Temperature Parameters of Humid to Mesic Forests of Eastern Asia and Relation to Forests of Other Regions of the Northern Hemisphere and Australasia

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By JACK A. WOLFE

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Analysis of temperature data from more than 400 stations in eastern Asia

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BY JACK A. WOLFE

ABSTRACT

Compilation of temperature data from more than 400 stations in the humid to mesic forests of Asia indicates that the boundaries of physiognomic units of vegetation approximately coincide with certain major temperature parameters. Most boundaries between broad-leaved forests coincide with mean annual temperature values; a mean temperature of the cold month of 1°C delineates dominantly broad-leaved deciduous forests from broad-leaved evergreen forests. Forests in which conifers are either dominant or a major emergent element typically are separated from broad-leaved forests by summer heat. Based on the approximate coincidence of certain mean annual temperature values with vegetational boundaries, a sixfold division of forest climates is proposed: tropical (more than 25°C), paratropical (20–25°C), subtropical (13–20°C), temperate (10–13°C), paratemperate (3–10°C), and subtemperate (less than 3°C).

Examination of latitudinal and altitudinal zonation of vegetation indicates that the concept of a given vegetational belt descending to lower altitudes in a poleward direction is at best a gross generalization and is in some respects invalid. Mesic broad-leaved deciduous forests do not live in areas in which the mean annual range of temperature is less than 19–20°C; hence such vegetation cannot be represented on tropical mountains. Mesic regions of Australasia have a low mean annual range and therefore have no broad-leaved deciduous forests.

Comparison of the climatic data from Asia with data from other areas of the Northern Hemisphere indicates: (1) A large area of eastern North America that might be expected to have broad-leaved evergreen forests has a broad-leaved deciduous forest similar to the secondary vegetation of some broad-leaved evergreen forest regions of Asia, probably as a result of geologically abnormal cold waves. (2) The "Mixed Mesophytic forest" of eastern United States is largely not the temperature analog of the Mixed Mesophytic forest of eastern Asia. (3) A large area of western Europe that might be expected to have a coniferous forest has a broad-leaved deciduous forest, probably as a result of historical factors associated with repeated glaciation. (4) Western United States has no temperature-vegetation anomalies based on the temperature parameters of eastern Asian vegetation. Comparison of the climatic data from western Europe and eastern North America indicate that the "nemoral" zones of the two areas are largely not temperature analogs.

The vegetation of New Zealand, which has been problematic in forest classification, is largely the vegetation expected in such temperature regimes. In certain given temperature parameters, mesic vegetation tends to be a microphyllous broad-leaved evergreen forest with an emergent stratum of conifers. Such forests can be observed in the Himalayas, as well as in New Zealand.

INTRODUCTION

For well over a century botanists and climatologists have attempted to relate the areal distribution of vegetation to climatic parameters. Some vegetational types have been successfully related to precipitation regimes and evapotranspiration rates, but areal distribution of principal forest types as a function of the temperature regime remains elusive. A correlation between forest types and temperature has been assumed to exist, and indeed the most commonly accepted definitions of the terms "tropical" and "subtropical" are based on the supposed limitation of "tropical" and "subtropical" forests by the 18°C and 6°C cold-month means.

Some botanists, among them Beadle (1951), maintain that given the same fundamental climatic regime in two widely separated areas, the vegetation (physiognomic type) may not necessarily be the same. These workers consider the physiognomy to be colored more by available plant materials than by environmental factors; that is, the presence or absence of certain physiognomic features is due mainly to the availability of plants having such features. While this concept may have some validity for geologically short periods of time, as, for example, in the development during the Holocene of broad-leaved deciduous forest in western Europe (see section "Forests of Europe"), when viewed over tens of thousands of years or millions of years, the concept must be considered invalid. Environmental factors are continually affecting lineages to select individuals and populations that are physiognomically best adapted to that particular environment. As this work indicates, physiognomically similar forest types typically do appear in widely separated areas that have similar major climatic parameters, irrespective of the lineages involved.

It is realized that some workers (for example, Küchler, 1967b) consider "vegetation" a general term that covers not only the physiognomy but also the phytosociology. In this paper the usage of "vegetation" is in the restricted sense of physiognomy rather than flora and floristic associations, a usage followed by many workers (see, for example, Richards, 1952; Webb, 1959; Beard, 1944; Dansereau, 1951; Fosberg and others, 1961). Some workers consider the phytosociological associations to be subdivisions of the physiognomic formations. Logically, however, such an approach is invalid; the formations and their subdivisions are an attempt to order the plant world strictly in terms of its physiognomy. Phytosociology attempts to order the same world in terms of associations of kinds (taxa) of plants. Vegetational groupings can be made in large part because of convergent evolution, whereas associations are by definition groupings based on the occurrence of two or more unlike plants produced by divergent evolution. Subdivisions of plant formations must, like the formations themselves, be based on physiognomic criteria. Webb's study (1959) of Australian rain forests provides an admirable example of such physiognomic subdivisions.

The structure and physiognomy of vegetation are the aspects by which analogous vegetation that is floristically distinct can be most readily recognized. The characters most commonly used are: the presence or absence of an emergent stratum (widely spaced trees that rise above the highest closed-tree stratum); number of closed-tree strata; presence (and density) or absence of a shrub stratum; presence (and density) or absence of lianes (woody climbers that reach the upper canopy) and other woody climbers; characters of tree trunks such as buttressing, height of stem relative to thickness, cauliflory; foliar characters (for example, evergreen, sclerophyllous, presence of drip tips, entire or nonentire margins, distribution of leaf-size classes); and diversity. Diversity is not a strictly physiognomic character except in the sense that a forest composed of a single tree species is apt to be far more monotonous in appearance than a forest composed of many tree species.

The average height of the canopy is a physiognomic character of limited value in distinguishing most forest types, as it is clearly dependent on a wide array of environmental factors, including soil type and exposure to strong winds. Broad-leaved forests tend to have the canopy about 20 to 30 m above the ground. Three exceptions are the short-statured Montane Rain forest, the tall Tropical Rain forest (about 50 m or higher), and the intermediate Paratropical Rain forest (about 35–40 m).

Particular attention is given here to physiognomic features of foliage. Many botanists have used such features as major defining characteristics of physiognomic units. Richards (1952, p. 77) states: "Many of these features *** are of considerable diagnostic value in the definition of tropical rain forest*** and in distinguishing it from other plant formations." And they are critical to the interpretation of fossil-leaf assemblages in relation to ancient vegetation and climate.

Some vegetational units that are validly physiognomic have been called by names of taxonomic categories. The term "oak-laurel forest," for example, actually is not an associational term (oaks and laurels are associated in a variety of vegetational types) but rather is used because of the dominance of these plants in a physiognomically distinctive forest, the Notophyllous Broad-leaved Evergreen forest. It is best to discard such a term as oak-laurel forest in preference for the physiognomic term.

The purpose of this study is (1) to delineate as accurately as possible the major physiognomic types of humid to mesic forests in eastern Asia; (2) to determine if the forest boundaries are related to any major temperature factors; and (3) to determine if the physiognomic groupings can be recognized in the same temperature parameters elsewhere in the world.

A part of this study was presented in preliminary version in an earlier paper (Wolfe, 1971). Some of the temperature parameters suggested then are now modified as a result of accumulation of more data, vegetational and climatic.

The emphasis here on temperature factors should not be construed to mean that precipitational factors are not critical to delimitation of vegetational types, for clearly precipitation is critical. But as significant precipitational deficits during the growing season generally do not exist in the study area chosen, the physiognomic differences recognized are expected to be the result of temperature factors. This study is in a sense an experiment in which one of the two major variables (precipitational and related factors) is taken to be constant in order to study the second major variable (temperature factors). If it is more clearly understood what physiognomic changes are primarily temperature related, then by additional studies it will be more clearly understood what physiognomic changes are primarily precipitation related.

For many fruitful discussions of the data and conclusions presented here, I thank H. D. MacGinitie and H. E. Schorn, both of the University of California (Berkeley). C. W. Wang, University of Idaho, has offered several comments on the vegetational types near specific Chinese stations; T. Tanai, Hokkaido University, has been of similar assistance in regard to Japanese vegetation. The personnel of the Environmental Science Services Administration Library have been particularly helpful in the search for climatic data. I also wish to thank F. R. Fosberg (Smithsonian Institution), W. H. Hatheway (University of Washington), and C. W. Wang for reading the manuscript and offering suggestions for improvement.

FORESTS AND CLIMATE OF EASTERN ASIA

VEGETATIONAL DATA

The delineation of forest types can at best be approximate. The various physiognomic units are concepts based on the physical characteristics of vegetation. Two workers may give different weight to two different characteristics, and consequently the physiognomic units and the areas occupied may not be equal. Nonetheless workers in eastern Asia have generally been able to recognize the same basic units in the same areas. Disagreements that do exist generally revolve around (1) reconstruction of the original vegetation in heavily cultivated areas, (2) the lumping or splitting of two or more vegetational types in a continuum (a problem inherent in any system of classification), and (3) whether a transitional vegetational type should be accorded a status distinct from adjacent types.

Most botanical mapping of the forests of eastern Asia has been reconnaissance. This has a distinct advantage, because reconnaissance mapping is generally concerned with the distribution of major physiognomic categories rather than phytosociological categories. The vegetational map compilation presented as plate 1 is based primarily on the work of Champion (1936), Richards (1952), Wang (1961), Lee (1964), Vidal (1956), Honda (1928), Miyawaki (1967), and Suslov (1961). Modifications of published maps fall into two main categories:

Modifications to accord with topography. For example, Champion (1936) shows broad belts of "subtropical" forest in mountainous areas of northeastern Burma, whereas Wang (1961) indicates that major valleys in China that extend into Burma are in fact occupied by "rain forest." Champion's data (1936) have been modified accordingly for incorporation into plate 1.

Modifications to accord with published statements. For example, Wang's map (1961) shows a broad belt of the Yangtze River valley and adjacent areas as Mixed Mesophytic forest, whereas his text makes clear that the Mixed Mesophytic forest is confined to altitudes greater than 500 to 1,000 m. Plate 1 has been modified to reflect Wang's statements rather than his map. Similarly, the distribution of physiognomic units proposed in this report (for example, Paratropical Rain forest) is based largely on information contained in textual statements rather than on published vegetational maps.

The reasons for selecting eastern Asia as a study area are several:

Except for alpine glaciation, the region was apparently unglaciated during the Quaternary; for this reason, historical factors associated with glaciation had a minimal impact on the vegetation.

The vegetation in general is more diverse than in any other area of the Northern Hemisphere; that is, more physiognomic units are represented in a continuum than in any other area. This stems in part from the size of the Asian continent and concomitantly the great temperature extremes in some areas.

In eastern Asia, unlike eastern North America, a series of east-west mountain ranges protect most of the forested area from frequent and intense outbreaks of low-altitude polar air. Such cold waves are probably atypical for most of geologic time.

The selection of eastern Asia as a study area does, however, have some problems:

In many areas, the vegetation has been profoundly altered by intensive agriculture. Consequently, the physiognomy has been interpreted from forest remnants; there are few areas of the Northern Hemisphere, however, where man has not significantly altered the vegetation.

Climatic data are few in eastern Asia relative to other regions, for example, eastern North America or Europe. This is particularly true for upland areas of Asia.

CLIMATIC DATA

Mean annual temperature and mean annual range of temperature have long been recognized as two of the most critical temperature parameters in describing climates. When the two values for a specific station are plotted against one another, the approximate warm and cold month means can be inferred, and the warm and cold month means, along with mean annual temperature, are generally thought to be the main values most likely to limit forest types. One of the main problems with the classification of vegetation and its relation to climate, suggested by Holdridge (1947) for example, is that mean annual range, and hence the means of the cold and warm months, are disregarded.

Climatic data for eastern Asia are widely scattered in the literature (table 1). Particularly useful sources are the various annotated bibliographies on specific areas of Asia produced by the Environmental Science Services Administration; nearly all the data on the temperature chart for eastern Asia, plate 2, have been taken from sources listed in those bibliographies.

TABLE 1.—*Location of stations and sources for temperature data used in compilation of plate 2*

Station name in plate 2	Name in source (if different name used)	Latitude	Longitude	Altitude (m)	Years of record	Source (see end of table)
A-306		37°52′ N.	127°43′ E.	78	4	10
Abashiri		44°01′ N.	144°17′ E.	37	30	5
Abu[1]		24°36′ N.	72°43′ E.	1,203	60	4
A-erh-shan		47°13′ N.	119°58′ E.	1,027	3	2
Ai-hui		50°15′ N.	127°29′ E.	131	6	2
Aikawa		38°01′ N.	138°15′ E.	34	41	14
Ajiro		35°03′ N.	139°06′ E.	67	14	14
Akita		39°43′ N.	140°06′ E.	10	30	5
Anpu		25°11′ N.	121°31′ E.	836	7	8
An-ta	Anta	46°24′ N.	125°21′ E.	151	20	2
An-tung		40°05′ N.	124°07′ E.	6	15	2
An-yüeh	Anyo	30°09′ N.	105°18′ E.	---	4	1
Aomori		40°49′ N.	140°47′ E.	5	30	5
Arkara		49°25′ N.	130°03′ E.	142	4	3
Asahikawa		43°46′ N.	142°22′ E.	111	64	14
Ashio		36°39′ N.	139°27′ E.	674	54	14
Asosan		32°53′ N.	131°05′ E.	1,143	20	14
Ayan[1]		56°28′ N.	138°17′ E.	10	9	3
Baguio		16°25′ N.	120°35′ E.	1,550	26	3, 10
Banmethuôt		12°41′ N.	108°05′ E.	536	---	11
Bao-Lôc		11°20′ N.	107°48′ E.	850	---	11
Bering Island[1]		55°12′ N.	165°59′ E.	6	30	5
Bhamo		24°15′ N.	97°15′ E.	118	50	4
Biak/Mokmer[1]		01°11′ S.	136°07′ E.	10	30	5
Bikin		46°49′ N.	134°16′ E.	73	12	3
Blagovescensk		50°16′ N.	127°30′ E.	137	30	5
Bolshaya Yelan		46°55′ N.	142°44′ E.	31	8	5
Bykov	Otiai	47°20′ N.	142°44′ E.	15	16	3
Cao Bang		22°40′ N.	106°15′ E.	270	8	10
Chai-sha	Liukiang	24°20′ N.	109°19′ E.	---	5	1
Chakrata		30°47′ N.	76°48′ E.	2,150	---	7
Chan-chiang		21°02′ N.	110°23′ E.	26	5	2
Chang-chia-k'ou	Kalgan	40°50′ N.	115°11′ E.	760	9	2
Ch'ang-chih		36°10′ N.	113°07′ E.	814	4	2
Ch'ang-ch'un	Changchun	43°52′ N.	125°20′ E.	216	36	2
Ch'ang-sha	Changsa	28°12′ N.	112°47′ E.	60	14	1
Ch'ang-te	Changteh	28°55′ N.	111°31′ E.	55	5	1
Chang-t'ing	Changting	25°45′ N.	116°20′ E.	200	5	1
Ch'ang-tu		31°11′ N.	96°50′ E.	3200	4	2
Chan-i		25°35′ N.	103°50′ E.	1,898.7	5	2
Chao-p'ing	Ali-shan	23°31′ N.	120°48′ E.	2,406	19	8
Chao-t'ung		27°10′ N.	103°45′ E.	1,930	4	2
Chao-yang		41°33′ N.	120°27′ E.	167	3	2
Chapa		22°22′ N.	103°52′ E.	1,640	10	3
Che-lang Chiao	Chilang Pt.	22°40′ N.	115°40′ E.	28	44	6
Ch'eng-te		41°58′ N.	117°45′ E.	850	8	2
Ch'eng-tu		30°40′ N.	104°04′ E.	498	21	2
Chen-hai	Chenhai	29°53′ N.	121°33′ E.	4	---	6
Chërnavo	Tchernaevo	52°47′ N.	126°00′ E.	212	16	3
Cherrapunji		25°15′ N.	91°44′ E.	1,314	35	4
Chia-mu-ssu		46°43′ N.	130°17′ E.	31	7	2
Chi'an		27°05′ N.	114°55′ E.	78	4	2
Chiang Rai		19°53′ N.	99°49′ E.	375	8	10
Chichibu		35°59′ N.	139°05′ E.	218	27	14
Ch'i-ch'i-ha-erh	Tsitsihar	47°20′ N.	123°56′ E.	147	20	2
Chieh-hsiu	Kiehsiu	37°00′ N.	111°55′ E.	---	5	1
Ch'ih-feng		42°16′ N.	118°54′ E.	571	11	2
Chi-hsi		45°17′ N.	130°57′ E.	219	3	2
Chi-nan	Tsinan	36°41′ N.	116°58′ E.	55	31	2
Ching Chuan		24°16′ N.	120°36′ E.	210	13	10
Chinhae		35°08′ N.	128°42′ E.	3	11	10
Chin-men	Chapel Is.	24°10′ N.	118°30′ E.	55	44	6
Chipo-ri		38°09′ N.	127°19′ E.	156	13	10
Chita		52°01′ N.	113°20′ E.	685	30	5
Chiu-chang	Kiukiang	29°45′ N.	116°08′ E.	55	44	6
Chiu-kan-yü	Kanyü	34°53′ N.	119°10′ E.	---	2	1
Ch'iung-shan	Kiungshan	20°01′ N.	110°16′ E.	3	14	1
Chonju		35°49′ N.	127°09′ E.	51	26	14
Choshi		35°43′ N.	140°51′ E.	28	30	5
Chugushi		36°44′ N.	139°30′ E.	1,335	9	14
Chungangjin	Chungkangin	41°47′ N.	126°53′ E.	312	31	14
Ch'ung-ch'ing	Chungking	29°30′ N.	106°33′ E.	261	28	2
Ch'ung-li	Hsiwantsu	40°58′ N.	115°18′ E.	1,165	44	6
Chunju (West)		36°58′ N.	127°55′ E.	82	12	10
Chutzehu		25°10′ N.	121°32′ E.	600	6	8
Ch'ü-wu	Küwo	35°39′ N.	111°33′ E.	---	5	1
Colombo[1]		6°54′ N.	79°52′ E.	7	30	5
Con Son		8°42′ N.	106°35′ E.	4	12	10
Coonor[1]		11°21′ N.	76°48′ E.	1,747	10	4
Dalat 1		11°44′ N.	108°22′ E.	962	11	10
Dalat 2		11°44′ N.	108°22′ E.	1,500	---	11
Dal'nyaya	Nisinotoro	45°54′ N.	142°05′ E.	46	10	13
Da Nang		16°02′ N.	108°12′ E.	10	12	10
Darjeeling 1		27°03′ N.	88°16′ E.	2,128	30	5
Darjeeling 2	Darjiling	27°03′ N.	88°16′ E.	2,266	50	4
Dolinsk		47°20′ N.	142°47′ E.	37	37	14
Donghoi		17°29′ N.	106°36′ E.	7	22	3, 10
En-shih		30°16′ N.	109°22′ E.	437	5	2
Esashi		41°52′ N.	140°08′ E.	30	12	14
Feng-ch'eng	Fynghuacheng	40°26′ N.	124°02′ E.	73	32	4
Fu-chou	Foochow	26°05′ N.	119°18′ E.	88	19	2
Fukushima		37°45′ N.	140°28′ E.	67	63	14
Funatsu		35°30′ N.	138°46′ E.	860	20	14
Gosh		51°24′ N.	129°12′ E.	213	7	3
Habarovsk		48°31′ N.	135°10′ E.	72	30	5
Hachijojima		33°06′ N.	139°47′ E.	81	30	5
Ha-erh-pin	Harbin	45°45′ N.	126°38′ E.	145	35	2
Hai-la-erh		49°13′ N.	119°45′ E.	677	31	2

TABLE 1.—*Location of stations and sources for temperature data used in compilation of plate 2*—Continued

Station name in plate 2	Name in source (if different name used)	Latitude	Longitude	Altitude (m)	Years of record	Source (see end of table)
Hai-lun		47°26′ N.	126°58′ E.	240	9	2
Haka		22°39′ N.	93°37′ E.	1,860	10	4
Hakoneyama		35°11′ N.	139°01′ E.	936	19	14
Ha-kuei-miao	Hakiao	41°15′ N.	113°24′ E.	1,000	3	6
Hang-chou	Hangchow	30°11′ N.	120°12′ E.	10	44	6
Han-k'ou	Hankow	30°35′ N.	114°17′ E.	37	44	6
Hanoi		21°02′ N.	105°51′ E.	14	22	4
Han-yuan		32°05′ N.	108°05′ E.	765	5	2
Hatinh		18°21′ N.	105°54′ E.	4	4	10
Heho		20°44′ N.	96°47′ E.	1,260	25	10
Heng-chun	Hengchun	22°00′ N.	120°45′ E.	22	56	8
Heng Shan		27°14′ N.	112°52′ E.	1,270	3	1
Heng-yang		26°56′ N.	112°36′ E.	95	12	2
Hensel AFB		13°51′ N.	108°03′ E.	771	7	10
Hikone		35°16′ N.	136°15′ E.	87	59	14
Hiroshima		34°22′ N.	132°26′ E.	30	30	5
Ho-ch'iu	Hochiu	32°22′ N.	116°15′ E.	---	44	6
Hoengsung		37°27′ N.	127°58′ E.	100	12	10
Hon-ba		12°05′ N.	108°45′ E.	1,484	12	3
Hongkong		22°18′ N.	114°10′ E.	33	30	5
Hsia-men	Amoy	24°27′ N.	118°04′ E.	41	25	2
Hsi-an	Sian	34°15′ N.	108°55′ E.	395	24	2
Hsiao-chin		31°00′ N.	102°22′ E.	2,465	4	2
Hsi-ch'ang		27°53′ N.	102°18′ E.	2,000	13	2
Hsien-hsien	Hsienhsien	38°12′ N.	116°07′ E.	14	44	6
Hsing-jen		25°25′ N.	105°15′ E.	1,412	5	2
Hsing-tzu	Singtze	29°37′ N.	116°03′ E.	---	7	1
Hsin-kao Shan	Mount Morrison	23°29′ N.	120°57′ E.	3,850	8	8
Hsun-k'o		49°15′ N.	128°28′ E.	90	3	2
Huai-jen	Hwaijen	39°50′ N.	113°07′ E.	---	5	1
Huai-te	Kungchuling	43°30′ N.	124°49′ E.	203	10	6
Hua-shan		34°25′ N.	109°57′ E.	2,074	4	2
Hua-tien	Huatien	42°58′ N.	126°45′ E.	76	2	6
Hue		16°23′ N.	107°42′ E.	15	42	10
Hui-li		26°50′ N.	102°15′ E.	1,920	3	2
Hun-ch'un	Hunchun	42°54′ N.	130°25′ E.	104	44	6
Hungnam	Kanko	39°54′ N.	127°32′ E.	---	16	3
Ibukiyama		35°25′ N.	136°24′ E.	1,376	34	14
I-ch'ang		30°42′ N.	111°05′ E.	133	14	2
Iida		35°31′ N.	137°50′ E.	481	55	14
I-lan	Ilan	24°46′ N.	121°45′ E.	7	8	14
I-lan	Sansing	46°19′ N.	129°34′ E.	100	12	6
Il'inskiy	Kvsyunnai	48°00′ N.	142°12′ E.	18	12	13, 14
I-mien-p'o	Imienpo	45°03′ N.	128°05′ E.	222	26	14
Inchon		37°29′ N.	126°38′ E.	69	40	14
Inje	Rintei	38°05′ N.	128°09′ E.	200	10	13
Irkutsk		52°16′ N.	104°21′ E.	485	30	5
Ishinomaki		38°26′ N.	141°18′ E.	45	30	5
Iwamizawa		43°13′ N.	141°47′ E.	33	6	14
Jefman/Sorong[1]		00°56′ S.	131°07′ E.	3	30	5
Juzno-sahalinsk		46°57′ N.	42°43′ E.	25	30	5
Kagoshima		31°34′ N.	130°33′ E.	5	30	5
K'ai-feng		34°50′ N.	114°20′ E.	75	9	2
Kalimpong		27°04′ N.	88°28′ E.	1,209	20	4
Kanazawa		36°33′ N.	136°39′ E.	29	30	5
Kan-chou		25°50′ N.	114°50′ E.	109	5	2
Kangnung		37°45′ N.	128°54′ E.	26	30	5
K'ang-ting		30°03′ N.	101°57′ E.	2,358	9	2
Kan-men-chen	Kanmen	28°05′ N.	121°16′ E.	60	6	1
Kanpetlet		21°12′ N.	94°02′ E.	1,927	10	4
Kan-tzu		31°38′ N.	99°59′ E.	3,320	5	2
Kao-hsiung	Kaohsiung	22°37′ N.	120°16′ E.	29	12	14
Kapsan	Kôsan	41°04′ N.	128°19′ E.	810	10	13
Karuizawa		36°20′ N.	138°36′ E.	934	20	14
Katmandu		27°42′ N.	85°20′ E.	1,324	10	5
Kengtung		21°18′ N.	99°37′ E.	850	7	10
Kholmsk	Maoka	47°03′ N.	142°03′ E.	27	38	14
Kirensk[1]		57°46′ N.	108°07′ E.	261	30	5
Kitamiesashi		44°56′ N.	142°35′ E.	6	10	14
Kochi		33°34′ N.	133°33′ E.	1	30	5
Kodaikanal[1]		10°14′ N.	77°28′ E.	2,344	40	4
Kontum		14°22′ N.	108°00′ E.	536	---	11
Korf[1]		60°21′ N.	166°00′ E.	---	30	5
Krasnoyarsk[1]		56°00′ N.	92°53′ E.	194	30	5
Kuala Lumpur[1]		3°07′ N.	101°33′ E.	17	30	5
Kuang-chou	Canton	23°00′ N.	113°13′ E.	18	26	2
Kuang-hua		32°25′ N.	111°29′ E.	91	5	2
Kuei-Lin		25°15′ N.	110°10′ E.	168	9	2
Keui-yang		26°35′ N.	106°43′ E.	1,057	30	2
Kumsan	Kinsan	36°07′ N.	127°30′ E.	163	10	13
K'un-ming 1	Kunming	25°02′ N.	102°43′ E.	1,834	16	2
K'un-ming 2	Yunnanfu	25°07′ N.	102°54′ E.	1,893	33	3
Kunsan		36°54′ N.	126°37′ E.	10	12	10
Kuo-ch'ien-ch'i		45°01′ N.	124°58′ E.	135	3	2
K'uo-hsien		38°49′ N.	112°47′ E.	838	3	2
Kuril'sk	Syana	45°14′ N.	147°53′ E.	38	10	13
Kurseong		26°53′ N.	88°17′ E.	1,500	---	7
Kurskaya		48°56′ N.	134°18′ E.	60	9	3
Kushiro		42°59′ N.	144°24′ E.	33	43	14
Kutchan		42°54′ N.	140°45′ E.	174	9	14
Kwangju		35°07′ N.	126°48′ E.	---	8	10
Lai Chau		22°04′ N.	103°09′ E.	160	6	10
Lang Son		21°50′ N.	106°46′ E.	259	22	3
Lao Kay		22°30′ N.	103°57′ E.	---	33	10
Laruce		15°51′ N.	107°50′ E.	715	---	11
Lashio		22°56′ N.	97°45′ E.	854	45	4
Leh		34°09′ N.	77°34′ E.	3,515	60	4
Lei-po		28°18′ N.	103°31′ E.	650	9	2

