4		Eastern S. slope	
Beech forest *F. crenata* 940m alt, lower zone beech forest upper zone Abies mariesii	Mt. Hakkôda, Aomori, Japan			Mt. Hakkôda (1,3600m)	Yoshioka and Kaneko, 1962
Beech forest *F. japonica* height 15–25m pure stand on S-slope	Mt. Ohmuro, Yamanasin Pref. below 1300m alt.			limiting factor: edaphic condition	Tohoyama, 1965
Beech forest *F. japonica* 500m above pure stand, 300– 500m beech-fir ecotone	Tôhoku District N.E. Honshu, Japan	11	1,154	sample Quadrat frequency 90–100% (beech)	Yoshioka,
Beech-oak forest *F. crenata* 3 stands data beech 5.2 → 74.3% oak 75.0 → 3.5% in volum percentage	Okutama, near Tokyo, 35°40′N 139°45′E			Analysis of Succession process	Nomoto, 1956
Beech forest *F. multinervis* pure stand	Is. Ulreung-do (984m) S. Korea 130°50′E 37°30′N	7–9	1,458	600–980m alt.	cha *et al.* 1975
Beech-maple forest *F. multinervis*	Is. Ulreung-do (984m) S. Korea	7–9	1,458	490–920 alt. 26° northern	Yim *et al.* 1980

A. mono var. *savatieri*	130°52′E	37°30′N	slope
A. takesimense			
Importance V.			
beech; 55 ~ 217			
maple: 21 ~ 117			

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摘 要

既存의 文獻에 의거하여, 北半球의 너도밤나무 屬에 드는 全 12種의 너도밤나무와 너도밤나무林의 分布를 氣候的 傾度에 따라 檢討하였다. 全體로 볼 때 *Fagus*屬은 平均 年氣温 4.5~20.0°C, 平均 年降水量 600~1000 mm 以上의 곳에 分布한다. 温度範圍의 上限附近에서는 生育期間에 比較的 降雨量이 많은 地帶에 나타난다. 또, 너도밤나무와 너도밤나무林은 濕하고 肥沃한 土壤에 나는 傾向이 있다.

너도밤나무가 優占하는 森林은 너도밤나무 屬의 氣候的 分布域의 限定된 一部地帶에 分布한다. 地球規模에서 보면 土壤條件이나 生物條件 등에 따라 局地的인 變異에도 不拘하고 氣候因子와 地史的 條件에 의하여 分布域이 크게 制限을 받고 있다.

REFERENCES

Anderson, J. M., 1973. Stand structure and litter fall of a coppiced beech *Fagus sylvatica* and sweet chestnut *Castanea sativa* woodland. Oikos., **24**: 128~135.

Benson, L. 1979. Plant Classification. 2nd ed., D.C. Health and Company. Lexington, Massachusetts.

Barry, J. M., 1980. Natural vegetation of South Carolina. University of South Carolina Press, Columbia.

Braun, E. L., 1916. The physiograghic ecology of the Cincinnati region. Ohio Biological Survey Vol. II(3). Bulletin No. 7, The Ohio State University, Columbus.

Braun, E. L., 1947 Development of the deciduous forests of eastern North America. Ecol. Monogr., **17**: 211~219.

Budyko, M. I., 1977. Climatic Changes. Translated by the American Geographic Union, Washington, D.C., from Russian ed. 1974.

Camp, W. H., 1951. A biogeographic and paragenetic analysis of the American beech (*Fagus*). Amer. Phil. Soc. Yrbk., **1950**: 166~169.

Cha, C. H., W. T. Lee and S. A. Lee, 1975. Climate and Vegetation of Korea. Seomun Munko No. 151. Seomundang Pub. Co., Seoul.

Chaney, R. W., 1947. Tertiary centers and migration routes. Ecol. Monogr., **17(2)**: 139~148.

Collins, C. W., 1975. Ohio, an atlas. American Printing & Pub. Inc., Madison Wisconsin.

Collins, C. W., 1978. New York, an atlas. American Printing & Pub. Inc., Madison, Wisconsin.

Daubenmire, R., 1978. Plant Geography. Academic Press, Inc., London.

