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Climate and Regional Composition of Deciduous Forest in Eastern North America and Comparisons with Some Asian Forests

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ABSTRACT

Deciduous Forest in eastern North America occupies a broad thermal range, even when transitional types (conifer-northern hardwoods and southern mixed hardwoods) are excluded. The Bailey System of Bioclimatology reveals differences in Warmth and Temperateness (equability) among syntaxonomic units of the Eastern Deciduous Forest (EDF), specifically the Maple Sub-Zone (northern), the Central Hardwoods Sub-Zone, and the Oak-Pine Sub-Zone (southern). Stations of the Maple Sub-Zone are coldest. Stations of the Oak-Pine Sub-Zone are warmer than most Central Hardwood stations and less temperate. When Mexican, European, west Asian and east Asian deciduous forests are analyzed similarly, by physiognomy, floristic composition, and Warmth and Temperateness of climate, some relationships with the eastern North American deciduous forest sub-zones are evident. In the mountains of eastern Mexico, the nomographed stations of the Mexican Holarctic Dicotyledonous Forest (MHDF) are congruent in Warmth with the Southern Mixed Hardwoods Forest and with the northern coastal stations of the Temperate Broad-Leaved Evergreen Forest (TBEF). Nomographed stations of the deciduous forests of Europe (England to the Balkan Peninsula) are congruent in Warmth with the combined Maple and Central Hardwoods Sub-Zones of EDF. However, the European stations are much more equable than their eastern North American counterparts, and they have many fewer hours of freezing temperatures. There is very little overlap in Temperateness between the nomograph-plotted deciduous forest stations in the two regions, which are separated by the Atlantic Ocean. In western Asia, the few stations of the Colchic-Hyrcanian-Talysch type that were plotted are nearly completely congruent in Warmth with the Oak-Pine Sub-Zone of EDF. However, they are more equable, with higher ratings of Temperateness, than EDF stations at the same Warmth, with one exception. Nomographed stations of the oak (*Quercus*)-dominated deciduous forests of China and the largely beech (*Fagus*)-dominated deciduous forests of Japan overlap the EDF Central Hardwoods Sub-Zone in Warmth, with the exception of one southern U. S. station. Japanese deciduous forests and all the northern stations of the EDF Central Hardwoods are congruent in Temperateness as well as Warmth. East Asian forests dominated by a combination of deciduous angiosperms, evergreen angiosperms and evergreen conifers, such as the Mixed Mesophytic Forest of China (MMFC), would appear to have, as their physiognomic counterpart in eastern North America, the Southern Mixed Hardwood Forest (SMHF; strictly, the DC of Greller 1989; in part, the Southern Evergreen Region of E. Lucy Braun). However, MMFC weather stations plotted on Bailey's nomogram are congruent in Warmth and Temperateness with stations of the Oak-Pine Sub-Zone of the EDF.

Keywords
Deciduous forest, climate, North America, Asia

РЕЗЮМЕ

Греллер А.М.

Климат и состав листопадных лесов востока Северной Америки в сравнении с некоторыми азиатскими лесами

Лиственные леса восточной части Северной Америки характеризуются широким спектром термических условий, даже если не принимать во внимание переходные типы (северные хвойно-широколиственные и южные широколиственные смешанные). Система биоклиматов Бейли показывает различия в теплообеспеченности и умеренности между разными растительными единицами Восточных листопадных лесов (ВЛЛ), и, в частности, между северной подзоной холодных кленовых, средней подзоной широколиственных и южной подзоной более теплых дубово-сосновых лесов. Поскольку аналогичные мексиканские, европейские, западноазиатские и восточноазиатские лиственные леса имеют сходные черты в их физиогномике, видовом составе, отношении к теплу и умеренности климата с восточными Североамериканскими листопадными лесами, можно предположить наличие взаимоотношений. В горах восточной Мексики леса, представленные видами двудольных, по уровню теплообеспеченности сходны с южными смешанными широколиственными лесами и умеренными широколиственными вечнозелеными лесами Североамериканского Северо-Востока. Листопадные леса Европы (от Англии до Балканского полуострова) по теплообеспеченности сходны с листопадными лесами подзон кленовых и широколиственных лесов зоны ВЛЛ. В Западной Азии, биоклиматические показатели области распространения растительности Колхидско-Гирканского типа сходны по тепловым индексам с климатическими условиями дубово-сосновых лесов в подзоне Североамериканских восточных листопадных лесов. Климатические условия дубовых, преимущественно листопадных лесов Китая и, в значительной степени, буковых лесов Японии показали сходство по индексам умеренности и температур с климатическими условиями лесов средней подзоны восточносевероамериканских листопадных лесов. Смешанные леса, представленные в Восточной Азии сочетаниями листопадных и вечнозеленых покрытосеменных и вечнозеленых хвойных деревьев, физиогномически сходны с лесами восточной части Северной Америки в южной подзоне смешанных листопадных лесов (а именно DC по Greller 1989, а также с регионом южных вечнозеленых лесов по Braun). Тем не менее, номограммы Бейли показывают, что смешанные мезофитные леса Китая по количеству тепла и умеренности соответствуют дубово-сосновым лесам восточносевероамериканской подзоны листопадных лесов. (Переведено редколлегией).

Ключевые слова
листопадный лес, климат, Северная Америка, Азия

INTRODUCTION

Since the late 20th century, scientists have been documenting the migration of plants upward on high mountains of the Northern Hemisphere (Grabherr et al. 1994, Pauli et al. 2003) and northward to the North Pole (Sturm et al. 2005), in response to warming winters. Small rises in summer temperatures are claimed to be responsible for the deaths, by bark beetles, of 40 million *Picea* (spruce) trees in the Kenai Peninsula of southern Alaska (Anonymous 2003). More recently, decline of the *Callitropsis nootkatensis* (= *Xanthocyparis nootkatensis* = *Chamaecyparis nootkatensis*, yellow-cedar) on nearly a million acres in the Alaska "panhandle", has been attributed to lower snowfall, causing the death of tree roots by freezing from exposure (Hennon et al. 2012). While phenological changes are widespread and have been summarized, latitudinal changes in contemporary forests have been demonstrated in only a few instances (Bertin 2008). Forests of the Northern Hemisphere showed major changes in the location and abundance of tree species during a 5 °C increase in temperatures between 15 000 and 7 000 years ago (Joyce et al. 1990). Forest tree species migrated at different rates (Davis 1981). In the early Holocene, under a rapidly warming climate regime, disassociation of forest tree species has been documented in migrating forests (Bernabo & Webb 1977). Greller et al. (2011) showed that *Magnolia* species, with centers of distribution in the southern Appalachian Piedmont and Mountains, have been establishing populations in oak (*Quercus*)-dominated forests of Long Island, New York, in which they had never before been documented. These range extensions, of many hundreds of miles in the case of *Magnolia macrophylla*, have no doubt been facilitated by local plantings of *Magnolia* species in local gardens and estates.

With the possibility of disassociation of the presently constituted forests of the Northern Hemisphere mid-latitudes, it is timely to examine their floristic compositions and documented distributions in the light of climatic parameters at their distributional limits. Because predominantly deciduous forests occupy the largest portion of eastern North America and Europe, and are represented in Asia by forests rich in endemic genera and species, deciduous forests have been chosen for examination in the present paper.

METHODS

Bioclimatic Analysis (from Greller 1989)

The present analysis of zonal climates uses the system of bioclimatology by Bailey (1960, 1964, 1966). This system has been applied intensively to modern aborescent vegetation in mid-latitudes (Axelrod 1965, 1968, Greller 1989), in a tropical area (Greller & Balasubramaniam 1988), and in near-shore paleontology (Hall 2002). Several thermal characteristics have proved useful in distinguishing vegetation, especially humid forests. Two of these characteristics are the Warmth (W) of climate and its Temperateness (M), which were defined and quantified by Bailey (1960, 1966).

Bailey measured the warmth regime by "Effective Temperature" (ET), the "one thermal level which best characterizes a temperature regime"; the temperature at which the growing season begins and ends. The equation (Bailey 1960) for Effective Temperature (Warmth) is:

$$ET(W) = (8T + 14A)/(8 + A),$$

where T = mean annual temperature (°C), and A = the annual range of mean monthly temperatures. [Bailey considered ET(W) greater than 18°C to be "Hot"; less than 18°C but greater than 15.7°C as "Very Warm"; 15.7°C to 14.7°C as "Warm"; 14.7°C to 12.5°C as "Mild"; 12.5°C to 11.5°C as "Cool"; and 11.7°C to 10.2°C as "Very Cool"]. Bailey obtained from ET a definition of growing season (and an estimate of its duration): the number of days (t^d) with mean temperature warmer than W (ET). The equation for (t^d) is given as:

$$t^d = 182.6 + 2.03 \text{ arcsine } (W - 14) / 4,$$

(in °C). Bailey (1960) created a measure of temperateness of climate, the statistic M, that provides an "index of thermal extremes that increase... from an ideal centered at T = 14°C (57.2°F) and A = 0°C, where T is the mean annual temperature and A is the annual range of mean monthly temperatures" (Axelrod & Bailey 1976). The formula is:

$$M = 109 - \log[(14 - T)^2 + (1.46 + 0.366A)^2],$$

with temperature in Celsius. Bailey (1964) rated temperateness (M) as follows: 100–80, Supertemperate (constant); 80–65, Very Temperate; 65–50, Temperate; 50–35, Subtemperate; 35–20, Intemperate; 20–0, Extreme.

From a table of probability values contingent on the mean annual temperature and annual range of temperature of any station, Bailey (1966) plotted on a nomogram the frequency of frost (*f* 0 in °C, *f* 32 in °F), in percentage hours of the year. For convenience in calculating ET and M, Bailey (1960) plotted these too on a nomogram. Warmth (W) was indicated as lines (radii) of effective temperature that "define the duration of the growing season as the number of days (t^d) with mean temperature warmer than [ET]". Temperateness of climate (M) was indicated on the nomogram as a "field of arcs nearly normal to the radii that increase in all directions from T = 14°C, and A = 0°C". Bailey's nomogram provides an accurate, simple, easy, graphic representation of several different thermal regimes on a single page, which facilitates comparisons of critical climate factors greatly (cf. Walter 1985). At the same time, the system does not assign detailed vegetational classifications to certain thermal regimes *a priori* (cf. Holdridge et al. 1971), rather it defines polar and tropical climates and locates vegetation with reference to these regimes. According to Bailey, moisture regime is third in importance for vegetation (after warmth and temperateness). This is because edaphic moisture (clay soil, springs, high water tables, rivers, etc.) can often compensate for low precipitation to permit the luxuriant development of forest vegetation that reflects the warmth and temperateness of the climate.

For a more detailled discussion of the Bailey Bioclimatology System, the reader is referred to Hall (2002: 34). The present study does not consider the moisture regime, so that the question of a "rainforest" designation, for example, is considered beyond its purview.

The nomograms used for calculation in this paper were provided by Harry P. Bailey (deceased) and Daniel I. Axelrod (deceased), from originals in the Department of Earth Sciences, University of California – Riverside. A simplified version of Bailey's nomogram appears as a graph in Greller (1980, Fig. 3). That version is used for Figures 1–5 in the present paper and is referred to as a nomograph. Climate Normals of mean annual temperature (T) and annual range of mean monthly temperatures (A) for the various stations were obtained from: Canada Department of Transport, Meteorological Branch (1968); [Mexico] García 1973; U.S. National Oceanic and Atmospheric Administration (1982); [world, general] Norwegian Meteorological Institute: eKlima.