TABLE 1.—*Location of stations and sources for temperature data used in compilation of plate 2*—Continued

Station name in plate 2	Name in source (if different name used)	Latitude	Longitude	Altitude (m)	Years of record	Source (see end of table)
Lesogorsk	Kitanayosi	49°27′ N.	142°08′ E.	7	10	13
Li-chiang		26°57′ N.	100°18′ E.	2,415	6	2
Lien-hsien		24°44′ N.	112°14′ E.	100	3	2
Lien-hua-feng Chiao	Breaker Pt.	22°56′ N.	116°30′ E.	17	44	6
Li-shui	Lishui	28°28′ N.	119°55′ E.	50	3	1
Loakan		16°22′ N.	120°37′ E.	1,310	10	10
Loikaw		19°41′ N.	97°13′ E.	---	10	12
Lo-tien		25°27′ N.	106°46′ E.	443	5	2
Lung-ching		22°22′ N.	106°45′ E.	128	15	2
Lung-yen		25°06′ N.	117°01′ E.	41	5	2
Lu Shan	Lushan	29°35′ N.	115°59′ E.	---	4	1
Lü-ta	Talien	38°54′ N.	121°38′ E.	96	40	14
Madang[1]		05°13′ S.	145°48′ E.	6	10	5
Maebashi		36°24′ N.	139°04′ E.	113	30	5
Mahabaleshwar[1]		17°56′ N.	73°40′ E.	1,382	10	4
Malaybalay		8°09′ N.	125°05′ E.	660	15	10
Man-chou-li	Manchouli	49°35′ N.	117°26′ E.	646	27	2
Mang-ting		23°33′ N.	99°07′ E.	500	3	2
Manila		14°35′ N.	120°59′ E.	5	30	5
Manokwari/Rendani[1]		0°53′ S.	134°03′ E.	3	30	5
Mat-su	Middle Dog	25°58′ N.	119°59′ E.	59	24	3
Matsumoto		36°15′ N.	137°58′ E.	611	30	5
Maymyo		22°01′ N.	96°28′ E.	1,081	40	4
Mazanovo		51°39′ N.	129°02′ E.	164	8	3
Mei-hsien	Meihsien	34°15′ N.	107°40′ E.	710	4	1
Meng-hai	Fuhai	21°55′ N.	100°25′ E.	---	3	1
Meng-tzu	Mongtseu	23°30′ N.	103°30′ E.	1,305	22	3
Mercara[1]		12°25′ N.	75°44′ E.	1,153	50	4
Mien-tu-ho	Mientuho	49°06′ N.	121°03′ E.	700	20	6
Min-hsien	Minhsien	34°29′ N.	104°01′ E.	2,246	4	1
Minusinsk		53°42′ N.	91°42′ E.	251	30	5
Mi-shan		45°33′ N.	131°45′ E.	134	4	2
Mito		36°23′ N.	140°28′ E.	29	56	14
Miyako		39°39′ N.	141°58′ E.	42	69	14
Miyazaki		31°55′ N.	131°25′ E.	8	30	5
Mokpo		34°47′ N.	126°23′ E.	31	30	5
Mo-mien	Mosimien	29°45′ N.	101°45′ E.	---	2	4
Mori		42°06′ N.	140°34′ E.	11	15	14
Morioka		39°42′ N.	141°10′ E.	155	29	14
Mosulpo		33°12′ N.	126°13′ E.	11	12	10
Mukteswar/Kumaun		29°27′ N.	79°41′ E.	2,311	30	5
Muroran		42°19′ N.	140°59′ E.	43	30	14
Murotomisaki		33°15′ N.	134°11′ E.	185	32	14
Mussooree		30°27′ N.	78°05′ E.	2,116	10	4
Mu-tan-chiang		44°35′ N.	129°30′ E.	234	38	2
Myitkina		25°23′ N.	97°24′ E.	145	35	4
Mys Vasileva[1]		50°00′ N.	155°23′ E.	16	10	7
Nagano		36°40′ N.	138°12′ E.	418	64	14
Nagatsuro		34°36′ N.	138°51′ E.	55	13	14
Nagoya		35°10′ N.	136°58′ E.	56	30	5
Naha		26°12′ N.	127°39′ E.	28	54	14
Namponmao		25°21′ N.	97°17′ E.	140	17	10
Namwon	Nangen	35°25′ N.	127°21′ E.	96	10	13
Nan-ch'ing	Nanking	32°04′ N.	118°47′ E.	62	16	2
Nan-ho-tien	Nanhotsien	41°05′ N.	113°53′ E.	1,684	44	6
Nan-p'eng Chün-tao	Lamocks Is.	23°16′ N.	117°19′ E.	58	44	6
Nan-p'ing		26°38′ N.	118°10′ E.	127	9	2
Nan-yang		33°04′ N.	112°32′ E.	125•	3	2
Nan-yueh		27°15′ N.	112°45′ E.	1,309	8	2
Nape		18°18′ N.	105°04′ E.	600	5	10
Naze		28°23′ N.	129°30′ E.	3	52	14
Nemuro		43°20′ N.	145°35′ E.	26	73	14
Nen-chiang		49°10′ N.	125°13′ E.	222	10	2
Nerchinskiy Zavod	Nertchinsky Zavod	51°19′ N.	119°37′ E.	620	35	3
Nevel'sk	Honto	46°40′ N.	141°52′ E.	4	25	14
Ngantong		40°06′ N.	124°21′ E.	9	---	6
Niigata		37°55′ N.	139°03′ E.	4	30	5
Niijima		34°22′ N.	139°15′ E.	9	7	14
Nikolayevsk na Amure		53°09′ N.	140°42′ E.	47	30	5
Ning-yüan	Ningyuan	27°55′ N.	102°18′ E.	---	12	3
Nuwara Eliya[1]		6°58′ N.	80°46′ E.	1,881	12	4
Obihiro		42°55′ N.	143°13′ E.	39	30	14
Odaigaharayama		34°11′ N.	136°06′ E.	1,566	22	14
Oita-handa		33°09′ N.	131°14′ E.	850	21	14
O-mei Shan		29°28′ N.	103°21′ E.	3,137	11	2
Onahama		36°57′ N.	140°54′ E.	5	42	14
Ootacamund[1]		11°24′ N.	76°44′ E.	2,245	27	4
Osaka		34°39′ N.	135°32′ E.	6	30	5
Oshima		34°46′ N.	139°23′ E.	191	13	14
Ostrov Baydukov	Langr	53°18′ N.	141°28′ E.	4	7	3
Ostrov Skryplëva	Skryplevsky Lighthouse.	43°02′ N.	131°57′ E.	46	17	3
Owase		34°04′ N.	136°12′ E.	5	20	14
Paengnyong Do		37°59′ N.	124°40′ E.	178	12	10
Pak-hoi	Pakhoi	21°29′ N.	109°05′ E.	5	44	6
Pak Song		15°11′ N.	106°12′ E.	1,200	11	10
Panasan[1]		7°31′ S.	110°45′ E.	110	14	10
P'an-hsien	Panhsien	25°47′ N.	104°39′ E.	---	2	1
Pao-shan		25°13′ N.	99°15′ E.	1,693	4	2
Pavlinovka		43°45′ N.	131°52′ E.	61	7	3
Pei-p'ei	Pehpei	29°49′ N.	106°20′ E.	298	6	1
Pei-p'ing	Peiping	39°57′ N.	116°19′ E.	52	78	2
Pei-shan-k'eng	Joyutang	23°53′ N.	120°51′ E.	1,015	10	8
Pei-yü-shan	Peiyushan	28°53′ N.	122°16′ E.	82	44	6
Petropavlosk Kamchatskiy[1]		52°59′ N.	158°39′ E.	28	10	5
Phu-lien		20°48′ N.	106°37′ E.	116	23	3
Piao Chiao	Cape of Good Hope.	23°15′ N.	116°48′ E.	46	44	6

TABLE 1.—*Location of stations and sources for temperature data used in compilation of plate 2*—Continued

Station name in plate 2	Name in source (if different name used)	Latitude	Longitude	Altitude (m)	Years of record	Source (see end of table)
Pi-chieh		27°18′ N.	105°14′ E.	1,511	12	2
P'ing-tu	Pingtu	36°50′ N.	119°56′ E.	---	6	6
Ping-tung		22°42′ N.	120°28′ E.	29	10	10
Plei-ku		13°58′ N.	108°02′ E.	750	12	10
Podkamennaya Tunguska[1]		61°36′ N.	90°00′ E.	60	30	5
Po-k'o-t'u		48°46′ N.	121°55′ E.	739	18	2
Pokrovka		53°24′ N.	121°33′ E.	317	8	3
Poluostrov Gamova	Gamov Lighthouse	42°33′ N.	131°13′ E.	50	8	3
Poronaysk		49°13′ N.	143°06′ E.	4	37	14
Pusan		35°07′ N.	129°05′ E.	13	30	5
Putao		27°20′ N.	97°25′ E.	432	7	10
Pu-t'e-ha-ch'i		48°00′ N.	122°44′ E.	310	25	2
Pyongyang		39°01′ N.	125°49′ E.	27	38	14
Quang-tri		16°44′ N.	107°11′ E.	7	22	3
Qui Nhon		13°45′ N.	109°13′ E.	6	21	10
R–813		35°08′ N.	128°41′ E.	2	11	10
R–815		35°59′ N.	129°25′ E.	21	7	10
Sachon		35°05′ N.	128°04′ E.	7	12	10
Saigo		36°12′ N.	133°20′ E.	26	13	14
Sakata		38°54′ N.	139°50′ E.	2	16	14
San-t'ai	Santai	31°06′ N.	105°04′ E.	---	10	1
San-tu-ao	Santuao	26°45′ N.	119°45′ E.	4	2	1
Sapporo		43°03′ N.	141°20′ E.	18	30	5
Seburiyama		33°26′ N.	130°22′ E.	1,053	7	14
Sendai		38°16′ N.	140°54′ E.	38	27	14
Seoul		37°34′ N.	126°58′ E.	86	37	14
Shang-hai	Shanghai	31°12′ N.	121°26′ E.	5	81	2
Shan-hou	Shanhou	41°05′ N.	120°10′ E.	---	44	6
Shan-t'ou	Swatow	23°21′ N.	116°40′ E.	4	17	2
Shen-yang	Mukden	41°46′ N.	123°36′ E.	42	40	2
Shillong		25°34′ N.	91°53′ E.	1,500	35	4
Shimonoseki		33°57′ N.	130°56′ E.	48	30	5
Shionomisaki		33°27′ N.	135°46′ E.	75	30	5
Shuang-liao	Liaoyüan	43°40′ E.	123°30′ E.	116	12	1
Silchar		24°49′ N.	92°48′ E.	29	40	4
Simla		31°06′ N.	77°10′ E.	2,202	45	4
Simushir[1]		46°51′ N.	151°52′ E.	26	30	5
Singapore[1]		1°17′ N.	103°51′ E.	5	30	5
Songjin		40°40′ N.	129°12′ E.	31	39	14
Son La		21°20′ N.	103°54′ E.	670	4	10
Ssu-p'ing		43°11′ N.	124°20′ E.	163	14	2
Stantsiya Reynovo	Reinovo	53°29′ N.	123°54′ E.	276	10	3
Su-hsien	Suhsien	33°41′ N.	117°02′ E.	---	15	1
Sui-fen-ho		44°23′ N.	131°09′ E.	512	8	2
Sui-ning	Suining	30°31′ N.	105°31′ E.	307	4	1
Sung-p'an		32°39′ N.	103°34′ E.	2,883	10	2
Suttsu		42°47′ N.	140°14′ E.	16	64	14
Suwa		36°03′ N.	138°07′ E.	760	8	14
Szu-mao		22°33′ N.	101°02′ E.	1,319	4	2
Taegu		35°53′ N.	128°37′ E.	58	37	14
Taejon		36°20′ N.	127°23′ E.	37	11	10
Tai-hsien	Taihsien	39°06′ N.	112°59′ E.	---	5	1
T'ai-ling	Taipinlin	44°33′ N.	130°41′ E.	561	20	1
T'ai-pei	Taipei	25°02′ N.	121°31′ E.	8	30	5
T'ai-tung	Taitung	22°45′ N.	21°09′ E.	9	44	14
T'ai-yüan	Taiyuan	37°55′ N.	112°34′ E.	782	13	2
Takada		37°06′ N.	138°15′ E.	13	31	14
Takayama		36°09′ N.	137°15′ E.	560	53	14
Ta-li		25°43′ N.	100°11′ E.	2,010	11	2
Tanabu		41°17′ N.	141°13′ E.	3	12	14
Ta-ming	Taming	36°18′ N.	115°18′ E.	---	44	6
T'ang-ku	Tangku	39°01′ N.	117°40′ E.	3	44	6
Ta-ning	Taning	36°25′ N.	110°44′ E.	---	5	1
Tan Son Nhut		10°49′ N.	106°39′ E.	8	31	10
Taunggyi		20°47′ N.	97°03′ E.	1,470	25	10
Te-hui	Jaomen, Tehhwei	44°32′ N.	125°43′ E.	178	14	1
T'eng-ch'ung 1	Tengchung	25°00′ N.	98°49′ E.	1,634	24	2
T'eng-ch'ung 2	Tengyueh	24°45′ N.	98°14′ E.	1,633	10	3
Than-hoa		19°48′ N.	105°52′ E.	4	22	3
T'ien-mu-shan	Tienmushan	30°20′ N.	119°27′ E.	1,060	2	1
T'ien-t'ai Shan	Tientaishan	29°18′ N.	121°05′ E.	960	2	1
Tigil'[1]	Tigil	57°45′ N.	158°19′ E.	22	3	3
Tokyo		35°41′ N.	139°46′ E.	6	30	5
To-lun		42°15′ N.	116°13′ E.	1,211	4	2
Tomakomai		42°38′ N.	141°36′ E.	5	20	14
Tomie		32°37′ N.	128°46′ E.	27	28	14
Tonaru		33°52′ N.	133°19′ E.	784	13	14
Toyama		36°42′ N.	137°12′ E.	9	14	14
T'si-shan		36°09′ N.	117°18′ E.	1,359	5	2
Tsukubasan		36°13′ N.	140°06′ E.	869	51	14
Tsuruga		35°39′ N.	136°04′ E.	1	55	14
Tsurugiyama		33°51′ N.	134°06′ E.	1,944	6	14
T'u-men-tzu	Tumentzo	43°12′ N.	131°02′ E.	210	4	14
T'u-mo-t'e-yu-chi	Salachi	40°33′ N.	110°30′ E.	1025	44	6
Tung-ch'uan	Tungchwan	26°30′ N.	102°50′ E.	---	11	3
T'ung-hua		41°43′ N.	125°55′ E.	491	4	2
T'ung-jen		27°35′ N.	109°04′ E.	602	6	2
T'ung-liao		43°40′ N.	122°15′ E.	178	8	2
Tung-p'ing	Tungping	35°59′ N.	116°17′ E.	67	6	1
Tung-t'ai		32°51′ N.	120°18′ E.	6.3	18	2
T'ung-tzu		28°08′ N.	108°49′ E.	---	11	2
Tung-yung	Tungyung	26°33′ N.	120°30′ E.	110	14	1
T'un-liu	Tunliu	36°19′ N.	112°54′ E.	---	5	1
Tu-shan	Tushan	25°50′ N.	107°32′ E.	---	3	1
Tuyen Quang	Tuyen-Quang	21°49′ N.	105°12′ E.	---	1	9
Ueno		34°46′ N.	136°09′ E.	159	15	14
Ullungdo		37°29′ N.	130°54′ E.	221	15	14
Unggi-up	Unggi	42°19′ N.	130°24′ E.	88	30	14

TABLE 1.—*Location of stations and sources for temperature data used in compilation of plate 2*—Continued

Station name in plate 2	Name in source (if different name used)	Latitude	Longitude	Altitude (m)	Years of record	Source (see end of table)
Unzendake		32°44′ N.	130°15′ E.	849	28	14
Unzen-koen		32°44′ N.	130°16′ E.	668	10	14
Urakawa		42°10′ N.	142°47′ E.	34	30	5
Ussuriysk	Nikolsk Ussurysk	43°47′ N.	131°57′ E.	25	27	3
Ust-Apuka[1]		60°27′ N.	169°35′ E.	8	30	5
Uwajima		33°14′ N.	132°33′ E.	42	30	14
Vinh		18°40′ N.	105°40′ E.	6	22	3
Vladivostok	Vladivostock	43°07′ N.	131°55′ E.	29	35	3
Vzmor'ye	Higasisiraura	47°51′ N.	142°31′ E.	4	10	13
Wajima		37°23′ N.	136°54′ E.	7	30	5
Wakkanai		45°25′ N.	141°41′ E.	3	30	5
Wamena[1]		4°04′ S.	158°57′ E.	1,660	4	5
Wei-ch'ang		41°56′ N.	117°34′ E.	850	5	2
Wei-ning		26°51′ N.	104°14′ E.	---	4	2
Wellington[1]		11°23′ N.	76°47′ E.	1,890	---	7
Wen-chou		28°01′ N.	120°49′ E.	5	17	2
Wonsan		39°11′ N.	127°26′ E.	35	40	14
Wu-ch'iu Hsü	Ockseu	25°00′ N.	119°27′ E.	62	44	6
Wu-chou		23°30′ N.	111°25′ E.	119	19	2
Wu-hu		31°20′ N.	113°21′ E.	13	11	2
Xien Khouang		19°30′ N.	103°30′ E.	1,060	10	9, 10
Ya-an		30°00′ N.	103°03′ E.	650	12	5
Yakushima		30°27′ N.	130°30′ E.	15	30	5
Yamagata		38°15′ N.	140°21′ E.	151	63	14
Yang-ch'ü	Yangchu	37°52′ N.	112°35′ E.	805	5	6
Ya-tung	Yatung	27°29′ N.	88°55′ E.	---	45	4
Yen-chi	Yenchi	42°55′ N.	129°30′ E.	168	15	6
Yeniseysk[1]		58°27′ N.	92°09′ E.	78	30	5
Ying-k'ou		40°40′ N.	122°12′ E.	4	42	2
Yogampo		39°56′ N.	124°22′ E.	13	26	14
Yokohama		35°26′ N.	139°39′ E.	40	30	14
Yu-ch'i		24°24′ N.	102°37′ E.	1,671	5	2
Yüeh-yang	Yoyang	29°24′ N.	113°10′ E.	---	14	1
Yu-lin-kang		18°14′ N.	109°32′ E.	2	5	2
Yun-ch'eng	An-i (Yun-ch'eng)	35°03′ N.	110°55′ E.	371	5	2
Yung-ning	Yungning	22°42′ N.	108°03′ E.	122	44	6
Yu-yang		28°48′ N.	108°46′ E.	629	11	2

[1] Station not shown on plate 1.

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13. The temperature of Japan, 1916–1925, v. 1, pt. 1: Central Meteorol. Obs. Tokyo, 1931.
14. Climatic records of Japan and the Far East area: Central Meteorol. Obs. Tokyo, 1954.

The climatic data used vary in quality. Although most data are based on long-term (30 years or more) records, many are based on short-term observations. More significant is the fact that even the long-term data are, in the life of a forest, short term; that is, climatic fluctuations could conceivably occur over a period of a century, but the forest boundaries would take centuries to adjust to such climatic changes. Some sets of data cannot be accurately compared with other sets; the daily readings, the basis for the data plotted, may have been taken at different times at different stations. Some short-term observations moreover are based on different intervals of years than other short-term (or even long-term) observations.

The term "mesic" is here used in a general sense to mean a climatic regime in which precipitation is well distributed throughout the growing season; in no more than 2 months of the growing season is precipitation less than 10mm. In this definition of mesic, some areas are included that have marked monsoonal climates; most have a dry season occurring between growing seasons. I have purposely excluded areas occupied by what Champion (1936) considered "semi-evergreen" or "deciduous" tropical forests; the forests in these areas display obvious modifications attributable to marked, lengthy dry seasons.