Delcourt, H. R. and P. A. Delcourt, 1977. Presettlement magnolia-beech climax of the Gulf Coastal Plain: Quantitative analysis from the Appalachicola River bluffs, north-central Florida. Ecology, **58**: 1085~1093.

Diller, O. D., 1935. The relation of temperature and precipitation to the growth of beech in Northern Indiana. Ecology, **16**: 72~81.

Espenshade, E. B., 1979. Goode's World Atlas, 15th ed. Rand McNally Co., Chicago.

Fukui, E., 1977. The Climate of Japan. Developments in Atmospheric Science. Kodan-sha Ltd., Tokyo.

Ganssen, R and F. Hädrich, 1965. Atlas zur Bodenkunde. Bibliographisches Institute, AG, Mannheim.

Geelan, D. J. M. and D.C. Twitchett, 1974. The Times, Atlas of China, Quadrangle. The New York Times Book Co., Time Newspapers Ltd., New York.

Gordon, R. B., 1969. The Natural Vegetation of Ohio in

Pioneer Days. Bulletin of the Ohio Biological Survey New Series III (2). The Ohio State Univ. Press, Columbus, Ohio.

Hicks, D. J., 1979. Forest microclimate in the Great Smoky Mountains. J. Tenn. Acad. of Sci., **54**(3): 84~88.

Horikawa, Y., 1972. Atlas of the Japanese Flora I. An Introduction to plant sociology of East Asia. Gakken Co., Ltd., Tokyo, Japan. p. 37.

Horikawa, Y., 1976. Atlas of the Japanese Flora II. An Introduction to Plant sociology of East Asia. Gakken Co., Ltd., Tokyo, Japan.

Küchler, A. W., 1964. Potential natural vegetation of the Conterminous United States. American Geographical Society. Special Publication 36, New York.

Lawrence, G. H. M., 1951. Taxonomy of Vascular Plants. Macmillan Publ. Co., Inc., New York.

Lee, S. C., 1973. Forest Botany of China Supplement. Taipei, Taiwan.

Lee, Y. N. 1967. Taxonomic studies on the *Fagus multinervis*, *Fagus japonica* and *Fagus crenata*. Journal of Korean Culture Research Institute. Ewha Woman Univ. Seoul, Korea. 10: 373~377.

Little, E. L., 1971. Tree. Vol. I. Conifers and Important Hardwood. USDA Forest Service, Washington, D.C.

Miyawaki, A. O. S., 1975. Actual Vegetation Map of Japan. Landscape of Japan Kokusai Johosha Ltd., Tokyo.

Nakane, K., 1978. Dynamics of soil organic carbon and its seasonal variation in a cool-temperate beech/fir forest on Mt. Odaigahara. Jap. J. Ecol., **28**: 335~346.

National Oceanic and Atmospheric Administration, 1977. Climatological Data. Annual Summary, **28**(13).

Nesom, G. L. and M. Treiber 1977. Beech-mixed hardwoods communities: A topoedaphic climax on the North Carolina Coastal Plain. Castanea, **42**: 119~140.

Nielsen, B. O., 1978. Above ground food resources and herbivory in a beech forest ecosystem. Oikos., **31**: 273~279

Nihlgård, B., 1970. Precipitation, its chemical composition and effect on soil water in a beech and a spruce forest in South Sweden. Oikos., **21**: 208~217.

Nihlgård, B., 1971. Pedalogical influence of spruce planted former beech forest soils in Scania., South Sweden. Oikos., **22**: 302~314.

Nihlgård, B. and L. Lindgren, 1977. Plant biomass, primary production and bioelements of three mature beech forests in South Sweden. Oikos., **28**: 95~104.

Nilsson, I., 1978. The influence of Dasychira pudibunda (Lepidoptera) on plant nutrient transports and tree growth in a beech *Fagus sylvatica* forest in southern Sweden. Oikos., **30**: 133~148.

Nixon, E. S., *et al.*, 1980. Woody vegetation of an American beech (*Fagus glandifolia*) community in eastern Texas. Castanea, **45**: 171~180.