For geographic distribution of forest types, the following publications were consulted: Forest products association of Canada (2013), Greller (1980, 1989, 1990), Numata (1974), Rowe (1972), Rzedowski (1978), UNESCO (1968, map), Wang (1961) as well as extensive personal observations in Europe.

Forest Regions and Associations Considered in the Present Study

A. North America

Deciduous Forest

For the present study, the Deciduous Forest (DF) is recognized as comprising only the following associations of Braun (1950; map): Oak-Pine (O-P), Oak-Hickory (O-H), Western Mesophytic (WM), Mixed Mesophytic (MM), Oak-Chestnut (O-C), Beech-Maple (B-M), and Maple-Basswood (M-B). To this group, Greller (1988) added a Beech-Birch-Maple-Basswood (BBMB) type in the higher elevations of the Southern Appalachian Mountains. Those Forest Zones are mapped in Greller (1989, Fig. 1). Following Braun's (1950) map, stations near the periphery of each of the seven associations were chosen to represent the DF climate. In addition, one station (Banner Elk, North Carolina) represents the BBMB Association.

Preliminary analyses of climates of the above types reveal that three more or less taxonomically, physiognomically and/or climatically distinct sub-groupings can be recognized:

1) the **Oak-Pine Sub-Zone** in the Piedmont, Inner Coastal Plains and lower Mississippi Valley north of the Southern Mixed Hardwoods zone;
2) a **Central Hardwoods Sub-Zone** comprising O-C, MM and some WM stations in the upper Mississippi Valley and Ohio Valley, and
3) a **Maple Sub-Zone** comprising B-M, M-B and BBMB associations.

Oak-Hickory association is not considered further because, although it mostly overlaps with O-C and MM, it exists in the Sub-Humid central portion of North America, where it often occupies river valleys under edaphic conditions that are more mesic than the surrounding upland soils. Western Mesophytic forest occurs mainly in the Mississippi Valley, and some of its stations overlap the O-P stations in Warmth and Temperateness (e.g., Memphis, Tennessee; and University, Mississippi). Western Mesophytic forest of the Mississippi Valley is here considered a mesic to hydromesic subsection of Braun's Oak-Pine region and relabeled as Oak-Pine Sub-Zone.

Central Hardwoods Sub-Zone. This forest region has, as arborescent dominants, taxa that are cold-tolerant and deciduous. Deciduous taxa also dominate a well-developed subcanopy tree layer, a discontinuous shrub layer, and a dense, rich, seasonally varied herb layer. Evergreen dicots, mainly the shrubs *Rhododendron* spp., *Kalmia latifolia* and *Leucothoe* spp., are confined to the subcanopy tree, shrub, and herb layers; they comprise little of the total basal area and involve only a few taxa. Most dominant deciduous trees have wide distributions in the eastern United States, for example: *Quercus, Fagus, Acer, Tilia, Carya, Fraxinus, Ulmus, Betula, Liriodendron*, and (formerly) *Castanea.* A few are centralized in this Sub-Zone, including *Aesculus glabra, Gymnocladus dioica* and *Cladrastis kentuckea*. Understory deciduous trees include: *Cornus florida, Oxydendron arboreum, Cercis canadensis, Magnolia tripetala, Halesia carolina* and *Diospyros virginiana. Tsuga canadensis*, an evergreen conifer, is a dominant on some mesic upland sites. *Pinus strobus* occurs in successional communities and is usually eliminated by shading of deciduous dicot species. The reader should consult Braun (1950) and Greller (1988) for a detailed description of this forest type.

Maple Sub-Zone. Comprising the Beech-Maple, Maple-Basswood and Beech-Birch-Maple-Basswood associations of Braun (1950), this sub-zone is characterized by cold-tolerant, deciduous trees in the canopy and understory. The shrub layer and herb layer are deciduous as well. Common trees are: *Acer rubrum, Acer saccharum* (co-dominant), *Betula allegheniensis (= B. lutea), Fagus grandifolia* (co-dominant*), Fraxinus americana, Magnolia acuminata, Quercus borealis, Tilia americana*; locally *Liriodendron, Quercus macrocarpa* (northwest); and in the higher elevations of the Appalachian Mountains *Aesculus flava (A. octandra)* and *Halesia monticola. Hamamelis virginiana* and *Viburnum* spp. are common in the sub-canopy. Beautiful spring wildflowers characterize this type.

Oak-Pine Sub-Zone. According to Braun (1950), the Oak-Pine (O-P) region of the Eastern Deciduous Forest reaches its northern limit in southern New Jersey. Braun considered the whole O-P region to be transitional between the Southern Mixed Hardwood Forest (SMHF) region (her Southeastern Evergreen Forest region; Greller's DEC, in part) and the Oak-Chestnut region (O-C). Evergreen dicots do not enter the canopy in the O-P forest zone. Mesic forests in the O-P are dominated by *Fagus grandifolia* (North Carolina, Nesom & Treiber 1977), *Liriodendron tulipifera* (Georgia, Skeen 1974, Skeen et al. 1980), as well as by many species of *Quercus, Carya, Pinus* and also *Liquidambar, Acer rubrum, Nyssa sylvatica* and others. *Pinus, Quercus* and *Carya* dominate on the drier sites. In the present study, upland forests of Cape May, New Jersey, dominated by deciduous trees of mainly southeastern United States distribution (Bernard & Bernard 1971), are classified in Braun's (1950) Oak-Pine (O-P) region, but transitional to Central Deciduous Hardwoods. As noted above, the Wes-

tern Mesophytic (WM) association of Braun (1950) is here considered a Hydro-Mesic subsection of the Oak-Pine Sub-Zone.

Conifer-Hardwood Forest

([Needle-Leaved] Coniferous / Deciduous [Broad-Leaved] Dicotyledonous Forest (Greller's [1989] CD)

In the present study this type is considered to be separate from the Deciduous Forest, a practice that Braun (1950) acknowledges as common. According to Braun this region ranges from "Minnesota to Atlantic Coast, occupying a position between the Deciduous Forest and the Boreal (Conifer) Forest." The CD, which Braun calls Hemlock-White Pine-Northern Hardwood Forest (HWPNH), is characterized by the pronounced alternation of deciduous dicot, coniferous, and mixed communities. The name Conifer / Deciduous Dicot Forest (CD), gives more emphasis to the physiognomy, and allows one to include Küchler's (1964) Spruce-Hardwood forest type as a subdivision of equal rank to the HWPNH. "[*Acer saccharum, Fagus grandifolia, Tilia americana, Betula lutea, Tsuga canadensis* and *Pinus strobus*] are the climax dominants of the region as a whole.... [*Pinus resinosa*] and, in the east, [*Picea rubens*], are characteristic species of the region, the former in dominantly coniferous communities, the latter in dominantly deciduous communities" (Braun 1950). Referring to Little (1971), it is clear that the arborescent dominants of the CD are broad-leaved deciduous taxa and evergreen conifers of northern distribution in eastern and central North America. In Wisconsin, Curtis (1959: 535) lists *Dirca palustris* and *Sambucus pubens* as characteristic shrubs of CD mesic forests; other common shrubs are *Corylus cornuta* and *Lonicera oblongifolia*. The diversity of shrub and herb layers is lower in CD than in DF mesic forests, and decreases with an increase of coniferous trees (Braun 1950, Rogers 1982). Curtis (1959) lists 21 common angiospermous herbs.

Southern Mixed Hardwood Forest

Located in the outer coastal plain and southern part of the Mississippi River Valley, this region has as its dominant life forms (1) deciduous trees (usually composing large parts of the canopy), (2) coniferous trees and (3) broad-leaved evergreen trees. Dominant trees are: (evergreen dicot) *Quercus hemisphaerica, Magnolia grandiflora, Ilex opaca* and *Magnolia virginiana* (wet); (deciduous dicot) *Acer barbatum, Carya glabra, C. tomentosa, Fagus grandifolia, Liquidambar styraciflua, Liriodendron tulipifera, Quercus austrina, Q. falcata, Q. nigra, Q. shumardii, Tilia caroliniana, T. floridana*; (evergreen conifers) *Pinus glabra* and *P. taeda*. The understory includes representatives of all these physiognomic types. The palms *Serenoa repens, Rhapidophyllum hystrix*, and *Sabal minor* may be locally abundant in the understory. Lianas are represented by *Gelsemium sempervirens, Bignonia* (= *Anisostichus*) *capreolata* and *Smilax laurifolia*. Herbs, especially ferns, are common locally (Braun 1950: 301). Cane (*Arundinaria tecta*), often reaching 6 m tall, was once abundant in the Loess Hills of the lower Mississippi Valley.

Mexican Holarctic Dicotyledonous Forest

Greller (1990) recognized four life zones for humid climates in eastem Mexico: (1) Selva Alta Perennifolia or Tropical Rain Forest (TRF), (2) Selva de Orizaba or Orizaban Rain Forest (ORF), (3) Bosque Mexicano de Dicotyledoneas Holarcticos or Mexican Holarctic Dicotyledonous Forest (MHDF), and (4) Bosque Mexicano de Abetos y Cipresos or Mexican Holarctic Coniferous Forest (MHCF). Of these, only the MHDF forest is considered comparable to Eastern Deciduous Forest of the continental United States. MHDF has a canopy dominated by taxa of Holarctic floristic affinities, deciduous (predominantly) and evergreen, as detailed by Miranda & Sharp (1950). It is endemic to Mexico and northern Central America, for nowhere else in North America do taxa such as *Clethra* (Clethraceae), *Dendropanax* (Araliaceae), *Oreomunnea (Engelhardia), Podocarpus* (Podocarpaceae) and *Weinmannia* (Cunoniaceae) dominate in the same stands as *Carpinus, Carya, Juglans, Liquidambar, Pinus* and *Quercus*. *Podocarpus* and *Weinmannia* (contra Good 1974) belong to the Austral or Southern Hemisphere Temperate Flora, and it is the admixture of southern taxa into a matrix of Holarctic dominants that makes this ZE unique. Miranda & Sharp (1950) emphasized this conglomeration of disparate floristic groups strongly in arguing for the uniqueness of their predominantly Holarctic forests. MHDF is distributed from approximately 1000 to 2000 m elevation and occurs above the Orizaban Rain Forest (e.g., Gómez-Pompa 1973: figs. 20, 21). Miranda & Sharp (1950) listed six types of forest dominated by dicotyledons: "oak-mixed hardwoods, *Liquidambar, Platanus, Fagus, Weinmannia* and *Engelhardia*". The first type is most widely distributed. The canopy averages 20 m tall, but reaches 40 m, and includes: *Quercus* spp., *Clethra quercifolia, Liquidambar [mexicana], Meliosma alba, Carpinus [tropicalis], Ostrya virginiana, Oreomunnea* (= *Engelhardia*) *mexicana*, and *Cornus* spp. There is a small-tree layer reaching 10 m tall, with *Cyathea* (a tree fern), *Inga* (Leguminosae), *Oreopanax* (Araliaceae), *Xylosoma* (Flacourtiaceae), *Turpinia* (Staphyleaceae), *Symplocos* (Symplocaceae), *Podocarpus [matudae]*, some other tropical taxa (*Beilschmiedia* and *Rapanea*) and other Holarctic taxa (*Vaccinium, Sambucus, Leucothoe* and *Cornus*). Epiphytes of Orchidaceae, Bromeliaceae, Cactaceae and Araliaceae are present. A shrub layer is present, containing a number of Holarctic taxa and some tropical taxa (*Drypetes, Randia*). Lianas and vines are present, as well as some dicotyledonous herbs.