Four main factors are probably responsible for the slight anomalies that appear on plate 2: (1) The vegetational boundaries are conceptual and, to varying degrees, imprecise; (2) the apparent parameters may be only approximations of the actual temperature limitations; (3) some of the data are short term; and (4) during periods of climatic change such as we are definitely in, a forest may take a few centuries to adapt to the climate in which it lives; that is, the dominant trees in a forest may be several centuries old and may have assumed dominance under a somewhat different climate than now prevails in that area.

TROPICAL RAIN FOREST

SYNONYMS

Southern tropical wet evergreen forests (Champion, 1936), Northern tropical wet evergreen forests in part (Champion, 1936), Dipterocarp forest (Brown, 1919), Rain forest in part (Wang, 1961), Tropical Rain forest in part (Richards, 1952).

STRUCTURE AND PHYSIOGNOMY

The Tropical Rain forest is broad-leaved evergreen and multistratal, always with three main closed canopies and typically an emergent stratum. Buttressing and cauliflory are common. Lianes are both diverse and profuse and are typically best developed along water courses and other openings. The shrub stratum is not well developed. Species diversity is high; stands dominated by a single species are uncommon. Leaves typically fall into the restricted mesophyll size class of Webb (1959); macrophylls are present, but typically in the shrub stratum. Drip tips are common, particularly on leaves of young trees of the upper canopy and trees of the lower canopies. Leaves are sclerophyllous; 75 percent or more of the species have entire margins; deeply dissected (lobed) leaves are rare (probably 5 percent or less of the species).

DISTRIBUTION (PLATE 1)

The distribution of Tropical Rain forest in southeastern Asia shown on the map is modified from Richards (1952). Exceptions to the distribution shown by Richards are: (1) The rain forest in upper Assam and northeastern Burma is excluded (see discussion of "Paratropical Rain forest"); and (2) the rain forest of southern Hainan is provisionally included, more on the basis of climate than on available physiognomic data.

FLORISTICS

The floristics of the Tropical Rain forest in southeastern Asia have been treated by a number of workers (for example, Brown, 1919; Champion, 1936; Richards, 1952; van Steenis, 1957). The most prominent group is Dipterocarpaceae, which typically forms the emergent stratum and upper canopy. Mixed with the dipterocarps, however, are a number of other groups, notably Meliaceae, Myristicaceae, Burseraceae, Lauraceae, Anacardiaceae, Myrtaceae, Palmae, Guttiferae, Ebenaceae, and Magnoliaceae. Holarctic groups are almost totally absent, except for Fagaceae. The lianes are members of families such as Annonaceae, Menispermaceae, Icacinaceae, Anarcadiaceae, Vitaceae, and Apocynaceae.

TEMPERATURE PARAMETERS (PLATE 2)

Much of the Tropical Rain forest in southeastern Asia is bounded by semievergreen forests, and hence the boundary there is determined more by precipitation than by temperature. In four areas, however, rain forest extends in an unbroken expanse from Tropical to Paratropical Rain forests: near Chittagong (eastern Bangladesh), in northeastern Burma, along the coast of Viet Nam, and in the uplands of the Philippine Islands. As discussed in the following section, the northern part of the Chittagong tract (Silchar) has physiognomic characteristics of Paratropical Rain forest, as does the forest in northeastern Burma (Bhamo, Lashio, Myitkina, Kengtung). In these areas, the mean annual temperature approaches, but does not reach, 25°C. Along the coast of Viet Nam, Tropical Rain forest reaches its northern limit south of Hatinh (mean annual temperature = 24.4°C) and north of Donghoi (mean annual temperature = 25.0°C). Along the flanks of the Vietnamese plateau country, stations such as Kontum and Banmethuôt are outside the Tropical Rain forest. On Luzon, Tropical Rain forest gives way to Paratropical Rain forest between altitudes of 450 to 700 m, that is, between a mean annual temperature of 24.0 and 25.8°C (Brown, 1919). Whether the mean annual range of temperature is low, as on Mount Maquiling on Luzon, or moderate, as along coastal Viet Nam, or intermediate, as in northeastern Burma, the transition from Tropical to Paratropical Rain forest takes place in areas where mean annual temperature is approximately 25°C.

PARATROPICAL RAIN FOREST

SYNONYMS

Northern tropical west evergreen forests in part (Champion, 1936), Mid-mountain forest (Brown, 1919), extratropical rain forest in part (Wang, 1961), Tropical Rain forest in part (Richards, 1952), Subtropical Rain forest (Richards, 1952), Submontane Rain forest (Richards, 1952).

The term "Paratropical Rain forest" was first proposed by Wolfe (1969a) as a substitute for Richards' (1952) "Subtropical Rain forest." As studies progressed, it became apparent that Richards' "Submontane Rain forest" (1952) was not formationally distinct.

STRUCTURE AND PHYSIOGNOMY

Paratropical Rain forest has a confused history of nomenclature, being sometimes grouped with Tropical Rain forest and sometimes excluded. The Paratropical Rain forest is preponderantly broad-leaved evergreen, but broad-leaved deciduous trees and conifers may be minor elements (particularly in secondary vegetation). To the casual observer, Paratropical Rain forest might resemble Tropical Rain forest. The most critical distinction is in the number of closed canopies. Wang (1961, p. 156) and Brown (1919) note that this forest is fundamentally composed of two closed canopies (in contrast to three in Tropical Rain forest), "with spreading crowns of large trees and palms protruding above the general canopy (Wang, 1961, p. 155)," that is, an emergent stratum. On Mount Maquiling, Brown (1919) shows that the emergent stratum of Tropical Rain forest gradually disappears, and the upper closed canopy gradually dissolves into the emergent stratum of Paratropical Rain forest. Champion (1936) has noted a similar breaking-up of the high canopy and irregularity of the emergent stratum in the rain forest on the upper part of the Chittagong tract, upper Assam, and northeastern Burma.

In other physiognomic features, Paratropical and Tropical Rain forest are closely similar. The leaves of Paratropical Rain forest may be slightly smaller than those of the Tropical Rain forest (Brown, 1919), but this needs verification because of the small sample size. Species that have entire-margined leaves, ranging from about 60 to 75 percent, are fewer in Paratropical than in Tropical Rain forest.

The recognition of Paratropical Rain forest as a major forest type is necessary, for this forest differs from other nontropical broad-leaved evergreen forests in a number of major physiognomic criteria: (1) The height of the canopy is greater than in any forest except the Tropical Rain forest; (2) an emergent stratum of broad-leaved evergreens is present; (3) the leaf size is very close to that of Tropical Rain forest and differs considerably from the smaller leaved Notophyllous Broad-leaved Evergreen forest; (4) the percentage of species that have entire-margined leaves is high; (5) the diversity of families, genera, and species is surpassed only by Tropical Rain forest (the notophyllous forest tends to be dominated by four families—Fagaceae, Magnoliaceae, Lauraceae, and Theaceae—whereas the Paratropical Rain forest has a wide array of families that may dominate); (6) buttressing and cauliflory are prominent; (7) lianes are prominent and very diverse. In general, the Paratropical Rain forest is much more closely allied to Tropical Rain forest than to any other forest type, a view supported by the work of Beard (1944) and Webb (1959). To label Paratropical Rain forest as another "subtropical" forest type obscures the close physiognomic relation between Tropical and Paratropical Rain forests and would seem to indicate a close relation between Notophyllous Broad-leaved Evergreen and Paratropical Rain forests, a relation that is in fact not close, either physiognomically or floristically.

DISTRIBUTION (PLATE 1)

The Paratropical Rain forest largely occupies lowland Taiwan (up to 500 m; Li, 1963), most of lowland Hainan, lowland southern China (up to 1000 m; Wang, 1961) and adjacent areas of Burma, Laos, and Viet Nam. As noted in the discussion of Tropical Rain forest, in northeastern Burma "Giant trees tend to be fewer and more grouped***" and "the bulk of the main canopy*** is perhaps less continuous and even***" (Champion, 1936, p. 42). The upper Assam rain forest is "Practically identical in form with the North Burma tropical evergreen forest***" (Champion, 1936, p. 47), whereas most of the Chittagong tract is three storied (Champion, 1936, p. 40, 49). On the larger islands of the Philippines, Paratropical Rain forest is confined to middle altitudes.

Lowland areas of the Ryukyu Islands are provisionally shown as Paratropical Rain forest. These lowland areas are almost entirely denuded of their original vegetation. The flora that is known, however, is composed primarily of species (Hara, 1959) that typically occupy coastal or disturbed sites in paratropical areas. The forest remnants in the uplands are part of the Notophyllous Broad-leaved Evergreen forest, judged by Walker's data (1957).

FLORISTICS

Part of the problem in the recognition of Paratropical Rain forest as a distinct vegetational unit is that it is very closely related to the Tropical Rain forest, having many families in common with it. Characteristic families include Meliaceae, Myristicaceae, Burseraceae, Lauraceae, Anacardiaceae, Myrtaceae, Palmae, Guttiferae, Ebenaceae, Magnoliaceae, Sterculiaceae, and Araliaceae (Wang, 1961). Dipterocarpaceae are represented, but much less abundantly than in Tropical Rain forest. Considering that the dipterocarps primarily occupy the emergent stratum and upper canopy of the Tropical Rain forest, their decrease in importance and diversity in the Paratropical Rain forest is expected.

The Paratropical Rain forest includes members of some genera typically thought of as "temperate": *Acer, Alnus, Berchemia, Ampelopsis, Celastrus, Celtis, Euonymus, Hydrangea, Koelreuteria, Myrica, Parthenocissus, Photinia, Pyracantha, Rhamnus, Rhododendron, Rhus, Rosa, Rubus, Salix, Styrax, Ulmus, Viburnum, Vitis,* and *Zelkova*. These "temperate" genera are better represented in areas geographically close to temperate regions than in the isolated occurrences of upland Paratropical Rain forest in equatorial regions. Most of these "temperate" genera are more typical of disturbed vegetation (particularly along streams) than of the primary forest (see habitats listed in Li, 1963). Some conifers—*Amentotaxus, Pinus, Podocarpus,* and the endemic *Glyptostrobus*—form a minor element in Paratropical Rain forest.

As winter cold increases in Paratropical Rain forest, the physiognomy appears from available data to remain unchanged, but floristically some changes do appear. Diversity does tend to lessen, as taxa sensitive to winter cold disappear. For example, Wang (1961) has noted that several Dipterocarpaceae present in the Paratropical Rain forest of Yunnan and adjacent Burma are lacking or rare in the rain forest in southeastern China.

TEMPERATURE PARAMETERS (PLATE 2)

The Paratropical and Tropical Rain forests are delineated approximately by the 25°C mean annual temperature, as discussed under Tropical Rain forest. The upper altitudinal limit (where not affected by light factors on equatorial mountains) and the northern latitudinal limit appear to be similarly limited by mean annual temperature. Along the coast of China, Paratropical Rain forest extends to the latitude of Fuchou and south of San-tu-ao (Wang, 1961), a boundary approximating a mean annual temperature of 20°C. In regions of low mean annual range of temperature such as Viet Nam and peninsular India, the Notophyllous Broad-leaved Evergreen forest extends into areas that have a mean annual temperature of approximately 20°C, whereas the Paratropical Rain forest altitudinally below extends upward to areas having a mean annual temperature of 21°C. The slight inconsistencies (for example, Abu, Che-lang Chiao) only reinforce the conclusion that some aspect of overall heat accumulation, which can be only approximately expressed by mean annual temperature, delineates Paratropical Rain forest from subtropical forests. Some of the data, moreover, are short term (for example, for Xien Khouang and Pak Song).

De Candolle's suggestion (1874) of the significance of the 20°C mean annual temperature in delimiting "megatherms" from "mesotherms" is remarkably intuitive, considering the lack of climatological data available at the time of his work. The concept of the significance of the 20°C mean annual temperature has persisted in the literature (for example, Beard, 1944) despite the lack of corroborating meteorological data. The data presented here, however, substantiate the significance of this mean annual temperature in delimiting two major forest types. Indeed, de Candolle's megatherms are largely restricted to areas in which the mean annual temperature is approximately 20°C or higher, because the megatherms are largely characteristic of the Tropical and Paratropical Rain forests.

Garnier (in Fosberg and others, 1961) suggested certain purely meteorological criteria for the recognition of the "humid tropics," including as primary that at least 8 months of the year have a mean temperature of 20°C or greater. This parameter, like the 20°C mean annual temperature, is an overall expression of warmth, and indeed it closely parallels the parameter suggested here and has the same exceptions (for example, Abu, Xien Khouang).

The occurrence or lack of freezing temperatures does not appear to have any significance in delimiting forest types in eastern Asia. Temperatures below −1°C have been recorded at many stations in the Paratropical Rain forest in Burma, Viet Nam, mainland China, and Taiwan. Temperatures as low as −2°C have been recorded in northern Hainan (Zaychikov and Panfilov, 1964, p. 508 of English translation). Other stations have not recorded subzero temperatures in this forest type. Freezing temperatures typically occur in cooler forest types, but stations such as Chapa (0°C), Haka (0.6°C), Kanpetlet (0.6°C), Cherrapunji (0.6°C), and Mahabaleshwar (6.7°C) in the Notophyllous Broad-leaved Evergreen forest and even Coonoor (2.2°C) and Kodaikanal (2.8°C) in the Microphyllous Broad-leaved Evergreen forest have not recorded subzero temperatures. Considering the fact that the Notophyllous Broad-leaved Evergreen forest occupies areas that regularly receive freezing temperatures (T'eng-ch'ung and most other Chinese stations, as well as all stations on Kyushu, Honshu, and Shikoku) or that have never experienced freezing temperatures, the occurrence of freezing temperatures—occasional or regular—has no significance to the physiognomy.

The value of 18°C for the mean temperature of the coldest month has traditionally been used for delineating tropical from subtropical climates. As can be seen from plate 2, this value bears no relation to the boundaries between major vegetational units. Perhaps one reason that this value seemed important to some climatologists is that the lowland boundary between the Tropical and Paratropical Rain forests does indeed come close to that cold month isotherm, and data previously available were largely on the lowlands. Only within the past several decades have upland data become available to indicate that the 18°C cold month mean is not critical to vegetational boundaries.

MICROPHYLLOUS BROAD-LEAVED EVERGREEN FOREST

SYNONYMS

Southern wet temperate forest (Champion, 1936), Northern wet temperate forest (Champion, 1936), Himalayan moist temperate forest (Champion, 1936), Broad-leaved Evergreen Sclerophyllous forest in part (Wang, 1961), Montane Rain forest in part (Richards, 1952).

STRUCTURE AND PHYSIOGNOMY

Few data are available on the structure of the Microphyllous Broad-leaved Evergreen forest. The bulk of the forest is broad-leaved evergreen, although Champion (1936) notes that in the upper part broad-leaved deciduous trees form a minor element. In areas that receive only moderate precipitation, conifers are present. Stratification is not clearly evident, and emergents—except for conifers—are absent. Large woody climbers are present but, according to Champion (1936, p. 218), are not conspicuous. The leaves are sclerophyllous. The full range of the percentage of species that have entire-margined leaves is not known; data from Simla based on Collett (1921) indicate a range centering around 45 percent. Structural and physiognomic data are more complete on this forest as it occurs in New Zealand (see "Forests of Australasia").

The absence of conifers in the Microphyllous Broad-leaved Evergreen forest in the isolated patches growing in peninsular India may be due to historical factors, that is, the isolation from sources of conifers—the Mixed Coniferous forest—to become an emergent stratum.

The Microphyllous Broad-leaved Evergreen forest could conceivably be confused with the bulk of Richard's Montane Rain forest (1952). Data presented by Brown (1919) and concurred in by Richards (1952) indicate that, at least in part, the scrubby Montane Rain forest results from a lack of light on many equatorial mountains. The true Montane Rain forest (Elfin woodland of some authors) is characterized by gnarled trees and shrubs, unlike the typically straight-boled Microphyllous Broad-leaved Evergreen forest. Because the distribution of the Montane Rain forest is controlled more by light conditions than by temperature, this forest is found in climates that on temperature alone are suitable for Paratropical Rain forest, Microphyllous Broad-leaved Evergreen forest, or Notophyllous Broad-leaved Evergreen forest. Because this report is concerned primarily with mesic forest distribution under "normal" light conditions, the Montane Rain forest is not discussed further.

DISTRIBUTION (PLATE 1)

The Microphyllous Broad-leaved Evergreen forest is primarily confined to high altitudes in the Himalayas and peninsular India (Champion, 1936). The type has not previously been recognized in China, but Wang (1961, p. 148) notes that the forest altitudinally above typical Notophyllous Broad-leaved Evergreen forest in Yunnan is dominated by "A species of small-leaved evergreen oak***" that forms a dense crown. The shrub layer includes broad-leaved deciduous species, and a few woody climbers are present; that is, this forest is an eastern extension of the Microphyllous Broad-leaved Evergreen forest of the Himalayas.

If the delimiting temperature parameters suggested here are valid, the temperature data for upland Taiwan indicate that altitudinally between the Notophyllous Broad-leaved Evergreen and Mixed Coniferous forests should be a narrow belt of Microphyllous Broad-leaved Evergreen forest. No vegetational studies have been made of this ecotonal region (1,800–2,000 m), but the microphyllous forest may indeed be recognizable. On Taiwan, the notophyllous forest is, as elsewhere in southeastern Asia, dominated by evergreen members of Fagaceae, Lauraceae, and Theaceae. From the lists and altitudinal ranges for members of these families given by Li (1963), about 60 percent of the members that occur between 1,800 and 2,000 m are, on the average, microphyllous. Wang (1961, p. 66), moreover, notes that the lower part of the coniferous forest contains "a considerable proportion" of broad-leaved evergreens; it also contains woody climbers and epiphytic forms. These features are more typical of broad-leaved than of coniferous forests.

FLORISTICS

This forest is floristically related to the Notophyllous Broad-leaved Evergreen forest. The broad-leaved evergreens are primarily members of Fagaceae and Lauraceae, although Theaceae, Magnoliaceae, and Ericaceae may be prominent. The coniferous element, which is not diverse, is composed of species that are also members of the Mixed Coniferous forest. The broad-leaved deciduous trees and shrubs are primarily of holarctic affinity (for example, *Deutzia, Rosa, Rubus, Euptelea, Viburnum, Carpinus, Acer, Alnus, Betula*).

TEMPERATURE PARAMETERS (PLATE 2)

The boundary between the Microphyllous and Notophyllous Broad-leaved Evergreen forests reflects some aspect of summer heat that approximates a warm month mean of 20°C. This may be the same factor that delineates broad-leaved deciduous from coniferous forests; in one sense, the microphyll leaf size of the plants may be analogous to the microphyll and nanophyll size of the conifers, which tend to be favored in areas of low summer heat accumulation. The boundary between the Microphyllous Broad-leaved Evergreen and Coniferous forests is not well controlled; more climatic data are needed from the upland forests of equatorial regions, where dominantly coniferous forests occur above dominantly broad leaved evergreen forests (van Steenis, 1935). It is tempting to suggest that a mean annual temperature of 13°C approximates the vegetational boundary.

NOTOPHYLLOUS BROAD-LEAVED EVERGREEN FOREST

SYNONYMS

Southern subtropical wet hill forests (Champion, 1936); Northern subtropical wet hill forests (Champion, 1936); Evergreen Sclerophyllous Broad-leaved Evergreen forest in part (Wang, 1961); "oak-laurel forest" of various workers.

STRUCTURE AND PHYSIOGNOMY

The primary forest is broad-leaved evergreen, but with minor admixtures of broad-leaved deciduous trees (but not typically in the crown) and shrubs and, less typically, conifers. Stratification is not clearly defined. Boles are thin and straight; buttressing and cauliflory are almost totally absent. Woody climbers may be profuse but are of far less diversity than in the Paratropical Rain forest. The leaves are typically sclerophyllous but without well-defined drip tips. The leaf size is the "small mesophyll" class of Sato (1946), that is, the notophyll size class of Webb (1959). The percentage of species that have entire-margined leaves varies from about 40 to 60 percent.

In individual stands of primary forest, broad-leaved evergreens are overwhelmingly dominant; Yoshino (1968) records that almost 95 percent of the basal area represents broad-leaved evergreens, while broad-leaved deciduous trees are less than one percent. From Sato's data (1946), the broad-leaved deciduous trees are typically not members of the crown. Wang (1961), however, notes that the secondary vegetation may be dominantly coniferous (primarily *Pinus*) or broad-leaved deciduous or mixtures of both.

DISTRIBUTION (PLATE 1)

The Notophyllous Broad-leaved Evergreen forest covers large upland areas of Burma, Laos, and Viet Nam, but the most extensive development is in central and southern China and southern Japan. The northern boundary in China is uncertain because of the extensive cultivation, but most workers (for example Grubov and Fedorov, 1964; Lee, 1964) consider that all the Yangtze River valley and the coastal area to about lat 35° N. was originally broad-leaved evergreen. Certainly the 8 members of evergreen Fagaceae and 15 members of Lauraceae Steward (1958) records from the lower Yangtze provinces of Kiangsu and Anhwei are indicative of notophyllous, sclerophyllous forest. In Japan, this forest cloaks the lower slopes of Kyushu, Shikoku, and southern and central Honshu.

The forests of Anhwei and Kiangsu are further interpreted to have a high proportion of deciduous species resulting from the same factor that affects the forests of eastern United States (see p. 25), that is, the intense winter outbreaks of polar air. In maritime areas of eastern Asia that have a cold month mean of 1° to 2°C (for example, coastal Korea and Japan), the proximity of the ocean probably yields a lower diurnal range of temperature than would continental areas of the same cold month mean.

Wang's map (1961) is, unfortunately, highly misleading. He shows most of the Yangtze River valley occupied by Mixed Mesophytic forest but makes clear in the text that Mixed Mesophytic forest actually has a lower altitudinal limit of 500–1,000 m (compare Wolfe, 1971).

FLORISTICS

The term "oak-laurel forest" has been applied to the notophyllous forest. Several genera of evergreen Fagaceae and Lauraceae accompanied by Theaceae and Magnoliaceae make up the bulk of the forest. Although broad-leaved evergreen species are the vegetational dominants, broad-leaved deciduous trees and shrubs make up 14 percent of the species (based on Yoshino, 1968). Holarctic elements are conspicuous; they include Salicaceae, Betulaceae, Juglandaceae, deciduous Fagaceae, *Liquidambar*, Rosaceae, and Aceraceae, elements particularly notable in disturbed or secondary vegetation. Thus while the dominants have tropical affinities, a considerable proportion of the species has temperate affinities.

TEMPERATURE PARAMETERS (PLATE 2)

According to Wang (1961) and Cheng (1939), dominantly broad-leaved evergreen forest extends up to about 2,200 m in western Szechuan, making stations such as Pi-chieh and Mo-mien (about 2,000 m) a part of the notophyllous forest; vegetation above this altitude tends to be an admixture including conifers and broad-leaved deciduous trees. Consequently, a mean annual temperature of 13°C approximates the upper boundary of the notophyllous forest. In Korea, stations such as Pusan and Mokpo—both slightly higher than 13°C—fall near the northern margin of the forest. The work of Yoshino (1968) indicates that stations such as Mito, Utsonimiya, and Maebashi are in an area in which the notophyllous forest is in ecotone with the Mixed Broad-leaved Evergreen and Coniferous forest, whereas Tokyo and Yokohama are in a definite notophyllous forest. Again, a mean annual temperature of about 13°C appears to approximate the boundary between the Notophyllous Broad-leaved Evergreen and Mixed Broad-leaved Evergreen and Coniferous forests.