Nomoto, N., 1956. Analysis of the succession process of the beech-oak forest. Jap. J. Ecol., **6**: 102~107.

Pearson, R., 1978. Climate and Evolution. Academic Press, London.

Quarterman, E. and C. Keever, 1962. Southern mixed hardwood forest: Climax in the southeastern Coastal Plain. Ecol. Monogr., **32**: 167~185.

Raven, P. H. and D. I. Axelrod, 1974. Angiosperm biogeography and past continental movements. Ann. Mo. Bot. Gard., **61**: 539~673.

Rehder, A., 1956. Manual of Cultivated Trees and Shrubs. The Macmillan Co., New York.

Rowe, J. S., 1972. Forest Regions of Canada. Dept. of Fisheries and the Environment. Canadian Service Pub. No. 1300.

Ruffner, A. and F. E. Bair, 1977. The Weather Almanac, 2nd ed. Gale Research Co. Book Tower. Detroit, Michigan.

Sasaki, Y., 1973. Plant Sociology. Ecological Studies 4. Kyoritsu Publ. Co., Tokyo (in Japanese).

Shanks, R. E., 1954. Climates of the Great Smoky Mountains. Ecology, **35**: 354~361.

Tanai, T., 1974. Evolutionary trend of the genus *Fagus* around the northern Pacific Basin. Symposium on Origin and Phytogeography of Angiosperms. Birbal Sahni Institute of Palaeobotany. Special Publ., **1**: 62~83.

Thompson, R. L., 1977. The vascular flora of Lost Valley, Newton County. Arkansas. Castanea, **42**: 56~60.

Tohoyama, M., 1965. Synecological study of the *Fagus japonica* forest on Mt. Ohmuro, Pref. Yamanashi. II. The forest vegetation of Mt. Fuji. Jap. J. Ecol., **15**: 139~142 (in Japanese).

Tralau, H., 1962. Die spattertiarten Fagus-arten Europas. Bot. Notiser, **115**(2): 147~176.

Trewartha, G. T., 1961. The Earth's Problem Climates. Univ. Wisconsin Press, Madison.

Tsin, C. P., *et al.*, 1975. The distribution of beech forest of Mt. Fangching Shan and its significance in plant geography. J. Plant Taxonomy, **13**(1): 5~18 (in Chinese).

Tsukada, M., 1967a. Vegetation in sub-tropical Formosa during the Pleistocene glaciations and the Holocene. Palaeoclimatol. Palaeoecol., **3**: 49~64.

Tsukada, M., 1967b. Vegetation and climate around 10,000 BP in central Japan. Am. J. Sci., **265**: 562~585.

Vankat, J. L., 1979. The Natural Vegetation of North America. John Wiley & Sons, New York.

U. S. Government., 1960. An Atlas of Chinese Climatology. Peiping, CCM Information Corporation, a subsidiary of Crowell Collier and Macmillan, Inc., New York.

Whittaker, R. H., 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr., **26**: 1~80.

Whittaker, R. H., 1975. Communities and Ecosystems. Macmillan Publ. Co., Inc., New York.

Wolfe, J. A., 1979. Temperature Parameters of Humid to Mesic Forest of Eastern Asia and Relation to Forests of Other Regions of the Northern Hemisphere and Australia. Geological Survey Professional Paper. 1106. U.S. Government Printing Office, Washington.

Wolfe, J. N., R.T. Wareham and H.T. Scofield, 1949. Microclimates and macroclimate of Neotoma, a small valley in central Ohio. Ohio Biol. Surv. Bull. 41.

Yim, Y. J. and T. Kira, 1975. Distribution of forest vegetation and climate in the Korean Peninsula. I. Distribution of forest vegetation of some indices of thermal climate. Jap. J. Ecol., **25**: 77~88.

Yim, Y. J. 1980. On the vegetation of Ulreung-do Institute of Technology and Science, Univ. of Chung-ang. Bull. 7: 1~12

Yoshioka, K. and T. Kaneko, 1962. The distribution of plant communities due to topography in a part of Mt. Hakkoda. Jap. J. Ecol., **12**: 26~31 (in Japanes).

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