Both Southern Mixed Hardwood Forest (SMHF) and MHDF are dominated by a mixture of deciduous, Holarctic dicotyledonous trees (*Quercus, Tilia, Magnolia, Fagus, Carya, Liquidambar*) and Holarctic evergreen dicotyledonous trees (*Quercus, Magnolia, Ilex, Prunus*). Pinaceae are widespread on drier sites in both zones. The two types differ in the widespread presence of *Podocarpus* and *Cyathea* and the more local presence of *Weinmannia* and *Drimys* in MHDF, and the absence of these taxa (and their families) from the region north of Mexico.

B. Europe

Deciduous Forests

The following geographic regions of Europe contain deciduous forest (Polunin & Walters 1985):

Atlantic Forest

Under "Atlantic Deciduous woodlands", Polunin & Walters (1985) list two oaks as dominants, *Quercus petraea* and Q.

robur (widespread) plus *Q. pyrenaica* (southwestern Europe). Other trees and shrubs include *Taxus baccata* (conifer), *Betula pendula, B. pubescens, Sorbus aucuparia* and evergreen *Ilex aquifolium*. In addition, other canopy constituents in *Quercus robur*-dominated woodlands are: *Alnus glutinosa, P. tremula, Betula pendula, B. pubescens, Carpinus betula, Malus sylestris, Populus canescens, Prunus avium* and *Ulmus glabra.* Beech (*Fagus sylvatica*) woods occur widely in the Atlantic region (northwest and central France, southeast England and in Belgium) and extend into Central Europe. In the Atlantic region the Beech Forest habitat appears to be excessively well-drained, with less fertile soils. Dominant trees are: *Fagus sylvatica*, *Fraxinus excelsior*, *Sorbus aria* and *Prunus avium;* with *Taxus baccata* and *Ilex aquifolium* in the understory. Forests on more extreme edaphic sites are excluded from consideration here.

Mediterranean Forest

This region extends from the Black Sea coast of Bulgaria, Romania and Turkey, west to the Iberian Peninsula, south of the Alps and the Pyrenees. Adjacent to the coast of the Mediterranean Sea, the forests are dominated by broad-leaved evergreen angiosperms and evergreen conifers: *Ceratonia siliqua, Olea europaea* (coastal Andalusia, AMG, pers. obs.; *Quercus ilex, Q. suber; Quercus coccifera, Q. calliprinos* (both shrub-like) and *Q. lusitanica* (semi-evergreen) and the pine, *Pinus halepensis*. Away from the coasts, deciduous angiosperms enter the forest canopy, especially *Quercus pubescens*. Inland and at higher elevations (to 900 m) in the Mediterranean region, deciduous and semi-evergreen forests are considered climax communities.

Dominant trees of the Mediterranean region are (Rivas Martínez et al. 2011): *Quercus ilex, Quercus lusitanica* (Spain: high elevations, semi-evergreen)*; Quercus pyrenaica* (Western Iberia)*, Quercus pubescens* (widespread, dominant in Corsica and Sicily); *Q. frainetto* (deciduous, enters Mediterranean forests away from coast; to Hungary); *Quercus cerris* (deciduous, widespread from southern Europe to Asia Minor), *Acer monspessulanum, A. obtusatum, A. opalus, Carpinus orientalis, Castanea sativa, Celtis australis, Cercis siliquastrum, Fraxinus ornus, Juniperus thurifera, Ostrya carpinifolia, Prunus mahaleb, Pyrus amygdaliformis, P. elaeagrifolia, Sorbus domestica* and *S. torminalis,* (Spain: southern mid-elevations). Polunin & Walters (1985) list *Quercus faginea, Q. petraea, Q. robur, Q. trojana, Sorbus aria, Acer granatense* and *Cornus mas* as occurring in deciduous oak woods, in addition to some of the other species listed above. Understory taxa include some evergreen angiosperms such as *Buxus sempervirens, Prunus lusitanica*, and *Hedera helix*. Polunin & Walters also list "Horse Chestnut and Walnut woods" as sub-Mediterranean type forests in "damp mountain ravines and valleys, from about 350 to 1350 m in eastern Greece, southern Albania and Macedonia". Here, the dominant trees are: *Acer campestre, A. pseudoplatanus, Aesculus hippocastanum, Alnus glutinosa, Carpinus betulus, Fagus sylvatica, Fraxinus excelsior, F. ornus, Juglans regia, Quercus* spp. and *Tilia cordata.*

Central European Forest

Polunin & Walters (1985) consider Beech (*Fagus*) to be the natural climax forest of Central Europe. Under "Beech and mixed Beech woods", Ellenberg (1988) lists the following genera as forest dominants on the best soils: *Acer, Carpinus, Fagus, Fraxinus, Tilia* and *Ulmus*. Trees grow in uniform stands, reaching 30 m in height. They achieve maturity in 60–100 years and trees decay after about 160 years. They allow very little light to penetrate to the ground layer. As one proceeds south from the Pyrenees, Alps, Carpathians, and central Balkans, beech forests occur higher up on mountains, for example in the Apennines south to Sicily where they occur at 2100 m on Mt. Etna. In southern Sweden and Britain they occupy lowland sites, reaching an upper limit of 300 m; in the northern Alps the upper limit is 1200 m, in the Pyrenees the limit is 1500 m, in Tirol 1550 m, and in the Apennines 1850 m. In the sub-Mediterranean region they show a lower limit of 700 m in the Rhodope Mts of Bulgaria to a lower limit of 1000 m on Mt. Olympus in Greece. *Fagus* often forms the upper limit of forest growth, mainly on limestone (pers. observ., Mt. Triglav, Slovenia).

A wide variety of combinations of beech, other trees and understory plants exists in Central Europe. Beech woods on limestone, beech woods on acid soils and beech woods in the sub-alpine belt are three distinctive types of forest. Beech woods on limestone have the following associated trees: *Abies alba, Ulmus glabra, Acer platanoides, A. pseudoplatanus* and *Fraxinus excelsior*. Beech woods on acidic soils have as associated trees: *Quercus petraea, Acer pseudoplatanus* and *Sorbus aucuparia*. Sub-alpine beech woods show decreasing tree size with increasing altitude. Sometimes they form the upper limit of forest growth on the mountain. Beech is accompanied by *Acer pseudoplatanus*. In southeastern Europe (Greece, eastern Bulgaria, Romania and European Turkey), *Fagus orientalis* is the dominant and forms extensive woods. Associated trees are: *Juglans regia, Quercus cerris, Q. frainetto, Fraxinus angustifolia* var. *oxycarpa* and *F. ornus.*

Pannonian Forest

The steppe region, stretching from central Asia, reaches its western limit in the Hungarian Plain, from a corridor along the Danube River in southern Romania and northern Bulgaria. Here, dry oak woods ("steppe-woodlands") predominate on the richest sites, with *Quercus cerris, Q. frainetto* and *Q. pubescens*. Of lesser importance geographically are *Quercus pedunculiflora, Q. polycarpa* and *Q. dalechampii*; other characteristic trees are listed as *Tilia tomentosa, Carpinus betulus, C. orientalis* and *Acer tataricum*. In *Quercus cerris*-dominated woods the following trees are common: *Carpinus betulus, C. orientalis, Ulmus minor, Pyrus pyraster, P. nivalis, Malus sylvestris, M. dasyphylla, Sorbus terminalis, Acer campestre, A. tataricum, Tilia cordata, T. tomentosa* and *Fraxinus ornus*. Woodlands dominated by *Quercus pubescens* have the following associates: *Quercus robur, Carpinus orientalis, Fraxinus ornus, Quercus petraea, Q. polycarpa* and *Sorbus domestica*; and *Prunus mahaleb, P. spinosa, Pyrus pyraster, Cotinus coggygria, Acer tataricum, Euonymus verrucosus, Cornus mas* and *Ligustrum vulgare.*

C. Caucasian Deciduous Forests

In the Caucasus Mountains of Southwestern Asia there are two major regions of deciduous forest, the Colchic and

Hyrcanic. The Colchic region occupies the eastern end of the Black Sea, the Hycanic region occupies the northern and southern slopes of the Elburz Mountains along the southern coast of the Caspian Sea. Another, small area of deciduous forests occupies the eastern slopes of the Talysch Mountains of Azerbaijan.

Colchic Forest

Colchic forests occupy ca. 3 million hectares. They comprise the following types of arborescent vegetation types: Lowland Hardwood Forest, Mixed Broadleaved Forest and Forests of Foggy Gorges, Sweet Chestnut Forest, Beech Forest, Dark Coniferous Forest (*Abies nordmanniana*, *Picea orientalis* and *Pinus sylvestris*).and Oak (*Quercus*) Woodland. The distinguishing characteristic of these forests is the presence of a tall (up to 4 m) understory, which is dominated by broadleaved evergreen shrubs and small trees (Nakhutsrishvili et al. 2010). Species typical of the Colchic forests are: *Quercus pontica*, *Betula medwedewii*, *B. megrelica*, *Rhamnus imeritina*, *Corylus colchica*, *Sorbus subfusca*, *Vaccinium arctostaphylos* and *Viburnum orientale.* Other trees and shrubs, often considered Tertiary relicts, are: *Quercus hartwissiana*, *Q. imeritina*, *Buxus colchica*, *Staphylea colchica*, *Philadelphus caucasicus*, *Hypericum inodorum*, *Daphne pontica*, *D. alboviana*, *Hedera colchica*, *Primula magaseifolia*, and others. Evergreen broadleaved taxa are: *Rhododendron ponticum*, *R. ungernii*, *R. smirnowii*, *R. caucasicum*, *Laurocerasus officinalis*, *Ilex colchica* and *Ruscus colchicus* (Zazanashvili 1999). Compositional data and a comprehensive list of flora for Colchic forests are available from Box et al. (2000).

Hyrcanian Forest

Hyrcanian forests occupy 1.96 million hectares, in the Talysch and Elburz Moutains. They differ from the Colchic forests in having fewer broadleaved evergreen species, but a greater number of woody taxa. Hyrcanic arborescent vegetation types are listed as: Oak (*Quercus*) Forest, Mixed Broadleaved Forest, Ironwood (*Parrotia persica*) Forest and Ravine Forests (with narrow endemics). Common "relict" species include: *Zelkova carpinifolia*, *Pterocarya pterocarpa*, *Diospyros lotus* and mountain cranberry (*Vaccinium arctostaphylos*). Prominent endemics are listed as: *Quercus castaneifolia*, *Parrotia persica*, *Alnus subcordata*, *Albizia julibrissin*, *Gleditsia caspia* and the lianes *Hedera pastuchowii* and *Danae racemosa.* Also noted are: *Ruscus hyrcanus*, *Ilex hyrcana*, *Buxus hyrcana* (Nakhutsrishvili et al. 2010).

In Azerbaijan, according to Scharnweber et al. (2007), the deciduous forests are represented in the Talysch: "The Talysch Mountains are located in southern Azerbaijan. The border to Iran in the West and South, the Kura-Araks lowland in the north as well as the Caspian Sea in the east, mark the boundary of the area. The altitude ranges from 12 m in Lenkoran up to 2400 m a.s.l. at the Iranian border. With an extension of 21.435 ha, the Hyrcan National Park (former Zapovednik) is embedded in the Talysch Mountains...