The boundary between the notophyllous forest and the Mixed Broad-leaved Evergreen and Deciduous forest is very uncertain because of the extensive disturbance of vegetation in central and northern China. The available data, however, indicate that possibly the same factor controlling the boundary between the Mixed Broad-leaved Evergreen and Coniferous and Mixed Mesophytic forests is operative in limiting the notophyllous forest, that is, a cold month mean of about 1°C.

The traditional lower boundary of subtropical climate has typically been placed along a cold month mean of 6°C (Landsberg, 1964). Such a boundary has no apparent relation to vegetational boundaries. The reason for selecting this value as a climatic boundary is not apparent.

MIXED BROAD-LEAVED EVERGREEN AND DECIDUOUS FOREST

SYNONYMS

Lower oak forest in part (Wang, 1961).

STRUCTURE AND PHYSIOGNOMY

Almost nothing is known of the original structure and physiognomy of the Mixed Broad-leaved Evergreen and Deciduous forest, because most of the areal extent is in a region that has been heavily cultivated for centuries. Wang (1961) is of the opinion that the forest was dominantly broad-leaved deciduous, and certainly the cultivated trees and secondary vegetation are preponderantly broad-leaved deciduous; a few species of broad-leaved evergreen trees and shrubs are known. As the secondary forest in the Notophyllous Broad-leaved Evergreen forest region also is mainly deciduous, the physiognomy of a secondary forest may have little bearing on the physiognomy of the original forest. In Korea, areas with basically the same temperature parameters as Mei-hsien must occur in the transect from Sachon to Kwangju; the forest in this area is considered to have a large proportion of broad-leaved evergreens.

The physiognomy of this original vegetation may, therefore, have been primarily broad-leaved evergreen or, more probably, a mixture of broad-leaved evergreen and deciduous plants. If, as the temperature parameters of the Mixed Mesophytic forest indicate, most notophyllous broad-leaved evergreens do not live in regions where the mean of the cold month is less than 1°C, then the forest would have been depauperate in regard to this element. Similarly, broad-leaved deciduous plants decrease significantly in diversity if the mean annual temperature is greater than 13°C, and consequently this element also would be depauperate. The forest might reasonably be expected to have resembled structurally the Mixed Mesophytic forest except for a higher proportion of broad-leaved evergreens and a more monotonous appearance resulting from lower diversity.

Physiognomic characteristics of the foliage are equally hypothetical. Bailey and Sinnot (1916) suggest that the cultivated flora in an area has about the same leaf margin characteristics as the native flora. If this is so, the short list given by Wang (1961, p. 92–92) indicates that the percentage of species that have entire-margined leaves is 41 for the area near Hsi-an.

DISTRIBUTION (PLATE 1)

Presumably most of the Mixed Broad-leaved Evergreen and Deciduous forest occupied a broad area centering in the valley of the Yellow River. Presumably this forest is present in a thin belt in southern Korea; investigations of this area should provide much data on the structure and physiognomy of the forest.

FLORISTICS

Some of the plants listed by Wang (1961) are clearly escapees from cultivation. Others he considers as native to the region. There is a notable occurrence of elements in the Mixed Broad-leaved Evergreen and Deciduous forest that also occur in the Notophyllous Broad-leaved Evergreen forest: *Quercus, Gleditsia, Paulownia, Hovenia, Pistacia, Broussonetia, Catalpa, Firmiana, Toona, Lindera, Machilus, Cocculus, Callicarpa.* Less prominent are elements that also occur in the Mixed Mesophytic forest: *Pterocarya, Kalopanax, Pteroceltis, Ulmus, Zelkova, Sophora.* Naturalized genera include: *Albizzia, Melia, Castanea, Juglans.*

TEMPERATURE PARAMETERS (PLATE 2)

This vegetation occupies the area not certainly occupied by contiguous forest types; the suggested parameters are therefore discussed under those forest types.

MIXED BROAD-LEAVED EVERGREEN AND CONIFEROUS FOREST

SYNONYMS

Evergreen oak and deciduous hardwood forest (Wang, 1961); Evergreen Sclerophyllous Broad-leaved forest in part (Wang, 1961); Cyclobalanopsis type (Yoshino, 1968); *Cornus kousa-Acer crataegifolium-Bobua myrtacea*-Association (Sato, 1946); Deciduous broad-leaved tree mixed with evergreen broad-leaved tree formation (Sato, 1946); *Tsuga sieboldii*-Association (Sato, 1946).

STRUCTURE AND PHYSIOGNOMY

Broad-leaved evergreens and needle-leaved evergreens are dominant in the Mixed Broad-leaved Evergreen and Coniferous forest; typically the broad-leaved evergreens predominate. In some parts of the range of this forest, conifers (except for pines) are lacking; whether this is a result of selective cutting or historical factors is uncertain. Broad-leaved deciduous trees may share in the dominance of the lower (second) tree stratum. Typically, woody climbers are present. Sato (1946) indicates that approximately 50 percent of the species are microphyllous. In basal area, Yoshino's (1968) data indicate that about 70 percent of the stands are broad-leaved evergreen, 27 percent coniferous, and 3 percent broad-leaved deciduous. The percentage of species that have entire-margined leaves ranges from about 30 to 35 percent (data based on lists from Wang, 1961; Sato, 1946; Yoshino, 1968).

DISTRIBUTION (PLATE 1)

Extensive areas on the flanks of the southwestern plateau of China are occupied by Mixed Broad-leaved Evergreen and Coniferous forest. The narrow ecotonal region between the Notophyllous Broad-leaved Evergreen and Mixed Mesophytic forests in the Yangtze River valley probably represents Mixed Broad-leaved Evergreen and Coniferous forest; the forest below Mixed Mesophytic forest on T'ien-mu Shan, for example, contains a mixture of broad-leaved evergreens and conifers, with broad-leaved deciduous trees a minor element. Yoshino (1968) recognized that her *Cyclobalanopsis* type contained a higher proportion of broad-leaved deciduous and particularly coniferous trees than the *Castanopsis* type (=Notophyllus Broad-leaved Evergreen forest); these two vegetational types form a mosaic in the hills rising from the Kanto Plain, the Mixed Broad-leaved Evergreen and Coniferous forest occupying cooler sites. This forest occupies certain belts in the altitudinal series of vegetation in Kyushu and Shikoku. Hara (1959) recognized the peculiar admixture of conifers and broad-leaved evergreens about 300–600 m above Izuhara (Tsushima Islands); on Ullungdo the vegetation is mixed broad-leaved evergreen and deciduous. Hara (1959, p. 56) considered remarkable the mixture of temperate conifers and broad-leaved deciduous trees in the dominantly broad-leaved evergreen forest of the Oki Islands in the Japan Sea. The climatic data for Saigo (almost at sea level) approach those for the Mixed Broad-leaved Evergreen and Coniferous Forest; a slight decrease in mean annual temperature (0.7°C), moving upslope on the Oki Islands, should in fact produce the climatic parameters under which the Mixed Broad-leaved Evergreen and Coniferous forest lives. Presumably the Mixed Broad-leaved Evergreen and Coniferous forest is developed on the Sea of Japan margin of Honshu in forests that have traditionally been interpreted as broad-leaved evergreen (similarly, the *Cyclobalanopsis* type has been traditionally interpreted as broad-leaved evergreen.)

FLORISTICS

The elements of the Mixed Broad-leaved Evergreen and Coniferous forest are drawn primarily from the adjacent vegetational types. Although the vegetation is broad-leaved evergreen and coniferous, Yoshino's data indicate that 28 percent of the species are broad-leaved deciduous and are species characteristically found in the Mixed Mesophytic forest. These include species of genera such as *Acer* and *Carpinus*. It was probably the high percentage of broad-leaved deciduous species characteristic of the Mixed Mesophytic forest that led Wang (1961) to include the Mixed Broad-leaved Evergreen and Coniferous forest in the Mixed Mesophytic forest. Typically, the broad-leaved evergreen elements are shared with the Notophyllous Broad-leaved Evergreen forest, and the coniferous elements are shared largely with the Mixed Coniferous forest.

TEMPERATURE PARAMETERS (PLATE 2)

Stations that are certainly in this forest type have one temperature factor in common, a mean of the cold month 1°C or higher. Stations in the Mixed Mesophytic forest all have a cold month mean less than 1°C. This cold month mean is apparently related to the factor that delimits most broad-leaved evergreens; indeed, the only main physiognomic feature that distinguishes Mixed Broad-leaved Evergreen and Coniferous from Mixed Mesophytic forest is the greatly reduced broad-leaved evergreen element in the Mixed Mesophytic.

MIXED MESOPHYTIC FOREST

SYNONYMS

Mixed Mesophytic forest in part (Wang, 1961); *Castanea* zone (Hara, 1959); *Acer sieboldianum-Carpinus tschnoskii-Ilex crenata*-Association (Sato, 1946); *Hamamelis japonica-Acer sieboldianum*-Association (Sato, 1946).

STRUCTURE AND PHYSIOGNOMY

Below the canopy in the Mixed Mesophytic forest smaller trees occur with poorly defined stratification (Wang, 1961). The dominant trees of the canopy are broad-leaved deciduous. Broad-leaved evergreen trees are a minor element, but broad-leaved evergreens are more prominent as small trees or shrubs. Conifers are typically a minor, though diverse, element in this forest. Woody climbers are present. From Sato's data, the leaf size is about evenly divided between notophylls and smaller size classes; nanophylls make up as much as 10 percent. It is emphasized, however, that Sato included all plants in his figures; many of the broad-leaved evergreens are microphylls, particularly among the larger trees. The percentage of species that have entire-margined leaves ranges from about 28 to 38 percent.

DISTRIBUTION (PLATE 1)

The distribution of the Mixed Mesophytic forest is modified from Wang (1961) to accord with his text statements regarding altitudinal range in China. The patch of this forest shown on the Shantung Peninsula is hypothetical, but this area has the temperature parameters occupied by Mixed Mesophytic forest elsewhere in Asia. Floristically, the Shantung Peninsula does have species common in the Mixed Mesophytic forest (Kazakova, 1964, p. 470 of English translation). The distribution shown for Korea is after Wang (1961). In Japan, the distribution shown is primarily after Wang (1961), but the southern boundary is in accord with Miyawaki (1967).

FLORISTICS

The floristic elements of Mixed Mesophytic forest have been exhaustively analyzed by Wang (1961). This forest is the richest of all broad-leaved deciduous forests, containing a diverstiy of members of Aceraceae, Betulaceae, Juglandaceae, Rosaceae, Fagaceae, and many other families. Wang has emphasized that no species or family is dominant in this forest. Other conspicuous elements are the many relicts, among them, *Cercidiphyllum, Euptelea,* and *Davidia,* although most of these are also present in the Notophyllous Broad-leaved Evergreen forest.

TEMPERATURE PARAMETERS (PLATE 2)

The Mixed Mesophytic forest occupies a very limited range of temperatures. Stations near the northern or upper altitudinal limit all have a mean cold month temperature of −2°C or somewhat higher, whereas stations that are in Mixed Northern Hardwood or Mixed Broad-leaved Deciduous forest all have a cold month mean below this value. As the Mixed Mesophytic forest differs from these forest types primarily by the presence of notophyllous broad-leaved evergreens, a limiting factor of winter cold is reasonable.

The hypothesis that the Mixed Mesophytic forest in central China lives under more equable conditions than the same forest type in eastern China, Korea, and Japan has apparently developed from extrapolating from climatic data for low altitudes and applying the precarious generality that mean annual range decreases upslope. In actuality, the climatic data from central and eastern China indicate little change in equability going upslope. Compare, for example, the pairs of data for T'ien-mu-shan and Han-k'ou, T'ien-t'ai Shan and Han-k'ou, Lu Shan and Chiu-chang, Heng Shan and Ch'ang-sha, Ya-an and Mo-mien, and Mo-mien and K'ang-ting, which show either a slight decrease or increase in equability. Moreover, the hazard of inferring from "normal" lapse rates the mean annual temperature of vegetation at higher altitudes is shown by data for Chinese stations, where lapse rates vary from about 0.4 to 0.6°C, that is, ±20 percent variation from the normal 0.5°C/100 m.

Extrapolating from the available climatic data, primary mesic broad-leaved deciduous forest could exist under a mean annual range of 19°C. The altitudinal range of a mean annual temperature of about 10°C, however, would be extremely limited, and consequently broad-leaved deciduous forest in an area of mean annual range of 19°C would be extremely limited areally. Indeed, it is probable that broad-leaved deciduous forest would not be recognized as a distinct formation in such an area but rather would form a mosaic with neighboring forest types.

MIXED BROAD-LEAVED DECIDUOUS FOREST

SYNONYMS

Lower oak forest in part (Wang, 1961); Upper oak forest (Wang, 1961); Temperate Broad-leaved Deciduous forest in part (Wang, 1961).

PHYSIOGNOMY

Mixed Broad-leaved Deciduous forest is two storied and has in addition a shrubby layer. All the broad-leaved trees are deciduous; broad-leaved evergreens are represented as shrubs by microphyllous species. Conifers are not typical of the mesic sites but rather are typically confined to secondary areas (pine forests) or to dry slopes. Woody climbers are present but not diverse. The percentage of species that have entire-margined leaves ranges from 27 to at least 33.

DISTRIBUTION (PLATE 1)

Mixed Broad-leaved Deciduous forest probably once covered the great plain surrounding Pei-p'ing and adjacent foothills (Wang, 1961). The forest is present in Korea, where it narrows from west to east. The Mixed Broad-leaved Deciduous forest has not been recognized by Japanese botanists as a physiognomic unit. In northern Honshu, Hara (1959) noted that topographically below the "Fagus zone" (= Mixed Northern Hardwood forest), deciduous oaks predominate; temperature data would be intermediate between those for Aomori and Fukaura. In central Honshu, Hara (1959) observed that the upper part of his "Castanea zone" (= Mixed Mesophytic forest) is characterized by deciduous oaks; stations such as Suwa and Takayama are near or in this oak-dominated zone. The prevalence of deciduous oaks in the Mixed Broad-leaved Deciduous forest in China suggests that this forest may be present to a limited extent on Honshu. Perhaps the reason the

Japanese have not recognized a distinct forest type is that in central Honshu, for example, the zone would cover only an altitudinal interval of about 100 m and would therefore be insignificant.

FLORISTICS

Several species of oak form the bulk of the Mixed Broad-leaved Deciduous forest. Many other genera not represented in the Mixed Northern Hardwood forest are present, native or introduced: *Broussonetia, Toona, Euodia, Pistacia, Schizandra, Catalpa, Diospyros, Gleditsia, Sophora, Albizza, Ailanthus, Koelreuteria, Hemiptelea, Paulownia, Zizyphus,* and *Hovenia.*

The dominance of oaks in the Mixed Broad-leaved Deciduous forest and their lack of dominance (except on drier sites) in the Mixed Northern Hardwood forest is indeed curious. The same phenomenon, however, apparently occurs in the broad-leaved deciduous forests of eastern North America. The vegetation dominated by oaks (specifically, the Appalachian oak and oak-hickory forests of Küchler, 1967a) extends northward into areas that have a mean annual temperature of about 10°C. In the cooler areas to the north of the oak forests, the vegetation tends to be dominated by *Acer, Tilia, Fraxinus, Ulmus,* and *Betula*—a combination of tree genera highly reminiscent of the Mixed Northern Hardwood forest of eastern Asia.

TEMPERATURE PARAMETERS (PLATE 2)

All stations in the Mixed Broad-leaved Deciduous forest have mean annual temperatures approximately 10°C or higher. Stations in the Mixed Northern Hardwood forest consistently have a mean annual temperature of 10°C or lower, whether in areas of high mean annual range (Shansi and Hopeh) or low mean annual range (southern Hokkaido). The narrowing of the area occupied by the Mixed Broad-leaved Deciduous forest in an easterly direction is understandable; mean annual range decreases in an easterly direction at middle latitudes in Asia.

The distinction between the Mixed Broad-leaved Deciduous and Mixed Northern Hardwood forests is not entirely satisfactory on a physiognomic basis. The structural similarities between the two forest types are great, and, except for the higher percentage of entire-margined species in the Mixed Broad-leaved Deciduous forest (largely a reflection of the higher mean annual temperature), no physiognomic differences are apparent. Wang (1961) considers that conifers are typically not present in the primary vegetation (they are present in the secondary forests) of the region occupied by the Mixed Broad-leaved Deciduous forest. Why this is so is not clear; presumably conifers respond more to summer warmth than to mean annual temperature, and the boundary between Mixed Broad-leaved Deciduous forest and Mixed Northern Hardwood forest almost certainly does not approximate any warm month mean. The floristic differences between the two forests are considerable, and the Mixed Broad-leaved Deciduous forest tends to be less diverse; this diversity, however, may be a reflection of the lack of extensive natural forests of this type at the present day. Certainly more fieldwork is needed, particularly in Honshu and Korea, to determine if the distinction between the Mixed Broad-leaved Deciduous and Mixed Northern Hardwood forests is physiognomically valid.

MIXED CONIFEROUS FOREST

SYNONYMS

Montane-Boreal Coniferous forest in part (Wang, 1961); Himalayan Moist Temperate forests in part (Champion, 1936).

STRUCTURE AND PHYSIOGNOMY

The Mixed Coniferous forest is dominated almost exclusively by needle-leaved evergreen species that form a closed canopy. Smaller broad-leaved trees are typically present, although they may not form a continuous stratum.

No attempt has been made to subdivide the Mixed Coniferous forest in eastern Asia, largely because climatic data and detailed physiognomic analyses are not available. At least one subdivision should be possible, however, when analyses are available. Both Wang (1961) and Champion (1936) note that the broad-leaved accessories of the coniferous forests in the Himalayas and Yunnan are typically evergreen and, based on Li's (1963) data, so also are the broad-leaved accessories in the coniferous forest of Taiwan, whereas the coniferous forests of northern China (excluding Taiga) and Japan have broad-leaved deciduous accessories. The temperature parameter dividing a coniferous forest with dominantly broad-leaved evergreen accessories from a coniferous forest with dominantly broad-leaved deciduous accessories would probably approximate a cold month mean between 1° and −2°C.

DISTRIBUTION (PLATE 1)

The occurrences of this forest are taken from Champion (1936), Wang (1961), Honda (1928), Miyawaki (1967), and Suslov (1961). The forest occurs at Chugushi and Tsurugiyama (Hara, 1959) and O-mei Shan (Cheng, 1939) in areas too small to show on the map.

FLORISTICS

The floristics of the conifer dominants have been thoroughly discussed by Wang (1961). Most of the members of this forest are Pinaceae: *Abies, Picea, Pseudotsuga,* and *Tsuga.*

In the Himalayas and the southwestern plateau of China, conifers, in particular Pinaceae, attain their greatest diversity. Associated with the conifers are evergreen shrubs such as *Rhododendron* and *Berberis.* Deciduous trees are uncommon and generally restricted to streamsides or to lower elevations in the forest. In some areas broad-leaved evergreen trees form a discontinuous lower tree stratum; these include *Quercus* and *Rhododendron.*

The Mixed Coniferous forest on Taiwan contains a number of broad-leaved adjuncts. These include deciduous Betulaceae, Ulmaceae, and Aceraceae, as well as evergreen Fagaceae and Lauraceae. The climbers include some of subtropical relation (*Schisandra* and *Akebia*) and some of temperate relation (*Hydrangea* and *Rubus*).

In Manchuria and Japan, the Mixed Coniferous forest typically includes a number of broad-leaved deciduous trees that are present in the Mixed Northern Hardwood forest. These include members of Betulaceae, Ulmaceae, Aceraceae, and Tiliaceae.

Conifers can be found throughout the broad-leaved spectrum. Their occurrence in forested regions that have high heat levels during the growing season is largely in secondary vegetation or in special edaphic situations, in particular for various species of *Pinus.* Other members of Pinaceae are primarily restricted to dominantly coniferous forests, although some species participate regularly as a minor element in broad-leaved forests such as the Mixed Northern Hardwood, Mixed Mesophytic, and Mixed Broad-leaved Evergreen and Coniferous forests. The Cupressaceae show divergent adaptations. Some genera, for example, *Chamaecyparis,* are largely members of coniferous forests; other genera, for example, *Fokienia,* are largely restricted to broad-leaved forests of at least moderate heat levels. The Taxodiaceae, in contrast, tend to be members of broad-leaved forests. *Glyptostrobus* is today restricted to Paratropical Rain forest. Although *Metasequoia* appears to be endemic to Mixed Mesophytic forest, the lists of Chu and Cooper (1950) include a sufficient number of broad-leaved evergreen trees to indicate that this genus may actually be endemic to Mixed Broad-leaved Evergreen and Coniferous forests. *Cunninghamia* is found in both Mixed Mesophytic and particularly in Notophyllous Broad-leaved Evergreen forest, and *Cryptomeria* occurs in both forests. The present range of *Taxodium* is largely in a region that, on major temperature parameters, is suitable for Notophyllous Broad-leaved Evergreen forest. In Asia, only *Taiwania* of all Taxodiaceae is restricted primarily to coniferous forests. In western North America, both *Sequoia* and *Sequoiadendron* are members of coniferous forests. The specific diversity of conifers, however, is not great in dominantly broad-leaved forests.

TEMPERATURE PARAMETERS (PLATE 2)

The boundary between Mixed Coniferous forest and Taiga appears to involve overall heat accumulation as approximately expressed by mean annual temperature. Hara (1959, p. 10–11) notes that in the Kurile Islands the boundary between the coniferous forest similar to that of Hokkaido (= Mixed Coniferous forest) and the depauperate Siberian vegetation lies along Miyabe's Line, which is south of Simusir. O-mei Shan, on the other hand, is by Wang's (1961) and Cheng's (1939) descriptions in a mosaic of Mixed Coniferous forest and meadows. These two stations, one of which is the most equable for Taiga, indicate that a mean annual temperature of approximately 3°C separates Taiga from Mixed Coniferous forest. Hara (1959, p. 12) notes that in areas of high mean annual range such as Sakhalin, Schmidt's Line is analogous to Miyabe's Line. If stations such as Kholmsk in Mixed Coniferous forest are compared with stations such as Bolshaya Yelan and Juzno-sahalinsk in Taiga, it is again apparent that a mean annual temperature of 3°C approximates the boundary between the two forests.

The climatic boundary between coniferous forests and the broad-leaved deciduous forests is shown as approximating a mean temperature of 20°C for the warmest month. This indicates that some aspect of high summer heat favors broad-leaved trees than conifers.

MIXED NORTHERN HARDWOOD FOREST

SYNONYMS

Fagus zone of Hara (1959); Mixed Northern Hardwood forest of Wang (1961); Upper oak forest in part (Wang, 1961); *Quercus mongolica* forest (Wang, 1961).

STRUCTURE AND PHYSIOGNOMY

The Mixed Northern Hardwood forest is two storied and has a shrub layer. All trees are broad-leaved deciduous; a few shrubs are microphyllous broad-leaved evergreen. Woody climbers are present but not diverse. Overall, diversity is lower in this forest than in all but one other broad-leaved forest. The percentage of species that have entire-margined leaves has a range of about 9 to 24. Nearly 20 percent of the species have lobed, palmately veined leaves, whereas this element constitutes only about 5 percent in the Mixed Broad-leaved Deciduous forest. Conifers are an important element in the Mixed Northern Hardwood forest, although accurate data are not available. On dry sites, the forest is dominated by one particular deciduous oak that forms a bushy open forest (Wang, 1961).

DISTRIBUTION (PLATE 1)

The forest occupies large areas of Manchuria and adjacent U.S.S.R. and Korea. Northernmost Honshu and most of lowland Hokkaido are occupied by this forest (Hara, 1959), which extends southward along mountains at moderate to high elevations.