...The vegetation represents a relict of the Arcto-Tertiary forests and comprises, in comparison to other European deciduous forests, a very rich flora of woody and endemic species. Examples of endemic tree species are *Parrotia persica*, *Gleditsia caspica*, *Albizia julibrissin* and *Quercus castaneifolia*. It is conspicuous that the flora almost completely lacks coniferous trees. Only a few yews (*Taxus baccata*) are noteworthy. Due to the high humidity epiphytes (mainly cryptogams) are abundant; sometimes bryophytes are completely covering the tree trunks."

Following Schmidt (unpublished, cf. Scharnweber et al. 2007), the main forest types are:

1. Hyrcanian or south Caspian hygro-thermophilous deciduous broad-leaved forests (species rich nemoral summer-green forests with evergreen understory species)

1.1. Hyrcanian lowland-colline mixed broad-leaved forests (south Caspian lowland forest with *Quercus castaneifolia*, *Parrotia persica*, *Zelkova carpinifolia*, *Diospyros lotus*, partly in combination with *Alnus glutinosa* ssp. *arbata-Pterocarya pterocarpa* alluvial forests)

1.2. Hyrcanian colline to montane oak (*Quercus castaneifolia*) and hornbeam (*Carpinus betulus*)-oak forests (oak and mixed hornbeam-oak forest of south Caspian mountains, partly with *Parrotia persica*, *Zelkova carpinifolia*, *Diospyros lotus*, *Acer velutinum*, *Gleditsia caspica*)

2. South Caspian Oriental beech forests

2.1. Montane Oriental beech (*Fagus orientalis*) forest with evergreen species (*Buxus hyrcana*, *Ilex spinigera*, *Ruscus hyrcanus, Danaé racemosa*, *Hedera pastuchowii*), alternating with mixed deciduous broad-leaved forests (*Quercus castaneifolia*, *Alnus subcordata*, *Acer velutinum*)

2.2. Altimontane Oriental beech forests without evergreen species

3. Xerophytic oak (*Quercus macranthera*) forest at the upper timberline (characterized by dry conditions because of its location above the cloud cover zone, distributed only in small parts of the Talysch Mountains)."

D. East Asian Forest

Chinese Deciduous Forest

Wang (1961) published a detailed and extensive review of the forests of China. He recognized two types of forest that resemble closely those of eastern North America as recognized in the present study. These forest types are his Temperate Deciduous Forest and Mixed Mesophytic Forest.

Temperate Deciduous Forest (DFC)

Wang listed three types of deciduous forest in China: 1) *Acer-Tilia-Betula* (northern hardwood species); 2) *Quercus mongolica*; 3) *Betula* forest (at highest elevations and latitudes). In the northeastern provinces, Wang listed 50 trees that are typical of the northern hardwoods forest (in adjacent northern Korea and eastern Siberia) and co-occur with the usual oak-dominated flora; there are numerous species of *Betula, Acer, Tilia, Ulmus, Fraxinus.* The following genera also occur only in this northeastern region: *Quercus, Juglans, Phellodendron, Populus, Maackia, Sorbus, Prunus, Morus, Carpinus, Alnus, Malus, Pyrus, Kalopanax* and *Zelkova; Cornus* and *Lindera* are represented by shrubby species.

Wang listed the following trees as dominants and often forming pure consociations: *Quercus mongolica, Q. dentata, Q. liaotungensis, Q. aliena, Q. acutissima, Q. variabilis and Q. serrata.* Accompanying the oaks are deciduous trees such as *Celtis, Fraxinus, Juglans, Populus, Ulmus, Carpinus, Acer* and *Pistacia.* Rare trees here are: *Ostrya, Euodia, Cornus* and *Sorbus.* Where the Temperate Deciduous Forest abuts the Mixed

Mesophytic Forest, Wang lists the following deciduous trees as occuring in the Deciduous forest (DF): *Magnolia, Cladrastis, Aesculus* and *Cercidiphyllum*. In addition, the following evergreen trees occur at that border: *Quercus baronii, Q. glauca* and *Q. spinosa*.

Mixed Mesophytic Forest Formation (MMFC)

Wang (1961) recognizes a Mixed Mesophytic Forest (MMFC) region in China as distinct from the Deciduous Forest of China (DFC). MMFC zone is centered on the Yangtze Province, extending for over 2000 km over the Lower and Upper Yangtze Valley in two distinct sub-sections. In one area it occurs as a montane belt above the Broad-Leaved Evergreen Forest and below the Montane Coniferous Forest. Climatically it is distinguished from DFC by a cold-month average temperature of 0°C or greater. Structure of the MMFC comprises a canopy crown layer, a lower tree layer, a tall shrub layer, a short shrub layer, an herbaceous ground layer of perennial shade-tolerant plants; there are climbers and epiphytes. Bamboo, although present, is rare in the understory. Wang (1961) compares it to the EDF Mixed Mesophytic association of Braun (1950).

MMFC is distinguished by the large number of species, mostly broad-leaved deciduous trees in a wide variety of families; and by the presence of mixed dominants, never a single dominant. This forest type has taxa derived from the "warm and moist part of the temperate region." It is rich in endemism and monospecific genera. Wang (1961) reports that there are 50 genera of broad-leaved trees occurring in the canopy and 12 genera of conifers. The following taxa are deciduous: *Acer, Aesculus, Albizia, Alnus, Betula, Carpinus, Castanea, Celtis, Diospyros, Euodia, Fraxinus, Gleditsia, Hovenia, Juglans, Kalopanax, Koelreuteria, Maackia, Magnolia, Malus, Morus, Ostrya, Paulownia, Phellodendron, Pistacia, Populus, Prunus, Pterocarya, Pyrus, Quercus, Salix, Sorbus, Tilia, Ulmus, Zelkova*. Taxa that are dominants in the Deciduous Forest of China (DF) are in the understory or are rare canopy dominants. Many tree genera of the Mixed Mesophytic Forest of China are not present in the Deciduous Forest of China: *Alniphyllum, Aphananthes, Camptotheca, Carya, Cercidiphyllum, Cladrastis, Daphniphyllum, Ehretia, Elaeocarpus, Emmenopteryx, Eucommia, Euptelea, Fagus, Firmiana, Gymnocladus, Halesia, Hamamelis, Idesia, Liquidambar, Liriodendron, Litsea, Mallotus, Meliosma, Nyssa, Platycarya, Pterostyrax, Rhus, Sassafras, Styrax,* and *Tetracentron*.

Evergreen broad-leaved trees are scattered throughout this mainly deciduous forest, especially *Castanea henryi, Castanopsis, Pasania* and *Quercus* [*Cyclobalanopsis*]. For a modern treatment of deciduous and evergreen species of *Quercus* and the genus *Cyclobalanopsis*, the reader is referred to Huang et al. 1999. In addition, the following genera occur at lower elevations and near the southern limits of the MMFC: *Cinnamomum, Machilus, Michelia, Phoebe* and *Schima*. Minor broad-leaved evergreen trees in the MMFC are listed as: *Eriobotrya, Illicium, Mangletia, Ormosia, Photinia* and *Ternstroemia*.

Important coniferous trees in MMFC forest are *Cryptomeria* and *Cunninghamia*. Other coniferous trees are scattered throughout the MMFC, within the matrix of deciduous trees: *Cephalotaxus, Juniperus, Nothotaxus, Pseudolarix, Pseudotsuga, Taxus, Torreya* and *Tsuga*. Along the southern border of MMFC with the Broad-Leaved Evergreen Forest are *Amentotaxus, Fokienia, Keteleeria* and *Podocarpus*. *Metasequoia* and *Taiwania* are endemic coniferous trees present in the MMFC; and *Ginkgo* (Ginkgophyta) may still occur naturally.

Japanese Deciduous Forest

Shidei (1974) describes the "Cool-Temperate Broad-Leaved Deciduous forest" of Japan as consisting mainly of beech (*Fagus*) trees with an admixture of large deciduous oak (*Quercus crispula, = Q. grosseserrata*) trees and a thick *Sasa* bamboo understory. The beeches are *Fagus crenata* and *Fagus japonica* (lower, warmer parts). *Abies homolepis* is mixed with beech on the Pacific Ocean side, often in pure stands on steep slopes. *Abies firma* pure stands border beech forest on the Sea of Japan side. Shidei notes that winters on the Pacific Ocean side are dry, whereas winters exhibit deep snows on the Sea of Japan side. The following deciduous trees are listed as components of the deciduous forest of Japan: *Acer mono, A. micranthum, A. japonicum, Acanthopanax sciadophylloides, Fraxinus lanuginosa, Kalopanax innovans, Magnolia obovata, Sorbus alnifolia* and *Tilia japonica*. Conifers, in addition to *Abies*, are *Chamaecyparis obtusa*, *Cryptomeria japonica, Sciadopitys verticillata* and *Thujopsis dolobrata*. Shidei speculates that ancient forests may have been composed of conifers and beeches, judging from sites preserved by traditional landowning clans. Shrub-layer woody plants are: *Benzoin umbellatum, Euonymus* spp., *Ilex macropoda, Hamamelis obtusata, Magnolia salicifolia, Rhus trichocarpa* and *Viburnum* spp. There are many broad-leaved evergreen shrubs on the Sea of Japan side, including *Camellia rusticana*. Herbs there are listed as: *Blechnum nipponicum, Carex conica, Mitchella undulata, Plagiogyria* sp., *Pyrola japonica* and *Shorta uniflora*, among others. In the richest sites and in valleys, the following woody plants occur: *Aesculus turbinata, Alnus maximowiczii, Betula grossa, Cercidiphyllum japonicum, Cornus kousa* and *Euptelea polyandra*. Northeastern forests lack beech trees, possibly due to deeper freezes. Common trees there are *Acer mono, Kalopanax innovans, Quercus crispula, Q. dentata, Tilia maximowicziana, Ulmus davidiana* var. *japonica* and *U. laciniata*.

RESULTS

Table 1 summarizes the Warmth and Temperateness of the deciduous forests and their related types under consideration as determined from plotting the representative weather stations on a Bailey nomogram.

Comparing Several North American Forest Regions that Involve Mainly Deciduous Forest

The present figure 1 is a Bailey nomograph, in which eastern **Deciduous Forest** (DF) is distinguished (approximately) from the **Southern Mixed Hardwood Forest** of Quarterman & Keever [1962] (the Deciduous-Evergreen-Conifer) Forest [DEC]; cf. Greller 1989); and from the **Conifer-Hardwoods Forest** (CD; Conifer-Hardwoods or Braun's (1950) Hemlock-White Pine-Northern Hardwoods). Measures of Warmth appear to be the most useful in distinguishing the range limits of the three. A radian of

Table 1 Warmth and Temperateness of Northern Hemisphere Deciduous Forests and Related Types

Forest Type, Location	Common Tree Species	est. Range of Warmth (W, °C) and Bailey Rating	est. Range of Equability (M, 0-100) and Bailey Rating
Conifer-Hardwood Forest (Hemlock-White Pine-Northern Hardwoods of Braun 1950; Red Spruce-Northern Hardwoods)	(deciduous dicots) *Acer saccharum, Fagus grandifolia, Tilia americana, Betula lutea*; also *Betula papyrifera, Fraxinus americana, Populus tremuloides,* (evergreen conifers) *Tsuga canadensis*, *Pinus strobus, Pinus resinosa*, *Picea rubens*	11.2–12.7 (Very Cool-Cool)	29.2–44.3 (Intemperate- to Sub-Temperate)
Deciduous Forest Eastern, North America – Maple Sub-Zone	*Acer pensylvanicum, A. rubrum, A. saccharum, A. spicatum, Aesculus flava, Amelanchier laevis, Betula alleghenensis, Carpinus caroliniana, Carya ovata, Fagus grandifolia, Fraxinus americana, Magnolia acuminata, Ostrya virginiana, Picea rubens, Populus grandidentata, Quercus alba, Q. borealis, Tilia americana, Ulmus rubra*	12.4–12.8 (Cool**)**	36–49 (Sub-Temperate)
Deciduous Forest Eastern, North America – Central Hardwoods Sub-Zone	*Acer pensylvanicum, A. saccharum, Aesculus flava, Betula lenta, Carpinus caroliniana, Cladrastus kentuckea, Cornus florida, Halesia tetraptera, Liriodendron tulipifera, Magnolia acuminata, M. fraseri, M. tripetala, Quercus alba, Q. coccinea, Q. rubra, Q. velutina, Ostrya virginiana, Prunus serotina, Tilia americana*	12.75–13.85 (Cool-Mild)	43–54 (Sub-Temperate-Temperate)
Deciduous Forest Eastern, North America – Oak-Pine Sub-Zone	*Acer floridanum, A. rubrum, Carpinus caroliniana, Celtis laevigata, Cercis canadensis, Cornus florida, Fagus grandifolia, Juglans nigra, Liriodendron tulipifera, Magnolia acuminata, Ostrya virginiana, Ulmus rubra*; (meso-xeric) *Carya glabra, C. ovata, C. tomentosa, Liquidambar styraciflua, Nyssa sylvatica, Oxydendrum arboreum, Pinus echinata, P. strobus, P. taeda, P. virginiana, Quercus alba, Q. rubra, Q. falcata, Q. stellata, Q. velutina, Sassafras albidum* (See Appendix for more detailed listings of EDF-Oak-Pine Sub-Zone trees in the Piedmont of North Carolina and Georgia)	(13.4–)14.25–14.65 (Mild)	47.5–52 (Sub-Temperate-Temperate)
Southern Mixed Hardwood Forest, se U.S.	(evergreen dicot) *Ilex opaca, Magnolia grandiflora, M. virginiana* (wet), *Quercus hemisphaerica*; (deciduous dicot) *Acer barbatum, Carya glabra, C. tomentosa, Fagus grandifolia, Liquidambar styraciflua, Quercus austrina, Q. falcata, Q. nigra, Q. shumardii, Tilia caroliniana, T. floridana*; (evergreen conifers) *Pinus glabra* and *P. taeda*	14.7–15.45 (Mild)	49–52.5 (Temperate)
Mexican Holarctic Deciduous Forest, Sierra Madre Oriental	*Carpinus [tropicalis], Clethra quercifolia, Cornus* spp., *Liquidambar [mexicana], Meliosma alba, Oreomunnea [Engelhardia] mexicana*, *Ostrya virginiana, Quercus* spp.; (small trees) *Cyathea* (a tree fern), *Inga, Leucothoe, Oreopanax, Podocarpus [matudae]* (a conifer), *Sambucus, Symplocos*, *Turpinia, Vaccinium, Xylosoma*; (other, tropical taxa) *Beilschmiedia* and *Rapanea*	14.6–16.45 (Mild-Warm)	64.5–73.5 (Very Temperate)
Deciduous Forest, Europe (graph not shown)	Sub-Mediterranean: *Acer campestre, A. pseudoplatanus, Aesculus hippocastanum, Alnus glutinosa, Carpinus betulus, Fagus sylvatica, Fraxinus excelsior, F. ornus, Juglans regia, Quercus* spp., *Tilia cordata*; Beech and Mixed Beech: *Acer, Carpinus, Fagus, Fraxinus, Tilia*, *Ulmus*; Pannonic: *Acer tataricum*; *Carpinus betulus, C. orientalis, Quercus cerris, Q. frainetto, Q. pubescens*, with *Quercus pedunculiflora, Q. polycarpa, Q. dalechampii*; and *Tilia tomentosa, Quercus cerris*-dominated Woodlands: *Acer campestre, A. tataricum, Carpinus betulus, C. orientalis, Fraxinus ornus, Malus sylvestris, M. dasyphylla, Pyrus pyraster, P. nivalis, Sorbus terminalis, Tilia cordata, T. tomentosa, Ulmus minor*; *Quercus pubescens*-dominated Woodlands: *Acer tataricum, Carpinus orientalis, Cornus mas, Cotinus coggygria, Euonymus verrucosus, Fraxinus ornus, Ligustrum vulgare, Prunus mahaleb, P. spinosa, Pyrus pyraster, Quercus robur, Quercus petraea, Q. polycarpa, Sorbus domestica*	12.4–14.6 (Cool to Mild)	49–73.5 (Temperate to Very Temperate)
Colchic-Hyrcanian-Talysch, Caucasus Mountains	Colchic: (deciduous dicots) *Alnus glutinosa*, *Carpinus betulus, C. orientalis*, *Castanea sativa*, *Fagus orientalis,* (evergreen conifers) *Abies nordmanniana*, *Picea orientalis, Pinus sylvestris*; Talysch: *Albizia julibrissin, Gleditsia caspica, Parrotia persica, Quercus castaneifolia* and *Taxus baccata;* Hyrcanian: *Diospyros lotus*, *Parrotia persica*, *Quercus castaneifolia*, *Zelkova carpinifolia*, with *Alnus glutinosa* ssp. *arbata-Pterocarya pterocarpa;* (colline to montane) *Acer velutinum*, *Carpinus betulus, Diospyros lotus*, *Gleditsia caspica, Parrotia persica*, *Quercus castaneifolia*, *Zelkova carpinifolia*; (montane oriental beech/evergreen dicots**)** *Fagus orientalis* with *Buxus hyrcana*, *Danaé racemosa*, *Hedera pastuchowii, Ilex spinigera*, *Ruscus hyrcanus*; (mixed deciduous broad-leaved forests) *Acer velutinum, Alnus subcordata*, *Quercus castaneifolia*	13.7–14.7 (Mild)	49.5–57.7 (Temperate)
China Deciduous Forest	(oaks) *Quercus acutissima, Q. aliena, Q. mongolica, Q. dentata, Q. liaotungensis, Q. serrata, Q. variabilis;* (other deciduous trees) *Acer, Carpinus, Celtis, Fraxinus, Juglans, Pistacia, Populus, Ulmus;* (rare trees) *Cornus*, *Euodia, Ostrya, Sorbus*	13.0–13.8 (Cool – Mild)	37.5–44.0 (Sub-Temperate)

Table 1 Continued

Forest Type, Location	Common Tree Species	est. Range of Warmth (W, °C) and Bailey Rating	est. Range of Equability (M, 0-100) and Bailey Rating
China Mixed Mesophytic Forest	(deciduous) *Acer, Aesculus, Albizia, Alnus, Betula, Carpinus, Castanea, Diospyros, Euodia, Fraxinus, Gleditsia, Hovenia, Juglans, Kalopanax, Koelreuteria, Maackia, Magnolia, Malus, Morus, Ostrya, Paulownia, Phellodendron, Pistacia, Populus, Prunus, Pterocarya, Pyrus, Quercus, Sorbus, Tilia, Ulmus, Zelkova*; (evergreen) *Castanea henryi, Castanopsis, Pasania, Quercus;* (conifers) *Cryptomeria, Cunninghamia*, *Cephalotaxus, Juniperus, Nothotaxus, Pseudolarix, Pseudotsuga, Taxus, Torreya, Tsuga*	13.35–14.55 (Mild)	47–49 (Sub-Temperate)
Japan Deciduous Forest	(deciduous) *Acer mono, A. micranthum, A. japonicum, Acanthopanax sciadophylloides, Fraxinus lanuginosa, Kalopanax innovans, Magnolia obovata, Sorbus alnifolia, Tilia japonica;* (conifers) *Abies* spp.*, Chamaecyparis obtusa, Cryptomeria japonica, Sciadopitys verticillata, Thujopsis dolobrata*	12.7–13.5 (Cool)	43–47.5 (Sub-Temperate)

Warmth of 12.7°C separates DF from CD clearly. DF appears to be separable climatically from DEC by an annual freeze period (f °C ≤ 0) of 3 % hr/yr.

In figure 2, the three sub-zones of the Deciduous Forest (*sensu* Greller 1989) can be characterized by Warmth (W) and Temperateness (M, 0-100), as follows:

1) Oak-Pine Sub-Zone (O-P Association of Braun 1950, with some stations of the WM Association):
   W varies from (13.4)14.25 to 14.65°C; M varies from 47.5 to 52.
2) Central Hardwoods Sub-Zone (O-C, MM and some WM):
   W: 12.75–13.85 °C; M: 43–54
3) Maple Sub-Zone (B-M, M-B, BBMB):
   W: 12.4–12.8°C; M: 36.0–49.

The Maple Sub-Zone occupies the coldest regions of the DF. The Warmth radian 12.8°C separates it approximately from the Central Hardwoods Sub-Zone. Central Hardwoods occupy an intermediate position in Warmth, with a Warmth radian of 14°C separating most of this region from the Oak-Pine Sub-Zone. The overlapping stations of the Oak-Pine Sub-Zone are along the Atlantic coast. Oak-Pine Sub-Zone occupies the warmest part of the DF. A freeze period of 4% hr/yr is congruent with the coldness limit of the Oak-Pine Sub-Zone. Inspection of Figure 2 shows that the Maple Sub-Zone ranges from marginally Temperate into the least equable climate of the DF (M = 36, marginally Intemperate), whereas the Central Hardwoods and Oak-Pine Sub-Zones both range from Temperate regimes into the Sub-Temperate.

Deciduous Forests (DF) of Europe in Relation to Eastern North America (not graphed)

A preliminary analysis of deciduous forest climates in Austria, the Czech Republic, England, France, Greece, Hungary, Spain, Portugal, and Turkey, reveals an estimated range of Warmth (W) from 12.4°C (England) to 14.6°C (Grenada, Spain), and a range of Equability (M, 0–100) from 48.3 (Ekisrhir, Turkey) to 72.9 (Cabo de Roca, Portugal). These are mainly lowland stations; the deciduous forests at higher elevations in central European mountains were not analyzed. For the European deciduous forests analyzed, there is nearly complete congruence in Warmth with the EDF Central Hardwoods Sub-Zone (plus some stations of the Western Mesophytic Association [WM] of Braun 1950), approximately W: 12.7–14.9°C. With regard to Temperateness or Equability (M), the DF of Europe ranges from M varies from 49 to 74 (Temperate-Very Temperate), whereas the Central Hardwoods Sub-Zone of the EDF shows a range of M 43–54 (Subtemperate-Temperate). Thus, there is little overlap in equability, with eastern North America being less equable (more extreme).

Deciduous Forests of the Caucasus Mountains in Relation to Eastern North America

Figure 3 is a Bailey nomograph of the Colchic-Hyrcanian-Talysch forests of the Caucasus Mountain region of Western Asia, compared with the Oak-Pine Sub-Zone of the southeastern United States. Most of the stations for both forest types range in Warmth from W = 13.8°C to W = 14.7°C. They are mostly separable by the M = 50 line of temperateness.