FLORISTICS

The dominants in this forest are members of *Quercus, Acer, Tilia, Betula,* and *Ulmus.* The forest contains other "northern" genera such as *Fraxinus, Sorbus,* and *Alnus,* and a few "southern" elements such as *Schizandar, Magnolia, Kalopanax,* and *Actinidia.* In Japan, the forest is dominated by *Fagus* (absent from the forest in mainland Asia) but is otherwise generically similar.

TEMPERATURE PARAMETERS (PLATE 2)

All stations in the Mixed Northern Hardwood forest have a mean annual temperature of 2.5°C or higher. The data for nearly all the stations near the boundary with the Simple Broad-leaved Deciduous forest, however, are short term. A mean annual temperature between 2.5 and 3.0°C appears to most closely approximate the boundary.

TAIGA

SYNONYMS

Montane-Boreal Coniferous forest in part (Wang, 1961).

STRUCTURE

Taiga is typically dominated by either a needle-leaved deciduous conifer or a needle-leaved evergreen conifer. There is but one tree stratum, and shrubs are sparse or absent.

DISTRIBUTION (PLATE 1)

The bulk of the Taiga forest is in the U.S.S.R. and adjacent parts of China. Taiga may be present on high mountains in Szechuan, but physiognomic analyses are lacking; Cheng (1939) notes that in various areas above Mixed Coniferous forest, the forest is composed entirely of a single species, and the species varies from one area to the next. Taiga is apparently not present on Taiwan; there, at least six species of conifers extend in mixtures up to the timberline of 3,000 m.

FLORISTICS

The two main Taiga species are members of *Larix* and *Pinus.* South of the main expanse of the Taiga along mountain ranges, it is probable that Taiga is formed by the most cold-tolerant local conifer.

TEMPERATURE PARAMETERS (PLATE 2)

See discussion, Temperature parameters, for Mixed Coniferous forest.

SIMPLE BROAD-LEAVED DECIDUOUS FOREST

SYNONYMS

Mixed Northern hardwood forest predominated by birch (Wang, 1961).

STRUCTURE AND PHYSIOGNOMY

The canopy of the Simple Broad-leaved Deciduous forest is typically formed by one or two species of broad-leaved deciduous trees. Lower tree strata are absent. Shrubs are scarce or absent. None of the species are entire margined.

DISTRIBUTION (PLATE 1)

Restricted to Manchuria in general, this forest may appear at high elevations farther south. The distribution of part of the birch forest is somewhat uncertain because birch dominates the secondary growth in coniferous regions.

FLORISTICS

The only tree species in the primary forest belong to *Betula.* Along streams, however, both *Populus* and *Salix* occur.

TEMPERATURE PARAMETERS (PLATE 2)

The temperature data used are confined to the main area of the Simple Broad-leaved Deciduous forest in Manchuria so that the analysis is not complicated by possible secondary forests. Birch forests or groves can also be found in regions that are coniferous; apparently birch can be a secondary tree in such regions after fire or clearing. And it is possible that the occurrence of birch forest at high altitudes above Taiga in Manchuria (Wang, 1961) results from the strong wind there, unfavorable to conifers at such altitudes. Birch forest clearly lives under the most severe and extreme temperature conditions of any broad-leaved forest; at Hai-la-erh, the mean January temperature is −28.3°C, the mean July temperature, 20.8°C. As no other mesic forested area of the world has such extremes, the Simple Broad-leaved Deciduous forest is present only in Asia.

FORESTS OF AUSTRALASIA

The most notable work on classifying the forests of Australasia on a purely physiognomic basis is that of Webb (1959) on the forests of eastern Australia (pl. 3). Webb recognized several rain forest types and noted their altitudinal distribution at selected latitudes. From comparison of Webb's physiognomic criteria with those used in this report, it is apparent that his Complex Mesophyll Vine forest, which he classifies as "tropical," is the same unit that I call "Paratropical Rain forest." Similarly, the smaller leaved Complex Notophyll Vine and Simple Notophyll Vine forests are physiognomically analogous to the Notophyllous Broad-leaved Evergreen forest. That overall heat accumulation delimits the Australasian Paratropical Rain forest from the notophyllous forests as in eastern Asia is indicated by comparing data for Gladstone to the data for Eagle Farm and Brisbane. As in Asia, the transition takes place between a 20° to 21°C mean annual temperature (pl. 3).

The Microphyllous Broad-leaved Evergreen forest has been studied in detail in one area of New Zealand by Dawson and Sneddon (1969). Although they consider the forest to be multistratal, the diagrams of Robbins (1962) indicate that the forest is probably fundamentally two storied (although stratification is poorly defined) and has an emergent stratum of conifers (primarily podocarps). Woody climbers are profuse in the New Zealand microphyllous forest. In leaf size, 68 percent are microphyllous (Dawson and Sneddon, 1969). Entire-margined species constitute 60 percent, a considerably higher proportion than in the Microphyllous Broad-leaved Evergreen forest of Asia. The higher percentage in Australasia (this is true for all forest types in Australasia) than in analogous Asian vegetation is apparently the result of historical factors (Bailey and Sinnot, 1916; Wolfe, 1971), that is, the absence of climates favorable to the development of broad-leaved deciduous forests (most species of which are nonentire). Consequently, a separate scale of leaf-margin percentages should be used for analyzing Australasian vegetation and probably that of other areas of the Southern Hemisphere. As a map of the physiognomic categories of New Zealand vegetation is not available, the temperature parameters of the Microphyllous Broad-leaved Evergreen forest in New Zealand are not known. The one station (Kaitaia; pl.3) that applies to Dawson and Sneddon's study area has temperature parameters that fall within the limit of the forest type in eastern Asia.

The forests of much of South Island and North Island of New Zealand have been the subject of much discussion (see Holloway, 1954; Robbins, 1962; Dawson and Sneddon, 1969). The problematic forests are those in which podocarps, which were apparently dominant, are giving way to broad-leaved forests dominated by the southern beech *Nothofagus*. As Dawson and Sneddon suggest, however, part of the problem may result from edaphic factors; that is, some areas are occupied by beech forest because of poor soils unfavorable to growth of "normal" forests. More significant is that most of lowland New Zealand has temperature parameters near the boundary between Microphyllous Broad-leaved Evergreen and Mixed Coniferous forests in Asia. The overall warming since the last major glaciation would tend to displace the coniferous forests in favor of the broad-leaved forests. The presence of coniferous emergents in a dominantly broad-leaved forest is not unique to New Zealand but rather characterizes the forests that occur in a similar climatic regime in Asia.

Many of the montane forests of Melanesia appear to be microphyllous broad-leaved evergreen, with an emergent stratum of conifers (Sachet, 1957, p. 45). Altitudinally below these forests, on mesic undisturbed sites, the forest appears to be Paratropical Rain forest from Sachet's brief descriptions (1957).

The reason for the close floristic relation between the montane rain forests of tropical South Pacific Islands and the lowland rain forests of extratropical Australia and New Zealand noted by several phytogeographers is clear. Both types of forests are Microphyllous Broad-leaved Evergreen forest, a forest type poorly developed in southeastern Asia south of the Himalayas except for isolated patches in peninsular India.

FORESTS OF WESTERN NORTH AMERICA

Western North America clearly has the greatest expanse of Mixed Coniferous forest of any region on the Earth. Despite the greatly reduced growing season precipitation in comparison with eastern Asia, most of the windward part of the Pacific Coast States from the northern Sierra Nevada north to Alaska can be classed as humid, even in dry years (Visher, 1966). This region can therefore provide information for interpreting physiognomic changes in relation to temperature changes in dominantly coniferous forests. As well, western North America has some broad-leaved forests, although none are dominantly deciduous.

Temperature data are numerous in western North America (pl. 3), although data for montane areas are, as usual, not as numerous as for lowland. All the data are from various publications of the National Oceanic and Atmospheric Administration.

BROAD-LEAVED FORESTS

Most of the broad-leaved vegetation of western North America appears in California as oak woodlands (Munz and Keck, 1950; Griffin and Critchfield, 1972). Temperature data (pl. 3) for stations in these woodlands indicate that the woodlands occupy the same temperatures as the Notophyllous Broad-leaved Evergreen forest of eastern Asia ("oak-laurel forest"). The oaks occurring in these woodlands include both evergreen and deciduous species.

On more mesic sites, the oak woodlands give way to what has been termed the Mixed Evergreen forest (Munz and Keck, 1950). This forest is dominated by notophyllous species of broad-leaved evergreens (for example, tanoak and California-laurel) but has some admixtures of conifers. The Mixed Evergreen forest of California could readily be classed with the Notophyllous Broad-leaved Evergreen forest of eastern Asia. As in eastern Asia, this forest or the derived woodland in western North America contains an "arcto-tertiary" element: *Aesculus, Cercis, Crataegus, Juglans, Ptelea, Staphylea, Styrax,* and *Vitis.*

Griffin and Critchfield (1972) note that in some areas of the southern Coast Ranges Coulter pine is a minor element in their Mixed Evergreen forest. In the Sierra Nevada, in areas altitudinally above the oak woodlands or the Mixed Evergreen forest (for example, near Placerville), conifers similarly play an increasingly important role, as they do in the Mixed Broad-leaved Evergreen and Coniferous forest of eastern Asia. All the stations that apply to Coulter pine, for example, have temperature parameters within the Mixed Broad-leaved Evergreen and Coniferous forest. In Oregon some of the stations (for example, Medford and Ashland) within the Interior valley zone of Franklin and Dyrness (1969) have a mixture of broad-leaved evergreens and some conifers, as well as broad-leaved deciduous trees.

Küchler (1946) was puzzled by the disappearance of broad-leaved deciduous forests from western North America. Except in isolated, small interior valleys (for example, Canyon City and Yreka), temperature parameters suitable for such forests are lacking in the Pacific Coast States. The lowered temperatures during glacial intervals must have had a profound effect on eliminating any surviving patches of broad-leaved deciduous forest in western North America.

CONIFEROUS FORESTS

MIXED CONIFEROUS FOREST

The subdivisions that have been previously proposed for the Mixed Coniferous forest in western North America have been based primarily on the dominance of one or two species (for example, Franklin and Dyrness, 1969; see pl. 3). The physiognomy of the various dominant conifers is, of course, monotonous, and it is in the broad-leaved adjuncts to the coniferous forest that physiognomic differences appear and allow subdivisions to be made. As noted below, some of these subdivisions apparently correspond very well with some of Franklin and Dyrness' (1969) phytosociological groupings (table 2).

LOW MONTANE MIXED CONIFEROUS FOREST

The Mixed Conifer forest of Griffin and Critchfield (1972) (pl.3) was defined on the basis of the admixture of several coniferous species, which occur together at middle altitudes in the Sierra Nevada and Cascade Range of California. This conifer forest occupies areas that have approximately the same temperature regime as the Mixed Coniferous forest in Szechuan (pl.2). As in Szechuan, the forest in California is dominantly coniferous but with some broad-leaved trees.

Both the Mixed Conifer forest and the *Tsuga heterophylla* zone (p. 3; table 2) represent the same basic physiognomic unit, which is here termed the Low Montane Mixed Coniferous forest. Although dominated typically by a closed canopy of high conifers, the forest includes a diverse woody broad-leaved element, both evergreen and deciduous. In terms of diversity, the broad-leaved element is far greater than the coniferous element, and quadrat studies (table 3) indicate that the broad-leaved plants are about four times as diverse as the conifers. Conifers typical of the Low Montane Mixed Coniferous forest include: *Pseudotsuga menziesii, Tsuga heterophylla, Pinus lambertiana, Thuja plicata, Abies concolor.* Broad-leaved trees and

TABLE 2.—*Comparison of proposed classification of coniferous forests with some previous classifications for the western United States*

This report	Munz and Keck (1950),Griffin and Critchfield (1972)	Franklin and Dyrness (1969)	Küchler (1967a)
Low Coastal Mixed Coniferous forest.	North Coastal Coniferous forest.	*Picea sitchensis* zone.	Spruce-cedar-hemlock forest.
High Coastal Mixed Coniferous forest.	Subalpine and Lodgepole forests.	*Tsuga mertensiana* zone.	Fir-hemlock and Lodgepole pine-subalpine forests.
Low Montane Mixed Coniferous forest.	Mixed Conifer, Redwood, and Douglas-fir forests.	*Abies concolor* and *Tsuga heterophylla* zones.	Cedar-hemlock-fir. Mixed conifer, Douglas fir.
High Montane Mixed Coniferous forest.	Red Fir forest	*Abies grandis* zone	Silver fir-Douglas fir, Red fir, and Grand fir-Douglas fir forests.
Taiga	Bristlecone Pine forest.		

shrubs are evergreen *(Arbutus, Quercus, Lithocarpus, Castanopsis, Umbellularia, Garrya)* or deciduous *(Acer, Cornus, Rhamnus, Quercus, Fraxinus, Alnus)*. The lowest shrubby groundcover, when present, is typically broad-leaved evergreen *(Gaultheria, Mahonia, Ceanothus, Arctostaphylos)*.

In California, the Mixed Conifer forest of the southern part of the Coast Ranges is shown on plate 3 as including temperatures typical of the Mixed Broad-leaved Evergreen and Coniferous forest of eastern Asia. California stations such as Cuyamaca (alt. 1,417 m) are in fact located in areas in which the vegetation is a mosaic of broad-leaved evergreen and coniferous trees (pl. 3) (Critchfield, 1971, p. 33).

In central California, other stations (for example, Mount Hamilton, Hetch Hetchy, Yosemite National Park) are also within temperatures typical for the Mixed Broad-leaved Evergreen and Coniferous forest of eastern Asia. The vegetation near these stations is in fact a strong mixture of broad-leaved and coniferous trees (Critchfield, 1971, p. 27, 36). This vegetation is physiognomically Mixed Broad-leaved Evergreen and Coniferous forest. One floristic feature of this vegetation is that white fir *(Abies concolor)* is absent, but white fir is present in the adjacent Mixed Coniferous forest.

Franklin and Dyrness' (1969) *Tsuga heterophylla* zone in the Pacific Northwest occupies approximately the same part of the temperature spectrum as the Mixed Conifer forest of Griffin and Critchfield in California. *Tsuga heterophylla* itself has a very limited distribution in California and is confined to moderate altitudes in the coastal region of northernmost California where precipitation is high. In northwestern North America the *Tsuga heterophylla* zone, except in southwestern Oregon, lacks most of the broad-leaved evergreen adjuncts that are typical of the Mixed Conifer forest of California. As discussed elsewhere (p. 34), the lack of these broad-leaved evergreens in the Pacific Northwest may be primarily a function of light conditions at more northerly latitudes.

The Interior Valley zone of Franklin and Dyrness (1969) (pl. 3), as they emphasized, contains divergent vegetational types in Oregon. In the Willamette Valley (stations such as Portland, Salem, Eugene), the oak-dominated vegetation is thought to be subclimax and will eventually be replaced by a climax forest of conifers. This concept is consistent with the temperature parameters for these stations. Although data are sparse, in the Umpqua Valley (a station such as Roseburg) also the climax is thought to be coniferous, again consistent with the temperature data. In the Rogue River valley (stations such as Medford, Ashland, Grants Pass), data are few, but apparently the climax is a mixed forest of conifers and broad-leaved trees (and possibly chaparral on some sites). The possible climax in the Rogue River valley would be consistent with the temperature parameters, which are suitable for a Mixed Broad-leaved Evergreen and Coniferous forest.

The redwood forest, particularly in the northern third of California, has a crown distinctly higher than that of Low Montane Mixed Coniferous forest; because of this distinction, the redwood forest could be recognized as a distinct physiognomic type. In the southern areas of the distribution of redwood, however, the forest has a physiognomy more characteristic of normal Low Montane Mixed Coniferous forest, with admixtures of small broad-leaved evergreen and deciduous trees. The redwood forest is therefore considered a variant of Low Montane Mixed Coniferous forest.

The temperature parameters of the redwood forest appear to be anomalously high in regard to mean annual temperature for Mixed Coniferous forest in eastern Asia. This anomaly is, however, probably an artifact of the meteorological stations being in clearings rather than in the forest proper. That is, the conditions in the forest proper are probably cooler than in adjacent clearings in the forest.

Redwood forest (pl. 3) appears to be limited, in part, by a cold month mean of about 7°C and by a warm month mean of about 15°C. Numerous workers have suggested that the absence of coastal fogs and their attendant moisture limit the distribution of redwood, but this may be only grossly coincidental. Redwood, for example, does not typically extend to the coast, where fog is abundant but the summer temperatures are low. Fog is not a notable feature of the climate at stations such as Ben Lomond, where redwood thrives, but fog is prevalent on the windward side of the Coast Ranges of northern California altitudinally well above the upper limit of redwood. Although fog may contribute to the high moisture regime in which redwood thrives, fog itself is not a limiting factor on the distribution of redwood.

The Closed-cone Pine forest of Munz and Keck (1950) (pl. 3) in California is not a satisfactory physiognomic unit. This forest is rather composed of "disjunct stands of closely related closed-cone pines and closed-cone cypresses" (Griffin and Critchfield, 1972, p. 9). Throughout much of its range, Closed-cone Pine forest has a lower tree story of broad-leaved evergreens. The Closed-cone Pine forest would probably be best classified as a variant of Mixed Coniferous forest.

Some of the stations plotted (for example, Betteravia, Pismo Beach, Lompoc, Santa Maria) are altitudinally below the Closed-cone Pine forest. Even the data for Monterey were collected below the forest. The closed-cone pines are not successfully cultivated in the

Pacific Northwest, apparently because of the low temperatures. The limiting factor on the natural distribution of these pines may prove to approximate a cold month mean of about 8°C.

HIGH MONTANE MIXED CONIFEROUS FOREST

Griffin and Critchfield (1972) suggest that the Red Fir forest of California (pl. 3) is not readily separable from their Mixed Conifer forest (= Low Montane Mixed Coniferous forest). As they note, both forests are characterized by tall conifers. As shown in plate 3, the two forest types have a common boundary that approximately coincides with a cold month mean of −2°C. A similar boundary-temperature relation is shown in northwestern North America (pl. 3) by the *Tsuga heterophylla* zone (= Low Montane Mixed Coniferous forest) and the *Abies grandis* zone of Franklin and Dyrness (1969).

In the broad-leaved forests of eastern Asia, the −2°C cold month isotherm approximately demarcates forests that contain some notophyllous broad-leaved evergreens from forests that lack these evergreens. A similar relation is apparent in transects in the Sierra Nevada (J. A. Wolfe, unpub. data; see also Critchfield, 1971); there, the Red Fir forest lacks notophyllous broad-leaved evergreens (some microphylls, for example *Quercus vaccinifolia,* may be present) in contrast to their presence in the lower altitude coniferous forest. The primary distinction between the Mixed Conifer forest of Griffin and Critchfield (1972) and the Red Fir forest is in the lack of notophyllous broad-leaved evergreens in the Red Fir forest. Coniferous forests in Hokkaido, which occupy the same temperature spectrum as the Red Fir forest, also lack notophyllous broad-leaved evergreens. Such physiognomic differences are fundamental and merit the recognition of the Red Fir forest (and its temperature analog in Hokkaido) as the High Montane Mixed Coniferous forest.

The Northern hardwoods-spruce forest of Küchler (1967a) of northeastern United States and adjacent Canada, as well as other related "forests" (for example, those with large amounts of *Tsuga* and *Abies*), occupy areas that have approximately the same major temperature parameters as the areas occupied by the High Montane Mixed Coniferous forest of western North America. This vegetation in eastern North America, however, has a higher proportion and diversity of broad-leaved trees than in western North America, where, except for two species of *Populus,* the broad-leaved woody plants are almost exclusively shrubby. In eastern North America, the coniferous forest contains species of *Populus, Quercus, Fagus, Ulmus, Betula, Ostrya, Acer, Tilia,* and *Fraxinus.* Most of these genera are represented in the conifer forest of northeastern China and Hokkaido areas (Wang, 1961, p. 39). I suggest that the poor representation of broad-leaved trees in the High Montane Mixed Coniferous forest in western North America is the result of historical factors: in both eastern Asia and eastern North America, the conifer forest is contiguous with large areas of climate favorable to broad-leaved deciduous forest, and this relation has prevailed in these areas throughout the Neogene. In western North America, in contrast, temperatures favorable to the development of broad-leaved deciduous forest disappeared in the mesic areas about 8 to 10 million years ago, so there has been no ready source for broad-leaved deciduous trees.

Dry stations in forested areas to the east of the crest of the southern part of the Sierra Nevada of California have generally not been included on plate 3. Stations at lower altitudes have temperatures as in the Low Montane Mixed Coniferous forest; the vegetation in such areas is typically dominated by yellow pine *(Pinus ponderosa).* At higher altitudes, where temperatures are as in the High Montane Mixed Coniferous forest, the vegetation is typically dominated by limber pine *(P. flexilis).*

LOW COASTAL MIXED CONIFEROUS FOREST

The coastal region of northernmost California, the Pacific Northwest, British Columbia, and southern Alaska is occupied by a forest that has been termed the *Picea sitchensis* zone (pl. 3; table 2) (Franklin and Dyrness, 1969) or the Spruce-cedar-hemlock forest (table 2) (Küchler, 1967a). Although broad-leaved trees and shrubs are present in this forest, they are of very low diversity. Small-scale range maps typically show many species of broad-leaved plants extending to the coast in the Pacific Northwest, but detailed range maps (for example, Griffin and Critchfield, 1972) for northern California show that many species of broad-leaved trees are actually not found within a few kilometers of the coast. The broad-leaved trees and shrubs that occur in this vegetation include both notophyllous evergreen (*Arbutus, Rhododendron*) and deciduous (*Acer, Alnus*) types. Because broad-leaved trees and shrubs are greatly reduced both in diversity and abundance in this vegetational type relative to the Low Montane Mixed Coniferous forest, this coastal forest is recognized as a distinct unit under the term Low Coastal Mixed Coniferous forest.

Notophyllous broad-leaved evergreen trees and shrubs (except for *Gaultheria*) are not known in the Low Coastal Mixed Coniferous forest north of southern British Columbia. As discussed below, the general absence of the notophyllous evergreens to the north is almost certainly a function of the light factor.

Quadrat studies in the lower part of the Smith River valley (Whitaker, unpub. data) and the adjacent Siskiyou Mountains (Wolfe and Schorn, unpub. data) of northernmost California indicate both (1) the physiognomic differences between the Low Coastal Mixed Coniferous forest and contiguous forest types (table 3) and (2) the fact that in a temperature regime similar to that at high-latitude localities, notophyllous broad-leaved evergreens occur in Low Coastal Mixed Coniferous forest. Although no temperature data are available from sites near the quadrats, the temperatures can be estimated from Elk River about 10 km from Whitaker's quadrats and about 70 m higher. The Smith River quadrats are clearly Low Montane Mixed Coniferous forest. In the classification of vegetation suggested here, the forest above Smith River is expected to be Low Coastal Mixed Coniferous forest and, even higher, High Coastal Mixed Coniferous forest.

The Low Montane Mixed Coniferous forest, as noted above, is a dominantly coniferous forest that has a significant element of broad-leaved deciduous and notophyllous evergreen trees and shrubs (table 3). In the lowest quadrats along Smith River, the conifers are dominant in terms of coverage, but in terms of species the broad-leaved are dominant by about 5:1. The next highest quadrats at about 1,000 m and extending up to just under 1,500 m on the Middle Fork of the Smith River also represent coniferous forest and have many of the species (including notophyllous broad-leaves) that occur in the Smith River quadrats. This higher vegetation, however, differs markedly in that conifers have a significantly higher coverage (approaching 100 percent) in the canopy, and in terms of species the broad leaves are only slightly more diverse than the conifers. The vegetation of these quadrats between 1,000 and 1,500 m is Low Coastal Mixed Coniferous forest. This vegetation, moreover, contains several notophyllous broad-leaved evergreens (*Arbutus, Castanopsis, Lithocarpus, Umbellularia*), despite the fact that the mean of the cold month is probably lower than in areas of southeastern Alaska where notophyllous broad-leaved evergreens are not native.