Deciduous Forests in China and Japan

Figure 4 and Table 1 show that the Deciduous Forest of Japan is nearly completely congruent in Warmth and Temperateness with the stations of the Central Hardwoods Sub-Zone of the eastern Deciduous Forest of North America (Albany, New York; Warren and Williamsport, Pennsylvania) that are colder and less equable than the other, more southern stations.

Further consideration of Figure 4 shows that the Deciduous Forest of China exhibits a range of Warmth (W = 13.0°C to 13.8°C) that is completely within the range of the Central Hardwoods Sub-Zone of the eastern Deciduous Forest of North America (W = 12.8°C to 14.4°C). In Temperateness, the DF of China ranges from M = 37.5 to M = 44 and is therefore less temperate than any of the stations of the Central Hardwoods of the EDF. The Maple Sub-Zone of the EDF (M varies from 36 to 49) overlaps completely the DF of China in Temperateness, but exists in a colder Warmth regime.

Mixed Mesophytic Forests in China

Figure 5 and Table 1 show that the Mixed Mesophytic Forest of China (Wang 1961) is nearly completely congruent

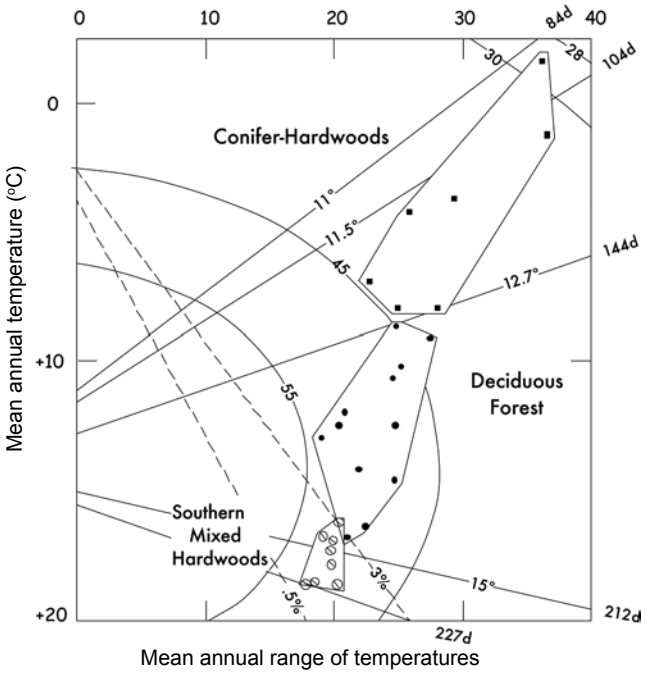

Figure 1 Bailey Nomograph of Deciduous Forest (DF; of Braun 1950) in Eastern North America, delineated by bioclimatic parameters (here and after: all stations in the United States unless otherwise indicated).

■ = Conifer-Hardwoods Forest (Hemlock-White Pine-Northern Hardwoods of Braun 1950). Stations: Abitibi, Ontario, Canada; Kenora, Ontario, Canada; Ludington 4SE, MI; Perce, Quebec, Canada; Pinkham Notch, NH; Sheboygan, WI; Sydney, Nova Scotia, Canada;

ɵ = Southern Mixed Hardwoods Forest (SMHF, Quarterman & Keever 1962; DEC of Greller 1989). Stations: Amite, LA; Columbus, GA; Florence, SC; Moorehead City, NC; Nacogdoches, TX; Vicksburg Mil Pk, MS; Waycross, GA; Wilmington, NC;

• = Deciduous Forest (Mixed Mesophytic, Western Mesophytic and Oak-Chestnut associations of Braun 1950). Stations: Albany, NY; Bluefield, WV; Boston, MA; Brevard, NC; Cairo, IL; Cincinnati, OH; Knoxville, TN; Memphis, TN; University, MS; Warren, PA; Williamsport, PA

Code: A = Annual Range of Mean Monthly Temperatures; T = Mean Annual Temperature; N = water need (not discussed); W = Warmth (temperature at which the growing season begins and ends), (8T+14A)/8+A; Td = number of days above W, 182.6+2.03 arc sin [W–14/4], length of the growing season; M = Temperateness (0–100), $109–30\log(14–T)^2 + (1.46+0.366A)^2$; % = percent of annual hours with sub-freezing temperatures from normal frequency distribution

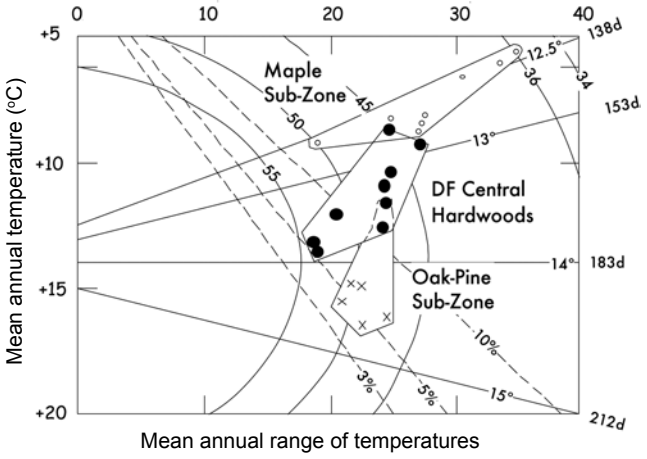

Figure 2 Bailey Nomograph of Deciduous Forest (DF) of Eastern North America, with three sub-zones of Braun (1950) delineated by bioclimatic parameters

● = Central Hardwoods Sub-Zone (Mixed Mesophytic and Oak-Chestnut associations of Braun 1950). Stations: Albany, NY; Bluefield, WV; Brevard, NC; Cape May Court House, NJ (transitional to Oak-Pine); Cincinnati, OH; Great Smoky Mountains Cove (425 m a.s.l.), NC; Knoxville, TN; Newark, OH; Warren, PA; Williamsport, PA.

x = Oak-Pine Sub-Zone (Oak-Pine association of Braun 1950; Mississippi Valley Western Mesophytic Forest (Braun 1950) stations, Memphis, TN and University MS, are equivalent to Greenwood MS). Stations: Atlanta, GA; Centerville, AL; Coalgate, OK; Greenwood, MS; Norfolk, VA

o = Maple Sub-Zone (Maple-Basswood, Beech-Maple associations of Braun (1950) and Beech, Birch, Maple, Basswood association of Greller (1989)). Stations: Banner Elk, NC (3750' a.s.l.); Buffalo, NY; Detroit, MI; Dubuque, IA; Erie, PA; Grand Rapids, MI; Minneapolis, MN; Winona, MN

Code as in Fig. 1

in Warmth and Temperateness with the Oak-Pine Sub-Zone of the eastern Deciduous Forest of North America. Warmth ranges for both are from about 13.7°C to 14.6°C. The range of Temperateness for both is about M=47 to M=52, although the MMFC does not exceed M=49.

DISCUSSION

Eastern Deciduous Forests of North America

Greller (1990, Table 2) outlined the Broad-Leaved Forest Zones of eastern North America, compared them with Walter (1985) Zonobiomes and gave ranges of Warmth, Temperateness, freeze frequency, length of growing season and Effective Precipitation for each. The following is Greller's (1989, 1990) summary of the bioclimatology of three zones of mainly deciduous forest zones in Eastern North America, and a separate type from Mexico.

1. Eastern Deciduous Forest (EDF): Deciduous [Broad-Leaved] Forest (Greller's [1989] DF**).** Walter's (1979) zone: ZB VI; W varies from 12.5 to 14.9°C (Cool / Mild); M varies from 36 to 53 (Subtemperate – Temperate); $f \leq 0$°C changes from 3 to 10 % hrs/yr; S varies from 6.8 to 13.3 inches (Subhumid – Humid); Growing season (t^d) changes from 137.9 to 209.0 days.

2. Conifer-Hardwood Forest (CD) **[**Needle-Leaved] Coniferous / Deciduous [Broad-Leaved] Dicotyledonous Forest (Greller's [1989] CD). Walter's (1979) zone: ZE VI-VIII ; W: from 11.5 to 12.5°C (Cool); M: from 32 to 51 (Intemperate – Subtemperate); $f \leq 0$°C >10 % hr/yr; Growing season (t^d) from 104.1 to 137.9 days; S: from 4.4 to 15.1 inches (Semiarid – Humid).

3. Southern Mixed Hardwoods Forest (DEC or SMHF) Forest of Quarterman & Keever (1962), excluding the stands where evergreen trees do not reach the canopy. Deciduous Dicot – Evergreen Dicot – Coniferous Forest (Greller's [1989] DEC). Walter's zone VI–V ; W: from 14.7 to 15.7°C (Mild to Warm); M: from 49 to 53 (Temperate); $f \leq 0$°C: from 0.5 to 3.0 % hrs/yr; Growing season (t^d): from 203.1 to 233.7 days; S: from 8.8 to 13.0 inches (Humid). One minor change between the present (Fig. 1) analysis

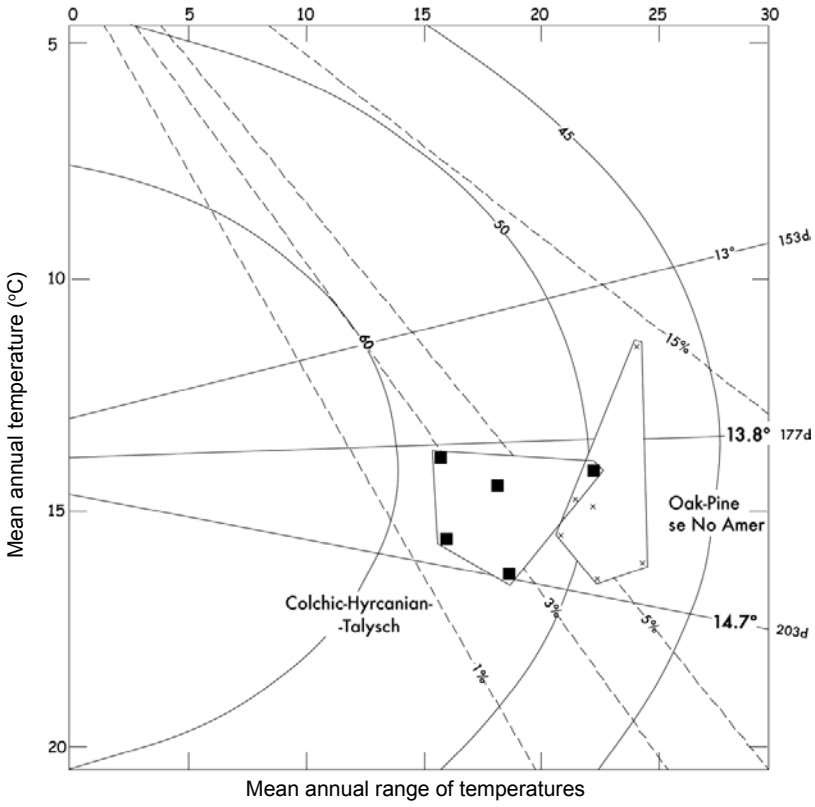

Figure 3 Bailey Nomograph of Colchic-Hyrcanian-Talysch deciduous forest (UNESCO [Mediterranean map] 1968) and Eastern Deciduous Forest of North America – Central Hardwoods Sub-Zone

■ = Colchic-Hyrcanian-Talysch deciduous forest: Batumi, Ajaria, Georgia; Lenkoran, Azerbaijan; Pahlavi, Iran; Sukhumi, Abkhazia; Trabzon, Turkey;

x = Eastern Deciduous Forest of North America – Oak-Pine Sub-Zone: Atlanta, GA; Cape May Courthouse; NJ (transitional to Oak-Chestnut Region); Centerville, AL; Coalgate, OK; Greenwood, MS; Norfolk, VA.