At about 1,500 m and higher near Sanger Lake and on Youngs Peak (Siskiyou Mountains), the notophyllous broad-leaved evergreens disappear (microphyllous species such as *Quercus vaccinifolia* and *Mahonia pumila* extend higher). These highest forests are dominated by *Abies procera* and *Picea breweriana*, but other conifers occur: *Abies concolor, Pinus jeffreyi, P. monticola, Calocedrus decurrens,* and *Tsuga mertensiana*. All the woody broad-leaved plants are shrubs. This vegetation is discussed immediately below.

TABLE 3.—*Comparison of physiognomy of vegetation in quadrats in northernmost California*

Location	Smith River	Middle Fork Smith River	Sanger Lake and Youngs Peak, Siskiyou Mountains
Vegetational classification	Low Montane Mixed Coniferous forest	Low Coastal Mixed Coniferous forest	High Coastal Mixed Coniferous forest
Altitude (m)	335–455	1,005–1,465	1,495–1,770
Number quadrats	6	10	8
Conifers:			
Percent basal area	79	99+	100
Number species	4	10	8
Number species/quadrat	2	5	5
Broad-leaved evergreen:			
Percent basal area	18	>1	0
Number species	10	9	2
Number species/quadrat	6	4	.5
Broad-leaved deciduous:			
Percent basal area	3	0	0
Number species	10	12	11
Number species/quadrat	5	3	3

HIGH COASTAL MIXED CONIFEROUS FOREST

Franklin and Dyrness (1969) segregated a zone dominated by *Tsuga mertensiana* in the Pacific Northwest. As Griffin and Critchfield (1972) noted, this zone appears to be the analog of Munz and Keck's (1950) Subalpine forest in California. The data presented in table 3 indicate that this vegetation is a dominantly coniferous forest that has broad-leaved deciduous or microphyllous evergreen shrubs. The vegetation is here termed the High Coastal Mixed Coniferous forest because the greatest expanse of this forest is present in the coastal area of southern Alaska.

In both eastern Asia and eastern North America, the High Montane Mixed Coniferous forest has a number of broad-leaved deciduous tree genera as adjuncts, including *Quercus, Fagus,* and *Ulmus* (p. 21). In eastern North America (for example, on Newfoundland), the broad-leaved deciduous trees typically disappear except for some species of *Betula* and *Populus,* and the temperature parameters on Newfoundland are approximately the same as those at localities in the High Coastal Mixed Coniferous forest in western North America.

TAIGA

Taiga has been uniformly recognized as the Alaskan and northern Canadian forest typically dominated by *Picea glauca* and (or) *P. mariana*. In structure, this forest conforms closely with Taiga in Asia, with a single tree stratum and shrubs typically few. In coastal southern Alaska, one area near Valdez has a forest that is typically considered to be *Picea sitchensis* zone (that is, Mixed Coniferous forest) rather than Taiga, although the mean annual temperature indicates a climate similar to that of Taiga. This vegetational assignment, however, is based more on the fact that the forest near Valdez is dominated by *Picea sitchensis* rather than the Taiga spruces. Whether the forest near Valdez is physiognomically more similar to Taiga than to Mixed Coniferous forest is not known.

Taiga is probably found on high mountains of British Columbia and conterminous United States. Franklin and Dyrness' summaries (1969) indicate that on some mountains the coniferous forest becomes depauperate near timberline, where the forest is composed of a single species of conifer (although the species differs from one area to another) and almost no shrubby growth in the forest. In California, however, Taiga-like vegetation is formed by pure stands of *Pinus contorta, P. albicaulis,* or, east of the southern part of the Sierra Nevada, *P. aristata.* Such vegetation was included by Griffin and Critchfield (1972) in Subalpine forest. In other words, in areas isolated from the bulk of the Taiga, a Taiga-like climate produces a forest that is physiognomically Taiga but differs floristically from the bulk of the forest. Indeed, the primary Taiga spruces of the Holocene are known to occur abundantly in Mixed Coniferous forest in the Pliocene of Alaska (Hopkins and others, 1971). This again emphasizes that floristic composition may not be a valid basis for segregating one vegetational type from another.

COMPARISON TO EASTERN ASIA

The profiles of altitudinal distribution of forest belts in China given by Wang (1961, figs. 23–25) support the delineation of coniferous forests proposed here. In Szechuan, for example, the descending order of vegetational types is:

Wang (1961)	*This report (fig. 1)*
Coniferous forest of *Abies* and *Tsuga.*	High Coastal Mixed Coniferous forest.
Deciduous and coniferous forest	Low Montane Mixed Coniferous forest.
Evergreen and deciduous broad-leaved forest and coniferous trees.	Mixed Broad-leaved Evergreen and Coniferous forest.
Evergreen broad-leaved forest	Notophyllous Broad-leaved Evergreen forest.

In Shensi, the descending order is:

Wang (1961)	*This report (fig. 1)*
Larix forest	Taiga.
Coniferous forest mixed with deciduous trees (*Picea-Abies* forest).	High Montane Mixed Coniferous forest.
Mixed deciduous and coniferous forest.	Mixed Northern Hardwood forest.
Deciduous forest	Mixed Broad-leaved Deciduous forest.

On Taiwan, the zonation is:

Wang *(1961)*; *Li (1963)*	*This report (fig. 1)*
Abies-Picea forest	Low Coastal Mixed Coniferous forest.
Coniferous forest (*Chamaecyparis*) with evergreen and deciduous broad-leaved trees.	Low Montane Mixed Coniferous forest.
Lower part of above with woody climbers and epiphytes.	Microphyllous Broad-leaved Evergreen forest.
Oak and laurel forest	Notophyllous Broad-leaved Evergreen forest.

In Japan, as noted above, the coniferous forest of Hokkaido is accompanied by broad-leaved deciduous or microphyllous broad-leaved evergreen adjuncts, and the broad-leaved deciduous trees and shrubs are diverse. This vegetation is thereby High Montane Mixed Coniferous forest.

FORESTS OF EASTERN NORTH AMERICA, THE CARIBBEAN, CENTRAL AMERICA, AND NORTHERN SOUTH AMERICA

Considerable confusion exists in the classification of forests in the Caribbean area (pl. 3). Lauer (1959) and Knapp (1965) recognize a broad-leaved evergreen lowland forest and a montane rain or cloud forest; Lauer (1959) suggests that the boundary between the two forests coincides with a mean annual temperature of 22°C. Knapp (1965) generally follows the treatment of Lauer (1959), considering the forest near Xilitla, Mexico, to represent the montane rain forest of the Tierra Templada. Rzedowski (1963), however, has demonstrated that the forest near Xilitla is physiognomically as well as floristically allied to the lowland rain forest (his tropical evergreen forest) of southern Mexico; Rzedowski apparently did not distinguish a forest with two closed-tree strata (such as that near Xilitla) from the three-layered forest characteristic of what is considered as Tropical Rain forest in this report. Consequently, the temperature data from Xilitla (pl. 3)) apply to Paratropical Rain forest. Rzedowski makes the distinction between the rain forest (= Tropical and Paratropical) and the montane broad-leaved sclerophyllous forest of the Tierra Templada and suggests that the two are delimited approximately by a mean annual temperature of 20°C. This temperature boundary is not supported by much the climatic data from the Americas but finds strong support in the Asian data.

Perhaps the most exhaustive treatment of the classification of primarily lowland vegetation in the Caribbean region is that of Beard (1944). Some of the units Beard recognizes are, as he suggests, produced by seasonality of precipitation. Critical to this discussion is Beard's Lower Montane forest, which Richards (1952) has subsequently included in his Tropical Rain forest (pl. 3). From Beard's description, the Lower Montane Rain forest is fundamentally two storied but is otherwise similar to Tropical Rain forest in structure; the Lower Montane Rain forest is therefore probably Paratropical Rain forest of this report. Above the

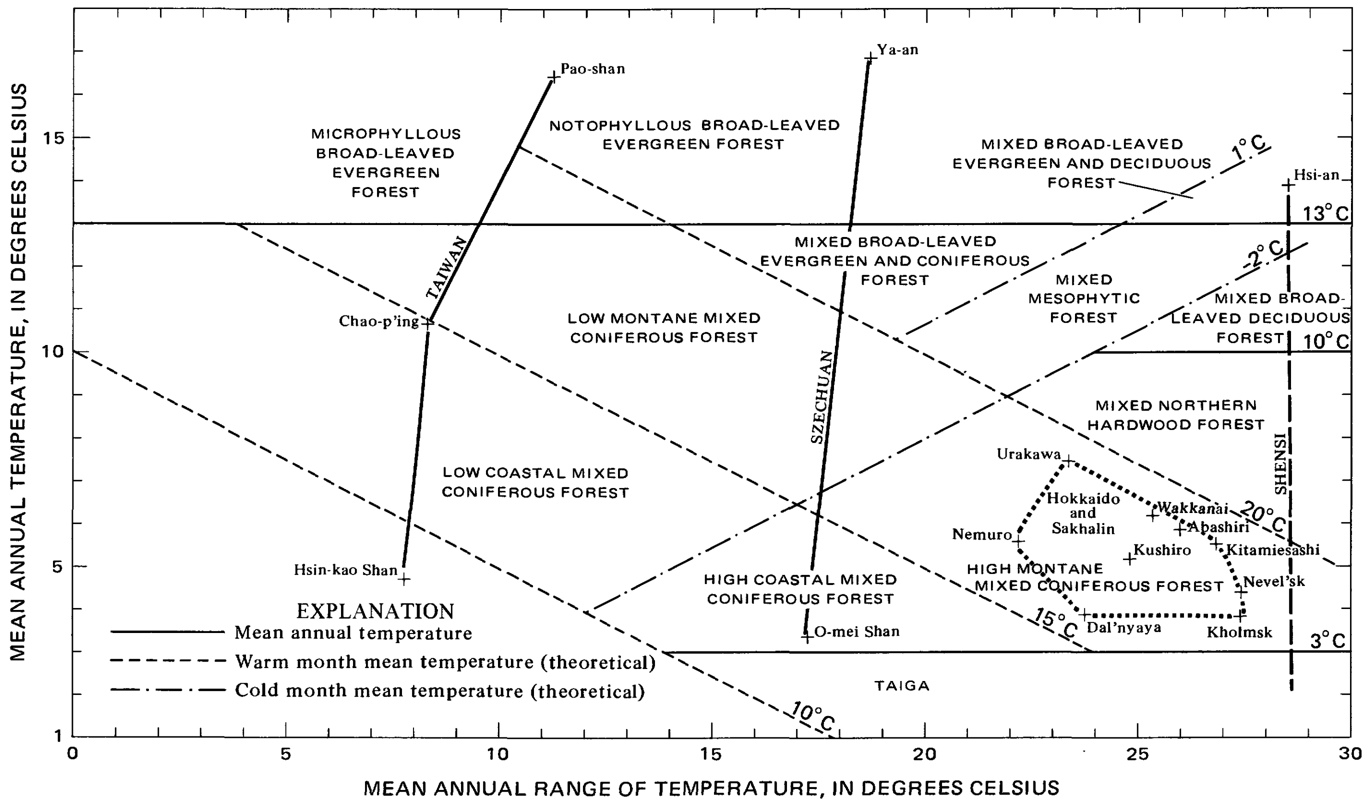

FIGURE 1.—Vegetational classification of the coniferous forests in parts of eastern Asia. Stations from plate 2; dashed lines indicate inferred temperatures; dotted line indicates temperature parameters around Hoikkaido and Sakhalin.

Lower Montane Rain forest is Beard's Montane Rain forest, presumably the same unit as Rzedowski (1963) recognizes above Xilitla. Like Rzedowski, Beard suggests that a mean annual temperature of about 20°C delimits the Lower Montane and Montane Rain forests.

The temperature parameters that delimit Tropical from Paratropical Rain forest in Central America and South America are not clear, largely because of the lack of physiognomic vegetation maps and climatic data. The Paratropical Rain forest on Trinidad (Beard's Lower Montane Rain forest) occurs about 30 m above the lowlands, where the mean annual temperature is about 25°C. Along the southern Brazilian coast, the emergent stratum (composed in part of *Hymenaea corbaril*) of the Tropical Rain forest disappears north of the latitude of Rio de Janiero, where mean annual temperature is 25–26°C. Tropical Rain forest there approaches a mean annual temperature of 25°C (for example, at Uaupes, Brazil) and Paratropical Rain forest approaches the same value (for example, the forests above Piarco, Trinidad).

The studies of Cain and others (1956) indicate that the distinction between Tropical and Paratropical Rain forests can also be made on a purely structural basis in South America. The Amazonian rain forest is unquestionably Tropical Rain forest. The main canopy is about 35 m high, with an emergent stratum extending about 10 m higher; two lower tree strata, one at 15–20 m and a second at 5–8 m, are recognizable. This forest has three closed stories plus an emergent stratum. Temperature data for the lowland Amazonian basin indicate a mean annual temperature above 25°C. At lat 26° S., the rain forest is of lower stature, and Cain and others (1956) note that probably only a few species would be megaphanerophytes (that is, would be sufficiently large to appear as emergents). Lianes are diverse and abundant in this rain forest, and the leaf size is dominantly mesophyllous (Cain and others, 1956, did not distinguish a notophyll size). This rain forest apparently fits the characteristics of Paratropical Rain forest. The mean annual temperature in this area of rain forest is about 20° to 22°C. Farther south at lat 32° S., the rain forest is of even shorter stature, and the leaf size is dominantly microphyllous. This type forest would be assignable to Microphyllous Broad-leaved Evergreen forest, and indeed the temperature parameters from a station somewhat farther south indicate that this forest should be microphyllous. Not recognized by Cain, Castro, Pires, and Da Silva (1956) is Notophyllous Broad-leaved Evergreen forest, but presumably this would be intermediate latitudinally between their two most southerly areas investigated.

The Holdridge (1947) system of vegetation classification has been extensively applied to the vegetation of Central America, particularly by Holdridge and coworkers (for example, Holdridge and others, 1971). From the descriptions of the physiognomies of the units recognized, the following are suggested as equivalents:

Holdridge and others (1971)	*This report*
Tropical Moist and Wet Forests	Tropical Rain forest.
Premontane Moist and Wet Forests	Paratropical Rain forest.
Tropical Lower Montane Moist and Wet Forests.	Microphyllous Broad-leaved Evergreen Forest.
Tropical Montane Rain Forest	Montane Rain Forest.

The meager (nine stations) temperature data given by Holdridge and others (1971) would suggest that the Tropical Moist Forest lives under mean annual temperatures as low as 22.4° and 23.6°C (Turralba-IICA and Quebrada Grande, respectively). The weather station at Quebrada Grande is at a higher altitude and some 25 km distant from the sites described. The Turralba station does apply to the site described (Holdridge and others, 1971), but there is considerable doubt as to whether the vegetation at this site is Tropical or Paratropical Rain forest. The vegetation here was interpreted as four storied, but "The separation of the lower-middle and lower level was not definite, and possibly these formed one stratum***" (Holdridge and others, 1971, p. 177). Further, the discontinuity described for the upper canopy could be readily interpreted as the emergent stratum above two closed canopies.

The data from the station at Turralba place this site in the Premontane zone of Holdridge and others (1971, fig. 8, p. 41). If the forest at Turralba is in fact Tropical Moist forest, then the data are anomalous in either Holdridge's system or the system proposed in this report.

The Holdridge system has yet to be applied to physiognomy of vegetation in humid to mesic forested regions outside Central America. Whether this system obtains on a worldwide scale has yet to be determined. Indeed, one of the fundamental concepts of the Holdridge system is that of biotemperature, and, as Holdridge and others (1971, p. 41) noted, the data from which biotemperatures must be calculated are rarely available.

One parameter of the Holdridge system that merits discussion is the so-called frostline or critical temperature line, which divides the premontane from the lower montane forests. Although Holdridge and others (1971, p. 13–14) state that this line has no significance for species diversity, their data contradict this statement. Average species diversity is clearly lower in the lower montane forests than in the premontane forests, as might be expected, because the lower montane forests typically have one less tree stratum than the premontane forests. The same factor probably results in lower diversity in the premontane forests relative to the tropical forests.

The subdivisions of the northern Andean forests by Cuatrecasas (1957) appear to be based on both physiognomic and floristic criteria. The Neotropical Rain Forest of Cuatrecasas (1957) is apparently a combination of the Tropical and Paratropical Rain forests. His (1957) Subandean Rain Forest apparently corresponds to the Microphyllous Broad-leaved Evergreen forest. Whether Notophyllus Broad-leaved Evergreen forest is represented is unknown; this vegetational type, floristically difficult to distinguish from adjacent units, would be confined to very narrow altitudinal limits in the northern Andes. Coniferous forests appear to be absent in the northern Andes (although these are present in Central America according to Holdridge, 1957). It is possible that the Andean Rain Forest of Cuatrecasas (1957), which is composed of broad-leaved evergreens, occupies the Mixed Coniferous forest temperatures because of a deficiency of light in the almost continuously mist-shrouded northern Andes. By this criterion, the Subandean Forest of Cuatrecasas (1957) is Montane Rain forest of various authors.

The sclerophyllous oak forests of the Tierra Templada (variously termed "Cloud forest," "Montane forest") are structurally the same forest as the Notophyllous Broad-leaved Evergreen forest of Asia. The forest in Mexico is two storied, dominantly broad-leaved evergreen, and has woody climbers. In leaf size, the species are dominantly notophyllous (Martin and others, 1962). Computation from lists given by Miranda and Sharp (1950) indicate that the percentage of entire-margined leaves is between 40 and 55 percent for various areas in the forest. The mixture of broad-leaved deciduous "arcto-tertiary" trees and shrubs, including *Liquidambar,* is not anomalous as some have thought (Hernandez and others, 1951); in eastern Asia, the notophyllous forest has representatives of many "arcto-tertiary" genera, and *Liquidambar* is more typical of the Notophyllous Broad-leaved Evergreen forest than of the broad-leaved deciduous forests.

The anomalous situation in eastern North America is not the mixture of broad-leaved evergreen and deciduous trees in upland Mexico but is rather in the almost exclusively broad-leaved deciduous (in some instances pines are dominants) forests of eastern United States. In eastern Asia, western North America, and southern Europe, areas that have major temperature parameters similar to those of the bulk of southeastern North America have dominantly broad-leaved evergreen forest or woodland. Eastern North America, unlike these areas comparatively shielded by mountain chains, is subjected to continuing, intense cold waves from the Arctic. Thus, despite the fact that the Potomac River floodplain has about the same cold month mean as the Kanto Plain of Japan, the absolute lows that can be expected in Washington, D.C., are lower than those that can be expected in Tokyo. It is probably this factor of prolonged cold spells in eastern United States that accounts for the existence there of broad-leaved deciduous forests rather than broad-leaved evergreen forests. Indeed, from available records, Washington, D.C., has recorded lower temperatures than many stations in the Mixed Mesophytic forest in Asia.

Until development of extensive ice sheets and an ice-covered Arctic Ocean in the late Cenozoic, cold waves from the Arctic probably would not have been as intense as at present. If this probability is valid, then it follows that Notophyllous Broad-leaved Evergreen forest occupied much of southeastern North America during the middle Cenozoic. Indeed, the flora of the Brandon lignitic beds of Vermont (Traverse, 1955) may well represent this forest, dominated by pollen of probable broad-leaved evergreens (*Cyrilla,* Sapotaceae); a subdominant, though diverse, element is probable broad-leaved deciduous *(Carya, Fagus, Liquidambar).*

The development of many of the broad-leaved deciduous forests in southeastern North America probably involves the gradual elimination of broad-leaved evergreens during the late Cenozoic, leaving the broad-leaved deciduous element, formerly subordinate, as dominant. By analogy, the secondary forest in the Notophyllous Broad-leaved Evergreen forest of Asia is composed primarily of broad-leaved deciduous trees along with pines. In this sense, the climax forests of much of eastern North America are, when discussed in terms of geologic history and vegetation in other areas of the world, secondary in nature. Certainly these forests are of little value in interpreting the vegetation of the Cenozoic prior to the development of intensive cold waves emanating from the Arctic.

Not only is the overall physiognomy of the vegetation of eastern United States not that typical for the major climatic parameters, but even detailed features are atypical. Only about 25 percent of the species in the flora of Washington, D.C., have entire-margined leaves; in areas of similar temperature parameters in eastern Asia, the proportion is about 40 percent. In Bailey and Sinnott's (1915, 1916) original compilation of leaf-margin percentages, the values obtained for eastern United States were thought to be directly applicable to fossil assemblages. It is clear, however, that figures based on what is basically secondary vegetation have little, if any, relevancy to interpretations of fossil assemblages.

Edaphic factors complicate the vegetational picture in eastern North America. For example, Braun's (1947) and Küchler's (1967a) Mixed Mesophytic forest is restricted to moist inceptisols. On the Atlantic Coastal Plain, where highly similar if not identical climates occur but inceptisols do not, the forest is classed as oak-pine.

The use of the term "Mixed Mesophytic forest" for Asian vegetation is in one sense unjustified. This term is applied in eastern North America to forests occupying the plateau country west of the Appalachian Mountains (see Küchler, 1967a). These forests are characterized by being dominantly broad-leaved deciduous with a minor element of conifers, primarily *Tsuga.* Broad-leaved evergreens are extremely minor and are not present in the tree stratum. In contrast, the Mixed Mesophytic forest of Asia (Wang, 1961), though similarly characterized by the dominance of broad-leaved deciduous trees, has a strong admixture of broad-leaved evergreen trees (Fagaceae, Lauraceae) and a diverse coniferous element. Physiognomically, then, the Mixed Mesophytic forest of Asia is not the same as the Mixed Mesophytic forest of eastern North America. The lack of broad-leaved evergreen trees in the American forest is almost certainly a function of the same factor as the lack of dominance of these trees in southeastern North America: the lesser diversity of broad-leaved deciduous trees and conifers in the American relative to the Asian forest can be attributed to the fact that the temperature parameters occupied by the American forest are unfavorable to most trees of these elements.

The fact that the American and Asian Mixed Mesophytic forests occupy different temperature parameters and that the two forests are not physiognomic analogs should make doubtful the widely accepted theory that the two forests are the lineal descendants of the same widespread, early Tertiary forest ("Arcto-Tertiary Geoflora") that purportedly occupied high latitudes. This is clearly impossible, for the lineages of the American and the Asian forest have had to adapt to different temperature parameters. It is not surprising, therefore, that extensive paleobotnical data indicate that the overall concept of an "Arcto-Tertiary Geoflora" is invalid (Wolfe, 1969a, 1972).

FORESTS OF EUROPE

In Europe, three major categories of forests are typically recognized: Mediterranean woodlands, Mid-latitude mixed forests (that is, broad-leaved deciduous forests typically dominated by oak and (or) beech), and boreal forest or Taiga (pl. 3). Physiognomically, the boreal forest is clearly the equivalent of the Taiga of Siberia and northern North America. Similarly, the Mediterranean woodlands are analogous to the dominantly broad-leaved evergreen Notophyllous Broad-leaved Evergreen forest of eastern Asia and the California woodlands. The Mid-latitude mixed forests, which are placed in the "nemoral zone" by some workers, appear as anomalies in the Northern Hemisphere.

In areas of the same temperature regimes as the nemoral zone of Europe (pl. 3), the forests are preponderantly coniferous. This is true in eastern Asia (compare Berlin to K'ang-ting; pl. 2, 3) and eastern North America (compare Duedde, Denmark, to Sable Island, Canada; pl. 3), where the regions receive more summer precipitation than in Europe, as well as in western North America (compare Berlin to Parkdale, Oreg.; pl. 3), where the region receives less summer precipitation than in Europe. Clearly, no present temperature or precipitation factor (or combinations of both) is responsible for the development of broad-leaved deciduous forest in much of Europe.

The vegetation preceding continental glaciation of the Quaternary in northern and central Europe was dominantly coniferous (Thomson, 1948; Szafer, 1954) as evident in pollen spectra. The same conclusion can be derived by the great diversity (16 genera, more than 30 species) of conifers, including many species of *Abies, Picea,* and *Tsuga,* in the megafossil assemblages. This forest had a number of broad-leaved adjuncts now restricted to eastern Asia, and many of these do occur as adjuncts to the Mixed Coniferous forest. In other areas of the world, the vegetation immediately preceding glacial advances was similar to the present vegetation in the same area; Europe appears to be the major exception. Not only is the present vegetation of Europe anomalous in terms of major temperature parameters, the vegetation is anomalous relative to preglacial vegetation.

If European interglacial pollen profiles and megafossil assemblages are perused (for example, Szafer, 1954), the decline of the Mixed Coniferous forest is clearly seen. Taking the known records, each succeeding interglacial has three or four fewer genera of conifers than the preceding interglacial. The coniferous lineages available became progressively fewer and presumably the collective tolerances of the remaining lineages more restricted. It is conceivable that the rapid migrations necessitated by glacial advances, concommitant with the narrowing of the Mixed Coniferous forest between the dry Mediterranean climate and the Taiga climates, created great stresses for the coniferous lineages. Following the last glaciation, the number of ecotypes remaining was apparently so limited (or nonexistent) that opportunistic broad-leaved deciduous trees were able to dominate.

It is reasonable to predict, however, that if the Earth is truly in a postglacial rather than an interglacial period, the coniferous lineages still represented in Europe will diversify ecologically. Most of the European beech and oak forests are doomed to eventual extinction as widespread vegetational types and will ultimately be supplanted by a Mixed Coniferous forest.

The term "nemoral" is used in Europe to indicate the broad-leaved deciduous forests (Sjörs, 1963), and Sjörs has applied the epithet to the broad-leaved deciduous forests of eastern North America and temperate eastern Asia. Sjörs (1963) was well aware that the broad-leaved deciduous forests of eastern North America and eastern Asia did not live under temperature regimes similar to those of the nemoral zone of Europe. What has not been evident before is that the bulk of the broad-leaved deciduous forests of eastern North America live under a mean annual temperature and mean annual range of temperature typical for broad-leaved evergreen forest regions and that fundamentally much of the broad-leaved deciduous forest of North America is an analog of the secondary vegetation of the Asian Notophyllous Broad-leaved Evergreen forest region. It has not been emphasized previously that the nemoral zone of Europe has a temperature regime best suited for a Mixed Coniferous forest; were it not for historical factors associated with glaciation, the nemoral of Europe almost certainly would have a Mixed Coniferous forest.

The axiom that the temperate flora of Asia is numbered in thousands of species, that of eastern North America in hundreds, and that of Europe in tens becomes readily understandable. Although the historical factors have undoubtedly contributed to the extinction of many lineages in Europe and North America, the difference in diversity of the deciduous floras of the three main "nemoral" regions is largely due to climate. Only the Asian region has a large area suitable for broad-leaved deciduous forests. Eastern North America has a smaller area (and range of climates) suitable for such forests. Europe has almost no mesic areas primarily suited for broad-leaved deciduous forests.

The various boreal zone and subzones recognized by Sjörs (1963) were conceptualized as a mixture of physiognomic and phytosociological categories. Although his boreal zone is in large part equivalent to the Russian Taiga, some problems remain. On physiognomic criteria, the boreal zone developed along the Norwegian coast may not belong in that zone. Considering that most of Scandanavia was glaciated, might not the dominance of the typical boreal conifers along the Norwegian coast be a function of the geographic proximity of this area to the sources of repopulation? Had the Norwegian coast a ready access to the nemoral populations during the Holocene, might not the typical nemoral zone be found as a thin strip (or in discontinuous patches)? As in the reverse case in Alaska (Valdez), where species of the Mixed Coniferous forest may well form the Taiga locally, the Norwegian coast may best be suited for Mixed Coniferous forest but is, because of geographic factors, populated by species of the Taiga.

Because of the problems associated with the Norwegian coast, only stations east of the Norwegian mountains have been used in plotting the data for Europe (pl. 3). The Taiga-nemoral boundary as commonly represented in various Russian atlases does indeed approximate a mean annual temperature of 3°C, as in Asia and North America (fig. 2).

The survival of several mixed mesophytic relicts in the Caucasus Mountains has long been recognized. I have found no climatic data for the specific area of this relictual forest, but altitudinally below the forest, data are available for Tbilis (pl. 3); it is reasonable to expect the temperature parameters for Mixed Mesophytic forest to be developed upslope from Tbilis. Certain other areas of eastern Europe have the temperature parameters for Mixed Mesophytic forest; in these areas, the Roumanian Plain, for example, precipitational deficits result in grassland vegetation.

DISCUSSION

A CLASSIFICATION OF FOREST CLIMATES

Some climatologists (for example, B. J. Garnier, *in* Fosberg and others, 1961) have argued that a classification of climates should be totally independent of other concepts such as the distribution of organisms. While such a philosophy is clearly valid, equally valid is the traditional approach championed by Köppen, Thornwaite, and other climatologists wherein climatic parameters selected for a climatic classification are the parameters that appear to delimit vegetational types. The advantage of the traditional approach is that areas for which little or no climatological data are known can be classified climatologically on the basis of the known or inferred natural vegetation.

Several major temperature parameters that have been suggested as coinciding with vegetational boundaries are, from the data presented here, invalid. These parameters include the 18°C cold month mean, which has been used to distinguish "tropical' from "subtropical" climates, and the 6°C cold month mean, which has been used to distinguish "subtropical" from "temperate" climates. More recently, Bailey (1960, 1964) has suggested a new classification of climates based on the significance of equability and certain characteristics of warmth during the warm season; comparison of Bailey's classification with plate 2 indicates that neither equability ("temperateness") nor the suggested characteristics of warmth ("effective temperature") are of significance in the distribution of vegetational types.

The data presented indicate that the boundaries between the major mesic forest types of eastern Asia approximately coincide with certain major temperature parameters, although in some instances the boundaries and hence the parameters are obscured by primarily human disturbance. It is emphasized here that the vegetation and climatic parameters investigated are in humid to mesic climates; the critical factor of precipitation in delimiting forest and other vegetational types has been ignored by restricting the discussion to mesic "temperate" or humid "tropical" climates. Nonetheless,

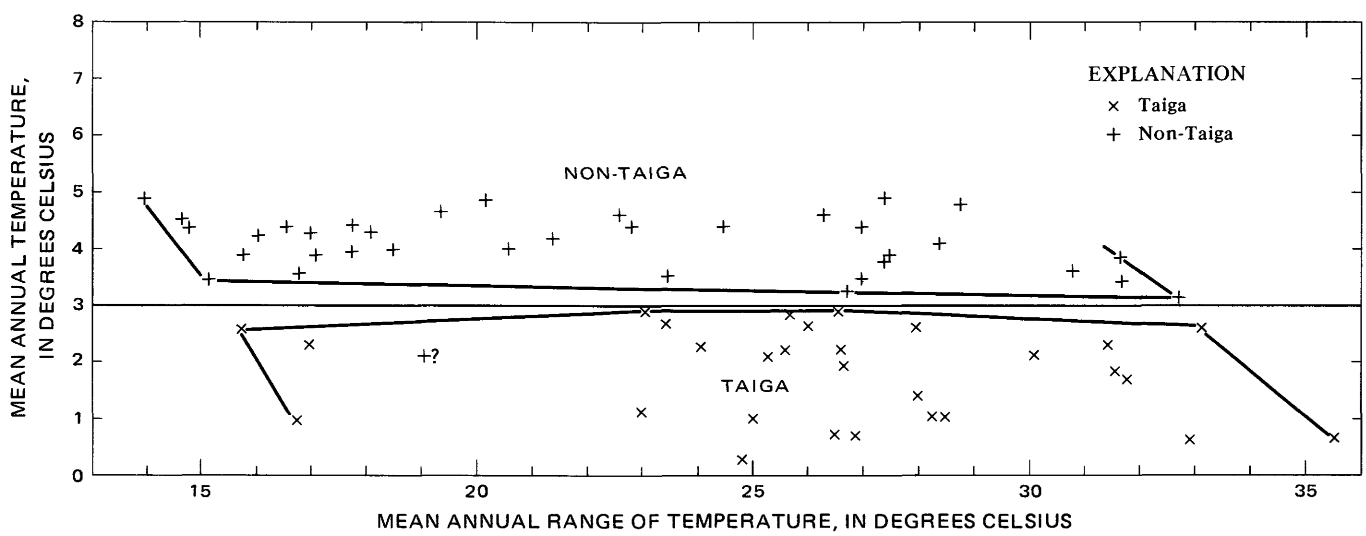

FIGURE 2.—Temperature data for Taiga and non-Taiga forests. Data from plates 2 and 3.

the significant climatic parameters offer a means of classifying climates.

The temperature parameters suggested here (mean annual temperature, mean annual range of temperature, mean temperature of the warm month, mean temperature of the cold month) are probably only approximations of the actual controlling parameters. Nevertheless, these approximate parameters are clearly closely related to the actual parameters; that is, the approximate parameters incorporate to a great extent the phenomena of temperature that are the controlling factors of forest distribution. The present advantage of the approximate parameters is that such values are readily available in climatological publications. When exact, or at least more valid, parameters are proposed, the suggested scheme of temperature classification should, of course, be modified.

It is difficult to express all major temperature parameters in readily usable terms without going into a complicated letter system of classification, such as that of Köppen. A complicating problem is that terms now in common use have various meanings for various workers; this is a problem of semantics. Japanese workers typically term "warm temperate" the entire area in Japan occupied by the Notophyllous Broad-leaved Evergreen forest, despite a cold month mean of 6°C or higher for much of that area (criterion for "subtropical" in the most widely accepted usage). Similarly, many American workers are loath to call "subtropical" large areas of southeastern United States occupied by broad-leaved deciduous forest.

In the classification proposed (fig. 3), only two terms, paratropical and paratemperate ("para," meaning "close"), are not commonly used at the present time The classification is simple, but it reflects known or inferred temperature parameters related to major forest boundaries. Some workers may object to labeling the climate of St. Louis as mild, warm subtropical (fig. 3), but the climate of any area falling near a boundary is apt to be subject to similar constraints. Were the area of St. Louis occupied by broad-leaved evergreen forests (as it would be without the excessive cold waves), botanists would probably be less inclined to object to calling the climate "subtropical."

The major disagreements on climatic terms probably revolve around the use of "tropical" verus "subtropical" versus "temperate." To a certain extent, "tropical" has a geographic connotation, that is, association with the area between the Tropic of Cancer and the Tropic of Capricorn. In the restricted sense of "tropical" proposed here, almost all tropical climate is within this geographic area. The greater part of paratropical climate

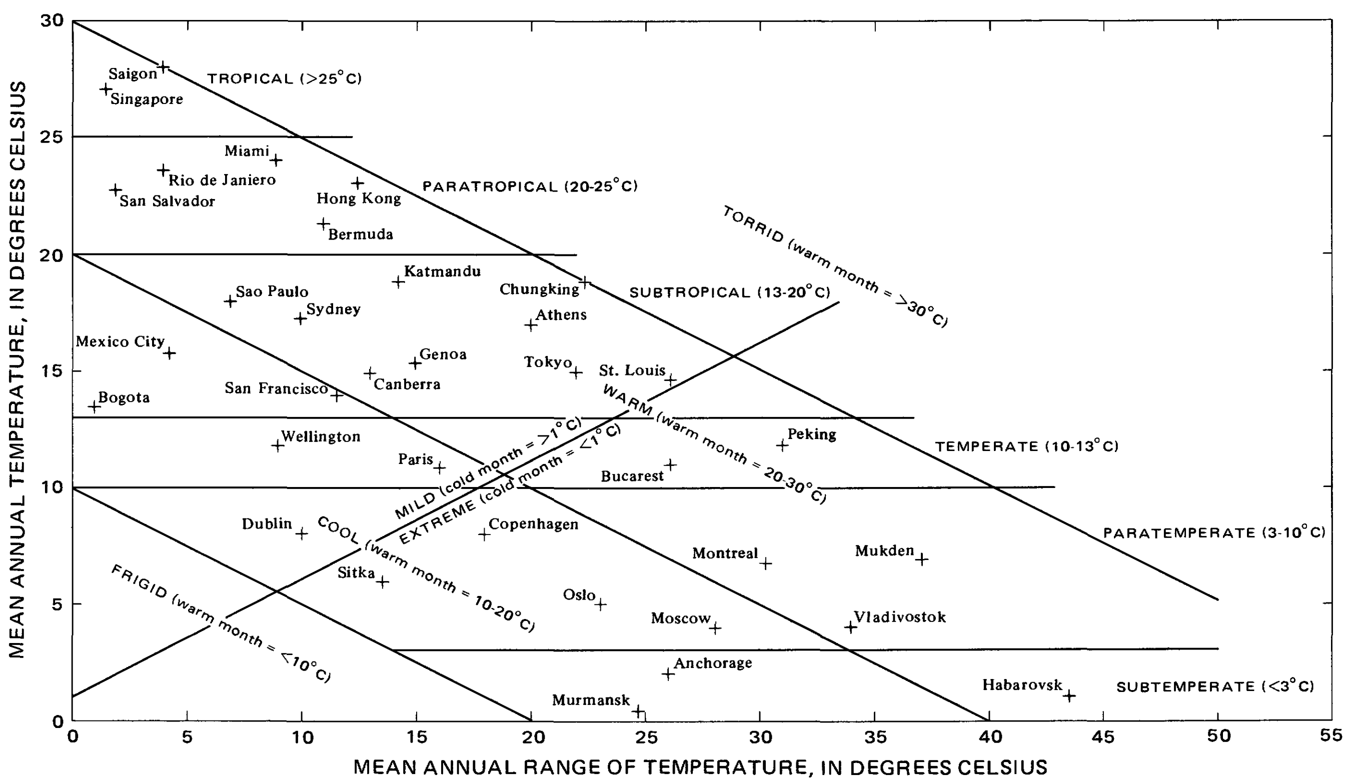

FIGURE 3.—Proposed classification of forest climates based primarily on the forests of eastern Asia. Data points show relation of classification to temperatures of major cities.

also falls between the Tropic of Cancer and the Tropic of Capricorn, whereas the lowland subtropical climate is extra-tropical in a geographic sense.

The use of "subtropical" here is different from any previously used definition. Areas are included that have been called "temperate" (for example, lowland areas of southern Honshu, Honan, and Shantung), and many upland areas of the tropics are excluded. Note that if the 6°C cold month mean is used to differentiate "subtropical" from "temperate" climates, treeless areas on tropical mountains (much of the Andean paramos, for example) must be classed as "subtropical."

"Temperate" has different connotations. Probably the most basic of these is the connotation of the climate being neither hot year round nor cold year round. Some workers, however, use "temperate" to connote climates of moderate heat but high equability. Bailey (1964) has argued for judging the "temperateness" of climates on the basis of their departure from a mean annual temperature of 14°C and a mean annual range of temperature of 0°C. The reason for selecting 14°C as a centrum is that this is approximately the mean temperature of the Earth at the present time. Considering, however, that the mean temperature of the Earth almost certainly has been higher than 14°C throughout most of geologic time, the selection of 14°C is of questionable value. As used here, "temperate" connotes only climates of a particular mean annual temperature and lacks any connotation of equability.

ALTITUDINAL ZONATION OF FORESTS IN EASTERN ASIA

An old concept of vegetational zonation holds that vegetational types or belts ascend altitudinally in an equatorward direction (Humboldt, 1817; Good, 1953, p. 22; Axelrod, 1966, p. 167). As Richards (1942, p. 372) has pointed out, the conclusions of Lam (1945), and particularly the conclusions of Troll (1948), are at strong variance with this older concept.

The altitudinal zonation of vegetation relative to latitude in Asia is complex. Considerable differences exist between the zonation in the major oceanic islands of the western Pacific, the zonation along the coastal mainland of China, and the zonation in the interior of China (fig. 4–6). The schematic zonation of figures 4–6 was constructed by using actual data at specific base stations (pl. 2)) and extrapolating the altitudinal zonation. The normal lapse rate of 0.5°C/100 m was used except between lat 20° and 30° in the interior of China (fig. 6), where an actual lapse rate of 0.4°C/100 m was used. The altitudinal zonation suggested (figs. 4–6) is close to observed zonation.

In regions of a high mean annual range (fig. 6), some vegetational types—Mixed Mesophytic, Mixed Conif-

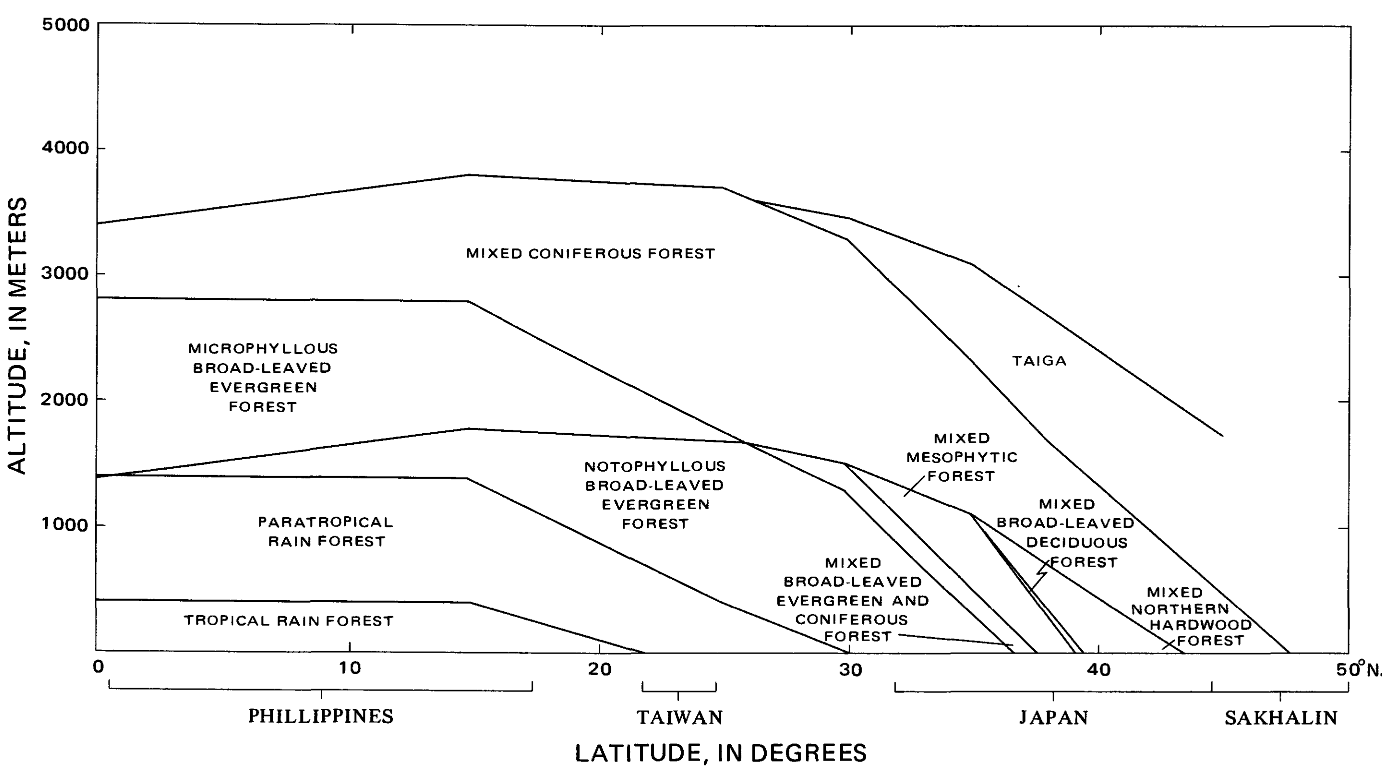

FIGURE 4.—Altitudinal zonation of forests on major islands of the western Pacific.

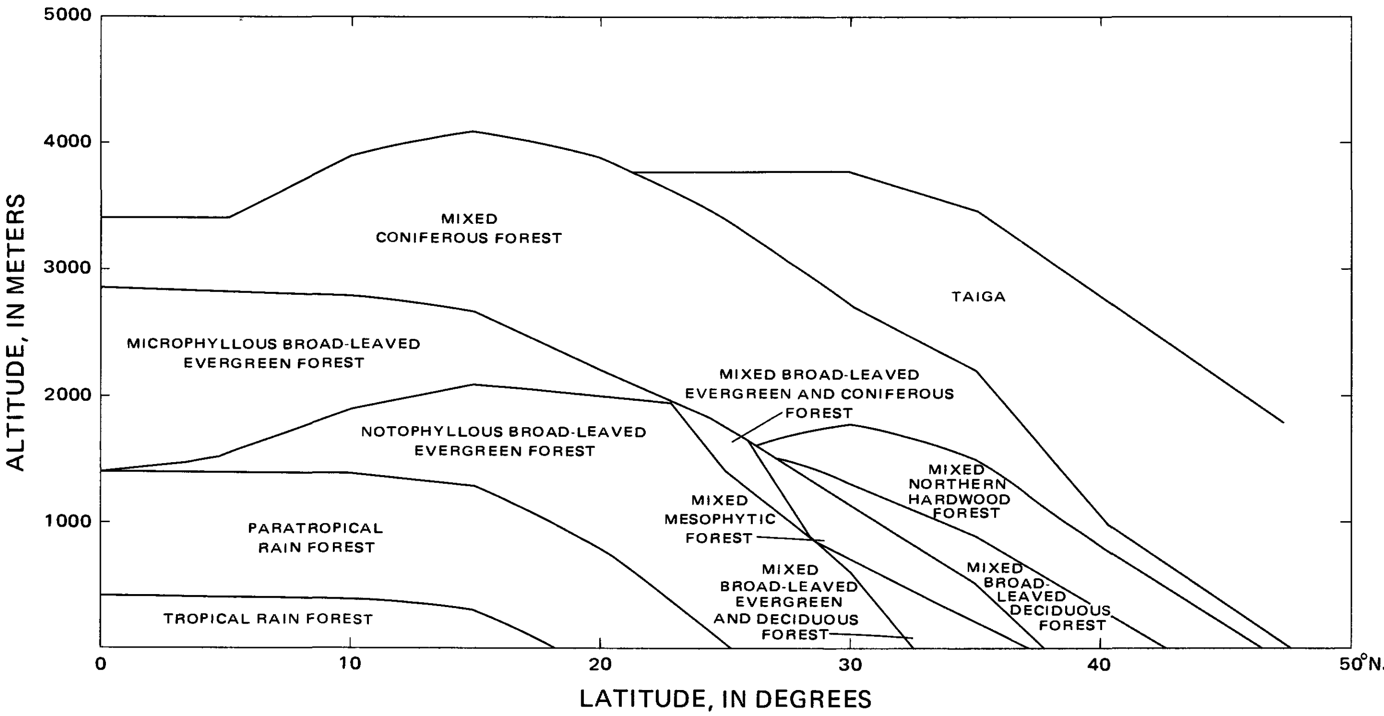

FIGURE 5.—Altitudinal zonation of forests along coastal mainland of China.