Code as in Fig. 1

and Greller's (1989, 1990) earlier analysis is the transfer of Tallahassee (Florida) from SMHF to Temperate Broad-Leaved Evergreen Forest (TBEF) region, attendant upon subsequent research.

EDF Comparisons with a Holarctic Forest in the Sierra Madre Oriental, Mexico (not graphed)

According to Greller (1990: 394, Fig. 3), Mexican Holarctic Dicotyledonous Forest (MHDF), with an elevation range of 700 m to 3000 m, has a Mild / Warm, Very Temperate climate. Specifically, this corresponds to Walter's zone: ZE VI–V; W(ET): from 14.3 to 16.5°C; M: from 64 to 74; f ≤0°C< 0.1 % hr/yr; growing season (t^d): from 202? to 261 days; Stations: Altotonga, Huachinango, Huatusco, Jalapa, Orizaba 1400 m, Tezuitlan. Mexican Holarctic Dicotyledonous Forest (MHDF) is most closely related to the Southern Mixed Hardwoods Forest (SMHF; DEC of Greller 1990). Nevertheless, the MHDF is much more equable (Very Temperate in Bailey's rating system) than the SMHF, showing no overlap in that statistic. The MHDF, however, also overlaps, in Warmth (W), the Temperate Broad-Leaved Evergreen Forest (TBEF) from central Florida north along the Atlantic coast, and overlaps all of the DEC/Southern Mixed Hardwoods Forest (SMHF). Thus, it is not strictly comparable to the Eastern Deciduous Forest (EDF) proper, but to the transitional forest area (including SMHF and coastal TBEF) to the south of the Oak-Pine Sub-Zone of the EDF.

Deciduous Forests of Europe

Climate is very broadly characterized by average July temperatures of 20–24°C and January mean temperatures ranging from 0 to 5°C. Total annual precipitation is 700–1000 mm/yr.

In Central Europe, the climate is mild with an average annual temperature of about 10°C. Average annual precipitation is about 1000 mm, although the amount may be lower in cooler regimes. Ellenberg (1988) listed the following tree genera as characteristic of the deciduous broad-leaved forests of Europe: *Acer, Alnus, Betula, Carpinus, Crataegus, Fagus, Fraxinus, Ilex, Malus, Populus, Prunus, Pyrus, Quercus, Salix, Sorbus, Tilia* and *Ulmus*.

Overall, the mainly lowland stations of the European deciduous forests show an estimated range of Warmth (W) from 12.4°C to 14.6°C , and a range of Temperateness (M, 0–100) from 48.3 to 72.9. There is **nearly complete congruence** in Warmth of these European, mainly lowland deciduous forests, with the Warmth regime of EDF-Central Hardwoods Sub-Zone (plus some stations of the Western Mesophytic association [WMA] of Braun 1950), approximately W varies from 12.7 to 14.9°C. With regard to Temperateness or Equability (M), there is nearly complete **separation** of the two geographical areas, with DF of Europe ranging from M = 49 to M = 74 (Temperate–Very Temperate), whereas the Central Hardwoods of the North American EDF range from M = 43 to M = 54 (Subtemperate–Temperate).

It is likely that European beech (*Fagus*) forests exist at similar warmth levels to the EDF-Maple Sub-Zone, where beech is often an important component of the forests, even forming relatively pure stands (Appalachian "beech gaps") at the elevational limits of deciduous forests.

Caucasian Deciduous Forests

The Colchic region has high rainfall, averaging 1 500–2 500 mm annually, with a maximum in excess of 4 000 mm, and has been designated a temperate rainforest (Nakhutsri-

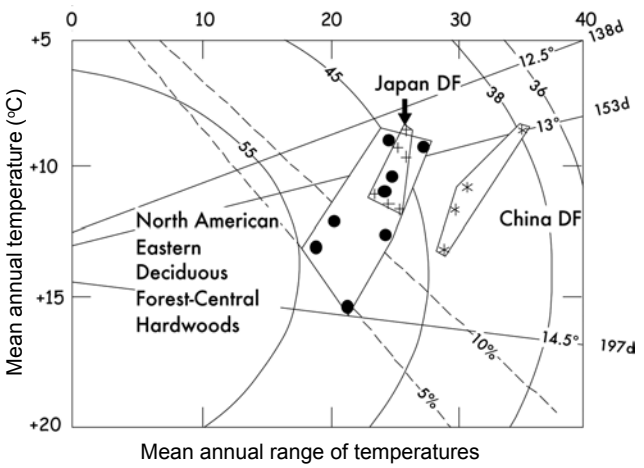

Figure 4 Bailey Nomograph of Deciduous Forest of China (follows Wang 1961); Deciduous Forest of Japan (follows Numata 1974); and Eastern Deciduous Forest of North America – Central Hardwoods Sub-Zone

∗ = Stations for Deciduous Forest of China: Chaoyang; Peking [Beijing]; Tsinan; Kaifeng;

+ = Stations for Deciduous Forest of Japan: Akita; Aomori/ Morioka; Miyako; Nagano; Sapporo; Tanabu;

● = Stations for Eastern Deciduous Forest of North America – Central Hardwoods Sub-Zone: Albany, NY; Bluefield, WV; Brevard, NC; Cape May CH, NJ (trans. to Oak-Pine); Cincinnati, OH; Great Smoky Mountains Cove, 425m asl; Knoxville, TN; Newark, OH; Warren, PA; Williamsport, PA;

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shvili 2010). Bioclimatically, in Warmth and Temperateness, the Caucasian mixed forests compare most closely with the Oak-Pine Sub-Zone of the eastern Deciduous Forest of North America (Fig. 3, Table 1). The North American forest (O-P Sub-Zone) occupies a less temperate regime, existing mainly in Sub-Temperate conditions, where M ≤ 50. The Caucasian forests range within the Temperate (M ≥ 50) regime.

Deciduous Forests of Eastern Asia

In their Figure 1, Nakashizuka & Iida (1995) show Temperate Deciduous Forest of eastern Asia as comprising two sections: CDF, the cool-temperate deciduous forest, and WDF, the warm-temperate deciduous forest. This deciduous forest region is shown ranging from 33°N to about 42°N latitude, and between 110° and 141°E longitude, occurring in China, Korea and Japan.

Box & Fujiwara (2012) discuss the zonation of bioclimates in the "temperate zone" and recognize three subzones. The second they list is: "a generally subcontinental 'typical temperate' zone with four seasons of roughly equal expression and more completely deciduous forests (without conifers [and broad-leaved evergreens] at maturity)..." In their Table 1, Box & Fujiwara define the climate limits of the "Temperate Zone" as "frost every year, to < –15°C; winter means > or < 0°C;" and describe the plant cover as "vegetation mainly winter-deciduous (conifers secondary or disclimax)." Their Table 2 lists three types of vegetation regions for the Temperate Zone: Beech forests (in Japan + Ulleung-do, Chinese S-central mtns; Mixed-oak forests (in N China, Korea, Japan, S Japan-Korea); Mongolian oak forests with *Carpinus* (in N China-Korea-China. This classification was adopted earlier by Nakashizuka & Iida (1995). The Beech forests are dominated by the following species: *Fagus crenata, F. japonica, F. multinervis, F. lucida, F. hayatae, F. engleriana, F. longipetiolata.* The mixed-oak forests are dominated (locally) by: *Quercus acutissima, Q. aliena, Q. variabilis, Q.dentata, Q. serrata.* Mongolian oak forests with *Carpinus* have: *Quercus mongolica, Q. liaotunensis* (N China) and *Q. mongolica-Carpinus* spp. (Korea-China). In their Table 3, Box & Fujiwara relate these East Asian oak and beech-dominated forests to the North American [lower elevation] "Mesophytic forests" (*Fraxinus*, etc.) *Quercus alba-Q. rubra* forests, with *Carya*; and drier versions with *Q. prinus* [=*Q. mon-*

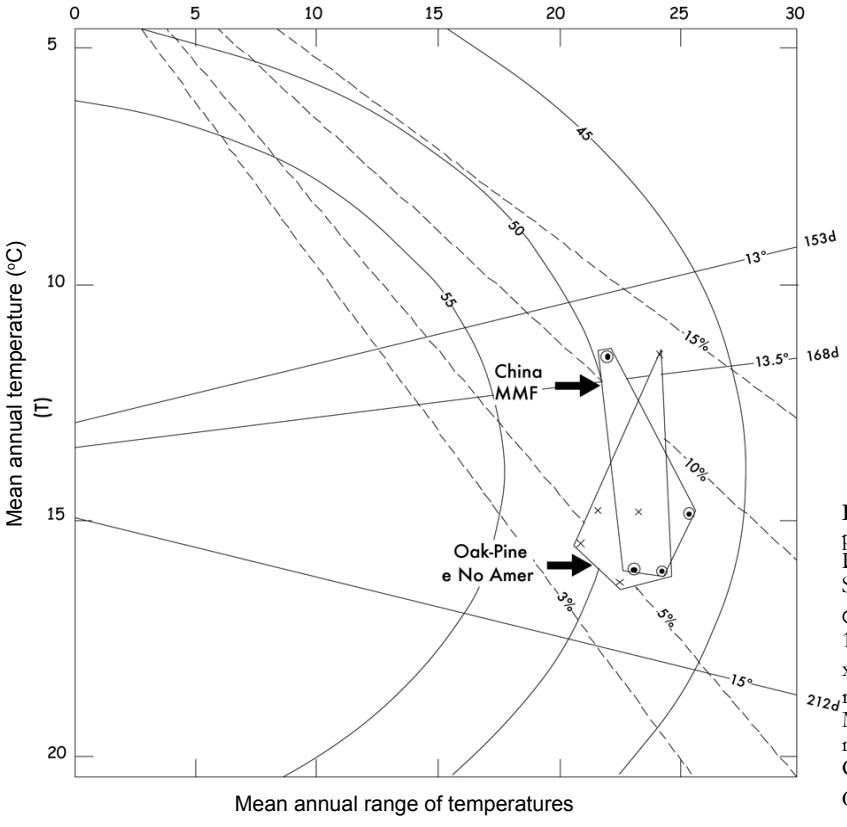

Figure 5 Bailey Nomograph of Mixed Mesophytic Forest of China (Wang 1960) and Eastern Deciduous Forest of North America – Oak-Pine Sub-Zone:

⊙ = Mixed Mesophytic Forest of China (Wang 1961): Engshih, Nanking, Hangchow, Kuling;

x = Eastern Deciduous Forest of North America – Oak-Pine Sub-Zone: Atlanta, GA; Cape May Courthouse; NJ (transitional to Oak-Chestnut Region); Centerville, AL; Coalgate, OK; Greenwood, MS; Norfolk, VA;

Code as in Fig. 1

tana]; [higher elevations] Appalachian "beech gaps" (*Fagus*), *Liriodendron* "cove forests", and [drier] *Quercus-Castanea* forests [formerly]. For Korea, Nakashizuka & Iida (1995) recognize a Warm-Temperate Deciduous broadleaf forest, dominated by *Carpinus tschonoskii, Quercus acutissima, Q. variabilis, Q. dentata, and Q. serrata.*

China

Nakashizuka & Iida (1995) recognize as occurring in China, only the Warm-Temperate Deciduous broadleaf forest. Dominant trees are listed as *Quercus acutissima, Q. aliena, Q. dentata, Q. variabilis and Q. serrata*. Wang (1961) lists the following stations as representative of the Temperate Deciduous Forest: Chaoyang, Peking (Beijing), Tsinan and Kaifeng. Climate data are presented in his Table 8. Wang calls this a "subhumid temperate forest."

Japan

Strictly speaking, this paper recognizes the "Temperate deciduous broad-leaved forest" of Shidei, which encompasses Nozaki & Okutomi's and Kira's *Fagus crenata* forest in the cooler portion and the Intermediate-temperate forest in the warmer portion of the deciduous broad-leaved forest region of Japan (cf. Nakashizuka & Iida 1995). Dominants are listed as: (cool-temperate deciduous broad-leaved forest of Japan) *Fagus crenata, Quercus crispula, Acer japonica, Betula maximowicziana;* (warm-temperate deciduous forest of Japan) *Fagus japonica, Quercus serrata, Carpinus laxiflora, C. tschonoskii* (Nakashizuka & Iida 1995).

CONCLUSION

In North America, and considering Eastern Deciduous (DF) Forest, a radian of Warmth of 12.7°C separates DF clearly from Conifer-Hardwood Forest (CD). DF appears to be separable climatically from Southern Mixed Hardwood Forest (DEC) by an annual freeze period (f °C $\leq$ 0) of 3 % hr/yr.

We see that eastern North American Central Hardwoods deciduous forests are congruent in Warmth with European deciduous forests; however, they live under a much more extreme regime of Temperateness. It is likely that European beech (*Fagus*) forests exist at similar warmth levels to the EDF-Maple Sub-Zone, where beech is often an important component of the forests, even forming pure stands (Appalachian "beech gaps") at the elevational limits of deciduous forests.

When the Colchic-Hyrcanian-Talysch forests of western Asia are compared with deciduous forests of eastern North America, the closest climatic relation is with the Oak-Pine Sub-Zone of the Eastern Deciduous Forest. Most of the stations for both forest types range in Warmth from W = 13.8°C to W = 14.7°C. They are mostly separable by the M = 50 line of temperateness.

The Deciduous Forest of Japan is nearly completely congruent in Warmth and Temperateness with the cooler, northern stations of the Central Hardwoods Sub-Zone of the Eastern Deciduous Forest of North America.

The Deciduous Forest of China exhibits a range of Warmth that is completely within the range of the Central Hardwoods Sub-Zone of the eastern Deciduous Forest of North America. In Temperateness, all the stations of the DF of China are more extreme, less temperate, than any of the stations of the Central Hardwoods Sub-Zone of the EDF.

The Mixed Mesophytic Forest of China (Wang 1961) is nearly completely congruent in Warmth and Temperateness with the Oak-Pine Sub-Zone of the eastern Deciduous Forest of North America.

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Appendix Trees that occur in the Piedmont Physiographic Region (**Oak-Pine Sub-Zone of EDF**) of North Carolina (adapted from Cook 2012) and Georgia, U.S.A (adapted from Brown & Kirkman 1990; based on range maps of Little 1971) that meet at least one of the following criteria for representing the EDF-Oak-Pine Sub-Zone:

1) they are cosmopolitan in the southeastern United States;
2) they have a range centered on or confined to the Southern Appalachian Piedmont in North Carolina and/or Georgia;
3) they are endemic to the Piedmont in Georgia

Code: Distribution of tree taxa in North Carolina: M = Mountains, P = Piedmont, CP = Coastal Plain; species attributes: (vc) = very common, (c) = common, (u) = uncommon, (o) = occasional, (r) = rare, (vr) = very rare. General distribution of tree taxa occurring in Georgia Piedmont: C = cosmopolitan; P = largely confined to or well-represented in the Georgia Piedmont; E = endemic to the Georgia Piedmont; I = introduced in the Georgia Piedmont

Species name	North Carolina			GA
	M	P	CP	
Acer floridanum		vc	u	
Acer leucoderme	r	o		
Acer negundo				C
Acer negundo var. *negundo*	u	c	o	
Acer rubrum var. *rubrum*	vc	vc	c	C
Acer rubrum var. *trilobum*		u	c	
Acer saccharinum	vc	vc	u	
Acer saccharum	c	r		
Aesculus flava	c	r		
Aesculus pavia var. *pavia*		r	o	
Aesculus sylvatica	r	u	r	P
Alnus serrulata	vc	vc	c	C
Amelanchier arborea	u	c	u	C
Amelanchier canadensis		o	u	
Aralia spinosa	vc	vc	u	C
Asimina triloba	o	u	o	C
Baccharis halimifolia		u	c	
Betula lenta	c	r		
Betula nigra	o	c	c	P
Bumelia lycioides				P
Carpinus caroliniana var. *caroliniana*		vc	c	C
Carpinus caroliniana var. *virginiana*	vc	c		
Carya carolinae-septentrionalis		u		P
Carya cordiformis	vc	vc	c	C
Carya glabra var. *glabra*	vc	vc	c	
Carya laciniosa		vc	r	
Carya ovalis	vc	vc	u	C
Carya ovata	vc	vc	u	C
Carya pallida	r	r	u	P
Carya tomentosa	vc	vc	c	C
Castanea dentata	c	r		
Castanea pumila	vc	vc	u	C
Catalpa bignonioides				P
Celtis laevigata var. *laevigata*	o	c	c	P
Celtis occidentalis var. *occidentalis*	vc	vc	r	
Celtis tenuifolia	o	u	u	P
Cephalanthus occidentalis				C
Cercis canadensis var. *canadensis*	u	c	u	C
Chionanthus virginicus	o	u	u	P
Cornus alternifolia	u	r		
Cornus florida	vc	vc	c	P
Cornus stricta (= C. foemina)				P
Crataegus alabamensis		vc	u	
Crataegus alleghaniensis	vc	u		
Crataegus aprica	vc	vc	u	
Crataegus berberifolia		vc	u	

Species name	North Carolina			GA
	M	P	CP	
Crataegus boyntonii	vc	u		
Crataegus buckleyi	vc	u		
Crataegus calpodendron	vc	u		
Crataegus coccinea	vc	r		
Crataegus collina	vc	u		
Crataegus crus-galli	vc	vc	u	
Crataegus flabellata	u	u	o	
Crataegus intricata	vc	u		
Crataegus iracunda	vc	vc	u	
Crataegus lassa		vc	u	
Crataegus macrosperma	vc	vc	u	
Crataegus marshallii		vc	u	
Crataegus munda	vc	vc	u	
Crataegus phaenopyrum	vc	vc	u	
Crataegus pruinosa	vc	vc	u	
Crataegus spathulata	vc	vc	u	
Crataegus viridis		o	u	
Crataegus visenda		vc	u	
Cyrilla racemiflora		r	c	
Diospyros virginiana	u	c	u	C
Euonymus atropurpureus	vc	r		
Fagus grandifolia var. *caroliniana*	c	c	u	C
Frangula caroliniana	vc	r		
Fraxinus americana	c	c	o	C
Fraxinus caroliniana		r	c	
Fraxinus pennsylvanica		c	u	C
Fraxinus profunda	r	r	u	
Halesia tetraptera var. *tetraptera*	c	o	r	
Hamamelis virginiana	vc	vc	c	C
Ilex ambigua	vc	vc	o	
Ilex decidua		vc	c	P
Ilex longipes		r		
Ilex montana	c	u		
Ilex opaca var. *opaca*	vc	vc	c	P
Ilex vomitoria		u	c	I
Juglans cinerea	o	r		
Juglans nigra	u	u	o	C
Juniperus virginiana var. *virginiana*	vc	vc	c	P
Kalmia latifolia	c	u	r	P
Liquidambar styraciflua	r	c	c	C
Liriodendron tulipifera	vc	vc	c	C
Magnolia acuminata	c	o		
Magnolia fraseri	c	r		
Magnolia grandiflora		vc	u	I
Magnolia macrophylla		r		P
Magnolia tripetala	vc	vc	u	

Species name	North Carolina			GA
	M	P	CP	
Magnolia virginiana		r	c	
Malus angustifolia	vc	vc	u	P
Morella [Myrica] cerifera		u	c	
Morus rubra	vc	vc	u	C
Nyssa biflora		r	c	
Nyssa sylvatica	vc	vc	c	C
Ostrya virginiana	vc	vc	u	C
Oxydendrum arboreum	vc	vc	c	P
Pinus echinata	c	c	o	P
Pinus palustris		r	u	
Pinus pungens	u	r		
Pinus rigida	u	r		
Pinus serotina		r	c	
Pinus strobus	c	o		
Pinus taeda		vc	c	P
Pinus virginiana	c	c	r	
Platanus occidentalis	u	c	u	C
Populus deltoides ssp. *deltoides*		vc	o	P
Populus heterophylla		r	u	
Prunus americana	vc	u		P
Prunus angustifolia		vc	c	P
Prunus caroliniana		r	u	I
Prunus serotina var. *serotina*	vc	vc	c	C
Prunus umbellata		vc	o	P
Ptelea trifoliata				P
Ptelea trifoliata	vc	vc	o	
Quercus alba	vc	vc	c	C
Quercus austrina		vc	r	
Quercus bicolor		vc	r	
Quercus coccinea	c	c	u	P
Quercus falcata	o	c	c	P
Quercus georgiana				E
Quercus imbricaria	o	r		
Quercus incana		r	c	
Quercus lyrata		o	u	P
Quercus margaretta		vr	c	
Quercus marilandica var. *marilandica*	o	u	c	C
Quercus michauxii		u	c	P
Quercus montana	c	u	r	
Quercus muehlenbergii	vc	r		P
Quercus nigra		u	c	P

Species name	North Carolina			GA
	M	P	CP	
Quercus oglethorpensis				E
Quercus pagoda		o	c	
Quercus palustris		o		
Quercus phellos		vc	c	P
Quercus prinoides	vc	vr		
Quercus rubra var. *rubra*	c	c	r	P
Quercus shumardii	r	u	r	P
Quercus stellata	u	c	vc	P
Rhamnus caroliniana				P
Rhododendron catawbiense	c	o	r	
Rhododendron maximum	c	o		
Rhus copallinum var. *copallinum*	vc	vc	c	P
Rhus glabra	c	c	r	C
Rhus typhina	c	r		
Robinia pseudoacacia	vc	vc	c	
Salix nigra	vc	vc	c	C
Sambucus canadensis				C
Sassafras albidum	vc	vc	c	C
Sorbus americana	u	r		
Staphylea trifolia	vc	vc	u	
Stewartia malacodendron	r	r	o	
Stewartia ovata	vc	r		
Styrax americanus	r	r	u	P
Styrax grandifolius		u	u	
Symplocos tinctoria	u	r	c	P
Taxodium distichum		r	c	I
Tilia americana var. *americana*	o	r		C
Tilia americana var. *caroliniana*		vc	o	
Tilia americana var. *heterophylla*	c	o	r	
Toxicodendron vernix	r	r	u	
Tsuga canadensis	c	r		
Tsuga caroliniana	u	r		
Ulmus alata	r	c	c	P
Ulmus americana	r	u	c	C
Ulmus rubra	c	c	r	P
Vaccinium arboreum	r	u	c	P
Viburnum cassinoides	c	r		
Viburnum nudum	o	u	c	
Viburnum prunifolium	o	u	o	
Viburnum rufidulum	r	u	u	P