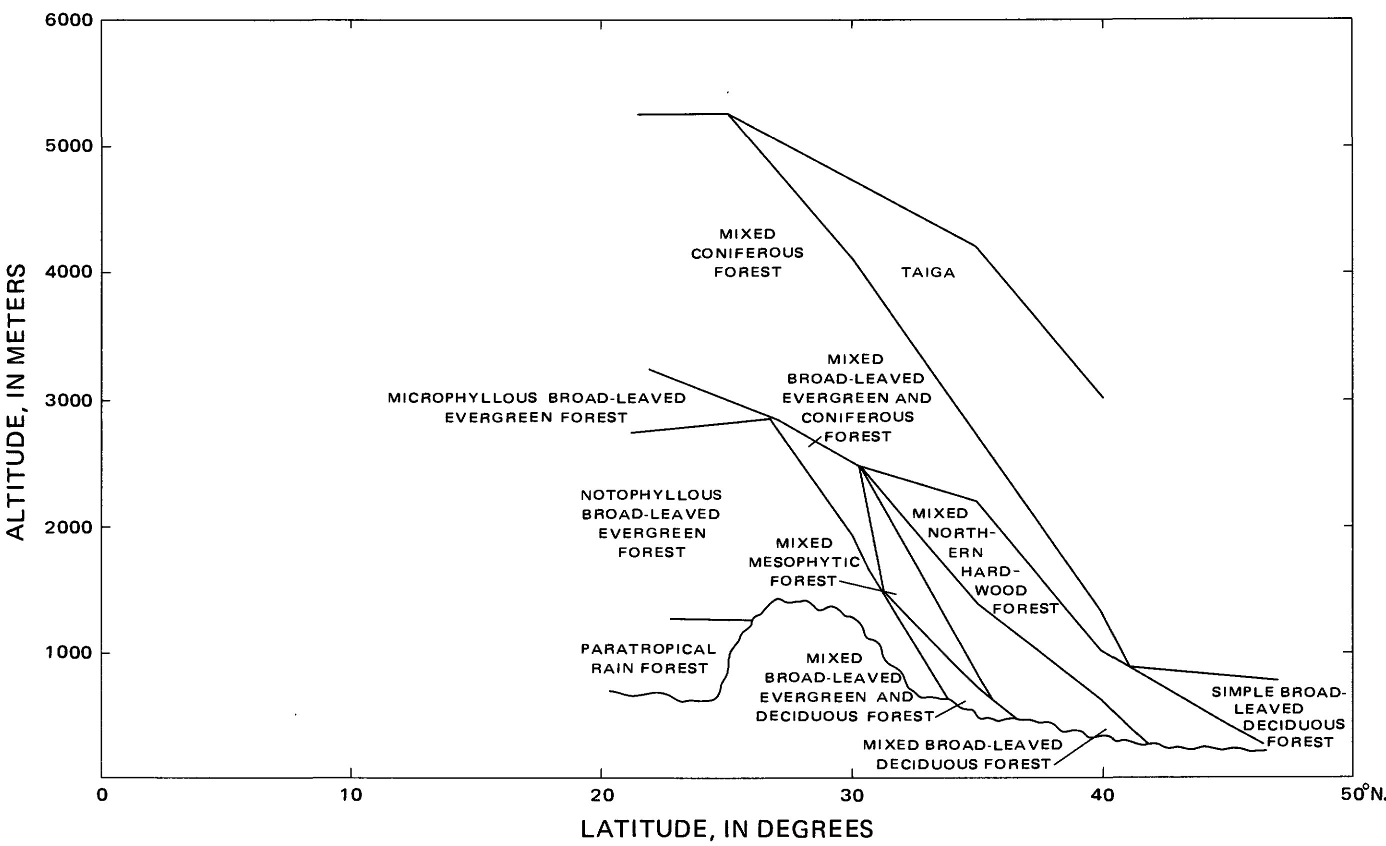

FIGURE 6.—Altitudinal zonation of forests in the interior of China.

erous, and Mixed Broad-leaved Evergreen and Coniferous forests—do not reach low altitudes. And vegetational types such as the Mixed Broad-leaved Evergreen and Deciduous forest are best (or only) developed under high mean annual ranges. Clearly, a high mean annual range is necessary to the development of broad-leaved deciduous forests over wide areas.

In regions of a low mean annual range of temperature (fig. 4), broad-leaved deciduous forests are poorly developed altitudinally and latitudinally. Evergreen forests, both broad leaved and needle leaved, on the other hand, are well developed.

An attempt to construct an idealized altitudinal and latitudinal zonation (fig. 7) is based on the following generalizations:

From lat 0°–10°, mean annual range of temperature varies from close to 0° to 2°C, and mean annual temperature is approximately 27°C;

From lat 10° to 45°, mean annual range of temperature increases by about 0.7°C/1° latitude, and mean annual temperature decreases by about 0.5°C/1° latitude;

From lat 45° to 60°, mean annual range of temperature increases by about 0.3°C/1° latitude, and mean annual temperature continues to decrease by about 0.5°C/1° latitude.

In the idealized zonation, all vegetational types but one are found at sea level. The best development of coniferous forest is at high altitudes at low middle and high low latitudes. Broad-leaved evergreen forests extend to lat 38°, well south of the light limitation (see discussion of light, p. 34). Broad-leaved deciduous forests are not particularly extensive and are represented by only two main types (a third, the Mixed Broad-leaved Deciduous forest is actually present at moderate altitudes as a sliver between the Mixed Mesophytic and Mixed Northern Hardwood forests).

APPLICATIONS TO PALEOBOTANY

One of the purposes of this study was to provide data that might help interpret fossil assemblages in terms of modern vegetation and climate. A given element (that is, coniferous, broad-leaved evergreen, or deciduous) tends to be floristically overrepresented in vegetation in which that element is a subordinate component. Broad-leaved deciduous plants, for example, form a higher percentage of the flora in broad-leaved evergreen forests than the percentage of basal area that the broad-leaved deciduous trees occupy. And broad-leaved deciduous trees may be prominent and even dominant in secondary forests in regions in which the primary forest is broad-leaved evergreen. Considering that many fossil assemblages represent vegetation that grew under disturbed conditions—highly volcanic terrain, flood plains, riverbanks—it is to be expected that species of secondary vegetation will be overrepresented. Indeed, the secondary or disturbed vegetation in many forest regions may have a high proportion of broad-leaved deciduous plants. Champion (1936) has shown that along streams of tropical regions in India, the vegetation may be dominantly deciduous—

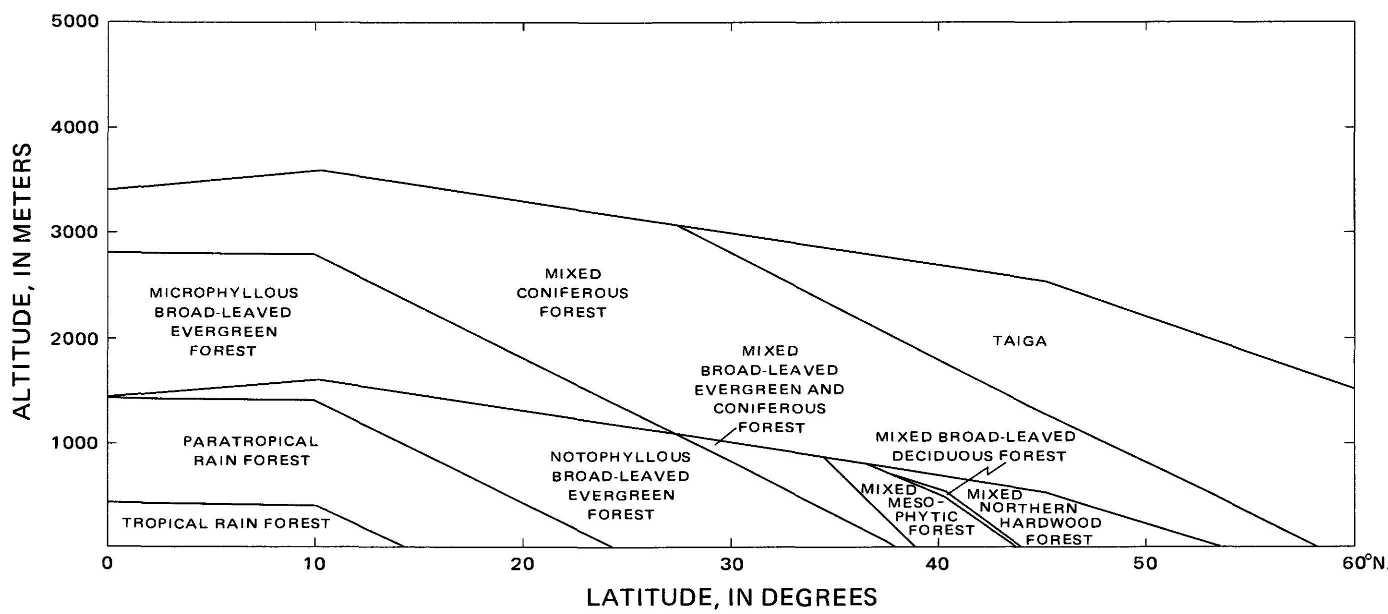

FIGURE 7.—Idealized altitudinal and latitudinal zonation of forests in the Northern Hemisphere.

including the typically "temperate" *Salix*. In the Paratropical Rain forest of Taiwan, disturbed vegetation similarly contains a high representation of broad-leaved deciduous trees and shrubs, including members of several "temperate" genera (*Salix* and *Pinus*, for example). In regions of dominantly coniferous forest, both Mixed Coniferous forest and Taiga, stream-side vegetation typically is broad-leaved deciduous.

Many paleobotanists have theorized that climates of the Paleocene, Eocene, and early Oligocene (about 32–65 million years ago) were characterized by high equability. Axelrod and Bailey (1969) have postulated a mean annual range of temperature of only about 11°C (or about 6°C fide Axelrod, 1966) at lat 45° N. during the Eocene. If indeed these values are even approximately correct, it follows that broad-leaved deciduous forests could not be present at midlatitudes at high altitudes and that mean annual range of temperature could not have been sufficiently great in combination with mean annual temperature at high latitudes to support a broad-leaved deciduous forest. Moreover, the fact that broad-leaved deciduous forests occupied large areas where coniferous forests now dominate (western North America) or should dominate (western Europe) indicates that Tertiary climatic changes have involved an increase in mean annual range of temperature during at least part of the early Tertiary to an even greater value than now and that subsequently there has been a decrease in mean annual range (Wolfe, 1971). Such possibilities indicate that Tertiary climatic changes and their concommitant effect on vegetation and the lineages of its floral elements are complex and that simplistic concepts of "Geofloral" migrations should be viewed with care.

Floristic criteria alone appear to be an inaccurate basis for inferring vegetational types from fossil assemblages. The ranges of many genera tend to be so broad as to be meaningless; for example, *Toona* ranges from Tropical Rain forest to Mixed Broad-leaved Deciduous forest. The ranges of some extant genera, judged by paleobotanical evidence, show a similarly broad adaptation that the extant representatives do not appear to have. For example, *Exbucklandia,* now restricted to broad-leaved evergreen forests in Asia, was of wide occurrence in Mixed Mesophytic forest in the Neogene of Oregon and Washington (Wolfe, 1969b); an even more striking example is the occurrence of *Glyptostrobus*—now restricted to Paratropical Rain forest—in High Coastal Mixed Coniferous forest in the Pliocene of Alaska (Wolfe, 1969b). Although the present ranges of bulk of the genera of a fossil flora do offer a clue to the vegetational type represented, a worker should be wary of trusting a small group of genera in that flora to determine more accurately the vegetation and climate. Physiognomic criteria of fossil-leaf assemblages, as Richards (1952) emphasized, offer a more direct and reliable means of correlating a fossil assemblage to a vegetational type and climate than do floristic criteria.

The physiological significance of some of the limiting temperature parameters to plants is generally clear. Mean annual temperature, being an approximate measure of overall heat accumulation, is an understandable limitation on the growth of various forms of plants. Similarly, the heat requirements of most broad-leaved trees is apparently higher than the heat requirements of conifers, and the boundary between broad-leaved forests and coniferous forests is understandable. That cold month means are critical to the limits of notophyllous broad-leaved evergreens would appear reasonable; if a tree or shrub must be dormant because of low temperatures incapable of sustaining physiological activity, it would seem that a deciduous or a microphyllous habit would be an advantageous adaptation.

The environmental factors that control leaf size of broad-leaved evergreen plants can only be conjectured. In areas of low summer heat (that is, the areas characterized by a warm month mean of 20°C or less), the forests are either coniferous (typically nanophylls) or microphyllous broad-leaved evergreen. If the forest is coniferous, the accessory broad-leaved evergreens are dominantly microphyllous, although some notophylls (or larger) may be present. In areas of moderate to high summer heat another factor is operative. Leaf size in broad-leaved evergreen forests appears to be related to overall heat (approximately expressed by mean annual temperature) rather than to any concept of equability (that is, a measure of warm or cold month means). Leaf size, for example, decreases going upslope on Mount Maquiling on Luzon, even though equability increases. The percentage distributions of leaf-size classes in the notophyllous forests of eastern Australia are approximately the same as in the considerably less equable notophyllous forests of Kyushu and Shikoku.

Despite the fact the broad-leaved deciduous trees dominate the Mixed Mesophytic forest, many of the associated broad-leaved evergreens are typically notophylls. If, however, the mean of the cold month is below −2°C, the broad-leaved evergreens fall into only the microphyll (or smaller) size class. Clearly more data on leaf size throughout broad-leaved forests are needed in order to attain a more accurate concept of the controlling factor(s) of leaf size. In general, in areas of moderate to high summer heat in which the mean of the cold month is at least −2°C, leaf size of broad-leaved evergreens appears to be related to overall heat accumulation.

A factor in the control of large-leaved evergreens in vegetation that has been largely disregarded in this discussion is light. In areas of high-heat accumulation and high equability such as tropical-latitude mountains, forests may be microphyllous. Brown (1919) suggested that the small leaf size can be correlated with the perennial dense cloudiness and concommitant reduction in solar radiation reaching the forest; Richards (1952) concurs in this suggestion. A similar phenomenon has been noted in the Caribbean region (Beard, 1944); Beard further notes that on mountains that rise above the dense cloud belt, vegetation above the belt may again be large leaved. These data would strongly support the concept that a lack of solar radiation has a causal relation to the small leaf size of many of these microphyllous montane forests and thickets (although not to the Microphyllous Broad-leaved Evergreen forest as herein defined).

The distribution of notophyllous broad-leaved evergreens poleward in the Northern Hemisphere also tends to support a concept of a limitation of solar radiation. In both eastern Asia and North America, notophyllous evergreens are limited by temperature to south of lat 45° (or even lower latitude). In Europe and western North America, the temperatures of the cold month are sufficiently high to support notophyllous evergreens as far north as lat 60°. In fact, in western North America, the two most northerly notophyllous evergreens, *Arbutus* and *Rhododendron,* extend only to about lat 51° N.; in Europe *Arbutus* extends to about 51°–52° N. It is notable that *Rhododendron* is found at lat 45° in mountains that have temperature parameters highly similar to those at lat 57° in southeastern Alaska, where *Rhododendron* is absent. These limitations indicate that the amount of solar radiation received during winter is insufficient to support notophyllous evergreens poleward of about lat 52° N. Such a radiational limitation would, as van Steenis (1962) noted, effectively prohibit migration of large-leaved evergreen lineages via areas such as the Bering Straits area under present light regimes irrespective of temperature regimes.

The second physiognomic character of foliage that has been used in this report is the type of leaf margin, whether entire or nonentire (lobed or toothed). The correlation of this character with climate was first pointed out by Bailey and Sinnott (1915, 1916). The major temperature factor that correlates with the type of leaf margin has been thought to be mean annual temperature (Wolfe, 1971), although some workers have maintained that equability was equally, if not more, significant (Axelrod and Bailey, 1969). Bailey and Sinnott's original compilations were based on floras primarily regional in scope, and thus a given leaf-margin percentage, in most instances, reflected a considerable range of temperatures. In two instances, however, Bailey and Sinnott (1916) demonstrated that percentages decreased from hot, tropical lowlands to cooler, more equable uplands. Brown's even more localized data (1919) indicated a similar relation.

In an attempt to resolve more accurately the correlation between leaf-margin type and temperature, the percentages of entire-margined species for many local floras in eastern Asia were plotted against mean annual temperature (fig. 8*A*) and mean annual range of temperature (fig. 8*B*). The plots for mean annual temperature leave little question that it is heat, rather than equability, that correlates best with the type of leaf margin. The closest fits are in instances in which extremely localized floras have been used and temperature data within the localized area of the flora are known, for example, Mount Maquiling and Chin-men, whereas floras that cover a considerable altitudinal interval are approximations, for example, T'ien-mu Shan and Lu-Shan. The approximate regression line indicates a relation of 3 percent/1°C.

Data for the Southern Hemisphere were not used in the leaf margin-temperature correlation (fig. 8). The higher proportion of entire-margined species in the Southern Hemisphere relative to the Northern Hemisphere has been noted by Bailey and Sinnott (1916), who attributed the difference to the low diversity of broad-leaved deciduous plants in the Southern Hemisphere. The few local floras for the Southern Hemisphere that have been plotted do substantiate the high representation of entire-margined species in these floras. The data can be interpreted as indicating that mean annual temperature is again the primary correlative with the type of leaf margin, although the relation appears to be about 4 percent/1°C.

In the eastern United States, leaf-margin percentages are anomalous. The percentage for Washington, D.C., for example, is 25 percent, rather than 40 percent as would be expected considering the mean annual temperature. Note, however, that secondary vegetation in an area of similar mean annual temperature on the Kanto Plain of Japan probably has a leaf-margin percentage considerably lower than the percentage for the primary vegetation, considering that the secondary vegetation is composed predominately of species that are dominant in the Mixed Mesophytic forest (Hara, 1959).

In dominantly coniferous forests, leaf-margin percentages do not appear to be related to major temperature factors. This may result from the fact that the bulk of the broad-leaved accessories are not exposed to the primary climate of the canopy and (or) primarily occupy streamside habitats or participate in secondary

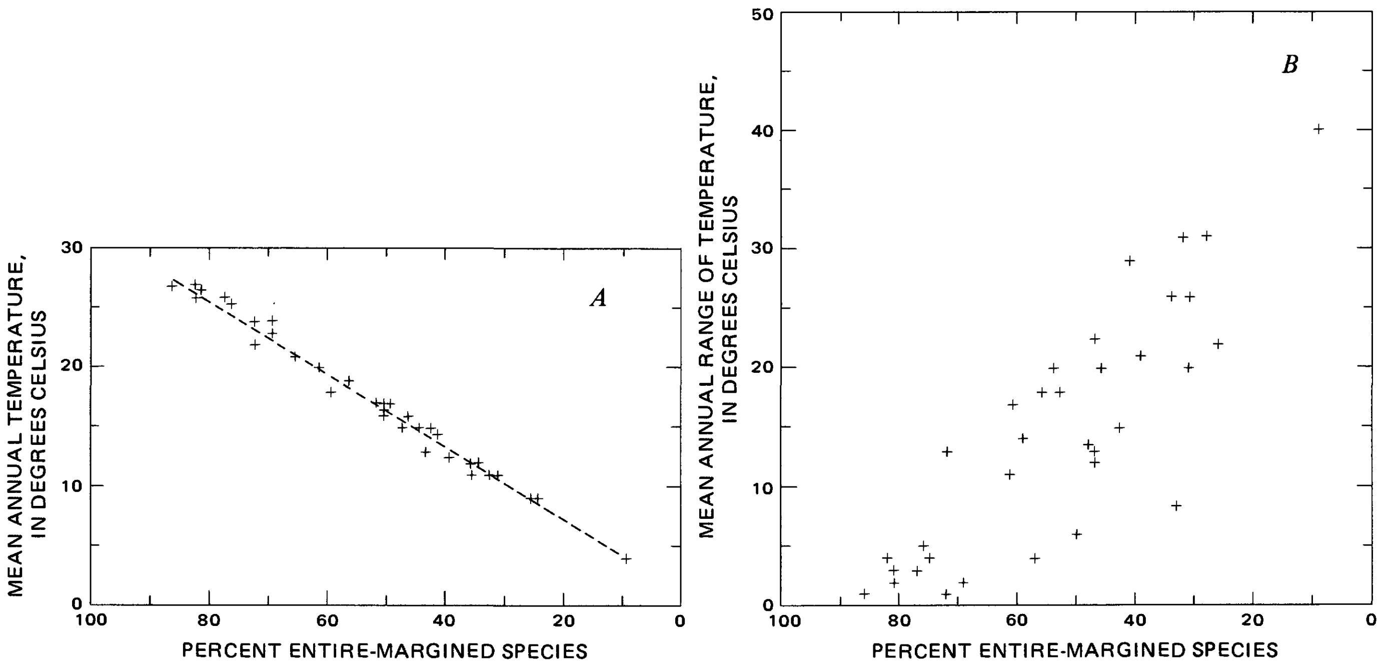

FIGURE 8.—Correlation of percentages of entire-margined species with temperature. *A*, annual temperature. *B*, mean annual range of temperature. Data based on local floras in the humid to mesic forests of eastern Asia. Dashed line is regression line.

vegetation. In coniferous forests in which broad-leaved trees regularly participate in the canopy (for example, the "Mixed Evergreen forest" of Whittaker, 1960), the leaf-margin percentage may be an accurate reflection of mean annual temperature.

The type of leaf organization, whether simple or compound, has been used by some workers as a physiognomic character. This feature may not be of more than taxonomic significance. The fact that woody members of families such as Leguminosae are typically compound in both tropical and temperate regions indicates that the type of leaf organization is strongly genetically controlled, and there is no reason to suspect that environmental parameters, even if exerted over many generations, would select in favor of a simple rather than a compound organization. As Richards (1952) has noted, the individual leaflets of compound leaves simulate in size, shape, and other features the simple leaves of associated species.

A point that deserves emphasis is that conifers may appear throughout the broad-leaved forest region. Some paleobotanists interpret a high proportion of *Pinus* pollen as an indicator of "temperate" climate. In fact, pines are well represented in truly tropical climates (especially in special edaphic situations) and are among the major components of secondary vegetation in subtropical climates. Other conifers, for example, *Fokienia*, are today typically associated with subtropical broad-leaved evergreen forests, and *Glyptostrobus* is today restricted to Paratropical Rain forest.

PROBLEMS

Clearly further work is needed to more accurately define the relation of humid and mesic forest types to temperature parameters in some areas:

Upland Taiwan. Does the Notophyllous Broad-leaved Evergreen forest indeed give way upslope to Microphyllous Broad-leaved Evergreen forest and does this in turn give way to Temperate Coniferous forest where mean annual temperature drops below 13°C?

Northern China. Can paleobotanical work of Holocene sediments aid in the reconstruction of the Mixed Broad-leaved Evergreen and Deciduous forest?

Central and northern Honshu. Is the Mixed Broad-leaved Deciduous forest recognizable between the Mixed Mesophytic and Mixed Northern Hardwood forests?

Korea. Is the Mixed Broad-leaved Evergreen and Deciduous forest a valid category and is the distinction between Mixed Broad-leaved Deciduous and Mixed Northern Hardwood forests valid?

Certainly much work is needed to determine the physiognomic changes that the humid to mesic forests undergo along moisture gradients leading to subhumid conditions. Do the Tropical and Paratropical Rain forests have subhumid analogs that are physiognomically separable? It is hoped that the present study, in attempting to show what physiognomic changes occur along temperature gradients under optimal (or nearly so) conditions of precipitation, will allow an understanding of what physiognomic features are primarily moisture related.

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