Ber. d. Reinh.-Tüxen-Ges. 27, 165-186. Hannover 2015

Quercus and *Fagus* Forests of Eastern North America

– Elgene O. Box, Georgia, USA –

Abstract

Eastern North America has a large region of temperate deciduous forest (southeastern Canada to the southeastern coastal plain and west to eastern Oklahoma and Texas), including a large "warm-temperate deciduous" forest area. Further south is a strip of warm-temperate, potentially evergreen broad-leaved forest on the coastal plain (North Carolina to Texas), which however is geologically young and covered by complex vegetation mosaics determined mainly by topography and substrate. Forests of both regions are dominated largely by species of *Quercus* (oak) or *Fagus* (beech), in various combinations and types. Beech and some oak species span the full north-south range of the deciduous forests and may extend further south. Oak-hickory forests cover the largest parts of this region, but other types include beech forests in the north and south, mesophytic forests with little oak or beech, so-called "southern mixed hardwoods", and rich southern bottomland forests. The deciduous region extends unusually far south, since evergreens are limited by infrequent but quite low temperature extremes. Questions about vegetation patterns involve the relative advantages of deciduousness and the role of topography or substrate in various situations.

Keywords: Absolute minimum temperature, deciduousness, evergreenness, forest types, southeastern US coastal plain, southern mixed hardwoods, temperate zonation, "wet beeches"

Introduction

Species of *Quercus* and *Fagus* occur primarily in the Typical Temperate (nemoral in Europe) and Warm-Temperate climatic zones (WALTER 1970, 1976; BOX, in press). The typical temperate zone (denoted VI by Walter) occurs within latitudes 30-60ºN on both the east and west sides of the Northern Hemisphere continents, while the warm-temperate zone (denoted Ve) occurs within 25-35ºN only on east sides (BOX 1995a,b; 2002). *Quercus* species also occur in Mediterranean-type climates, which are warm-temperate thermally but occur only on continental west sides.

The zonal vegetation (WALTER 1954, 1970; BOX & FUJIWARA 2013; BOX, in press) of the typical temperate zone is summergreen (deciduous) broad-leaved forest, as occurred naturally over large areas of East Asia, eastern North America, and (at higher latitude) Europe (e.g. WALTER 1968). The zonal vegetation of the warm-temperate zone is glossy-leaved, evergreen ("laurel") forest, still with mainly temperate taxa, as is best developed in East Asia but occurs also in small areas of southeastern Brazil, eastern Australia and northern New Zealand (e.g. TROLL 1948, 1961; SCHMITHÜSEN 1976; KLÖTZLI 1988, TAGAWA 1997).

In the 1940s, though, Tatsu KIRA (1949) observed that deciduous forests could also form permanent communities in drier parts of the warm-temperate zone in interior Japan, where values of his Coldness Index were below about -10ºC, i.e. too cold for broad-leaved evergreen trees (KIRA 1977, 1991). Such "warm-temperate deciduous forests" occur around the Northern Hemisphere (BOX & FUJIWARA 2015) and are significant in the present context because

they contain many *Quercus* species, often also *Fagus*. Such forests occur over large areas of the southeastern USA, as well as northern China and southern Europe (cf. so-called "thermophilous" and "submediterranean" forests).

Zonation and Regions of Eastern North America

Eastern North America has all three of these forest zones: typical temperate (VI), with summergreen forests involving both *Fagus* and *Quercus*; warm-temperate deciduous (Ve-VI), often dominated by *Quercus* (but including *Fagus*); and warm-temperate (Ve), with a climatic potential for evergreen broad-leaved forests, despite many topographic and substrate complications. The map of eastern North America (see Figure 1) shows the deciduous forest region

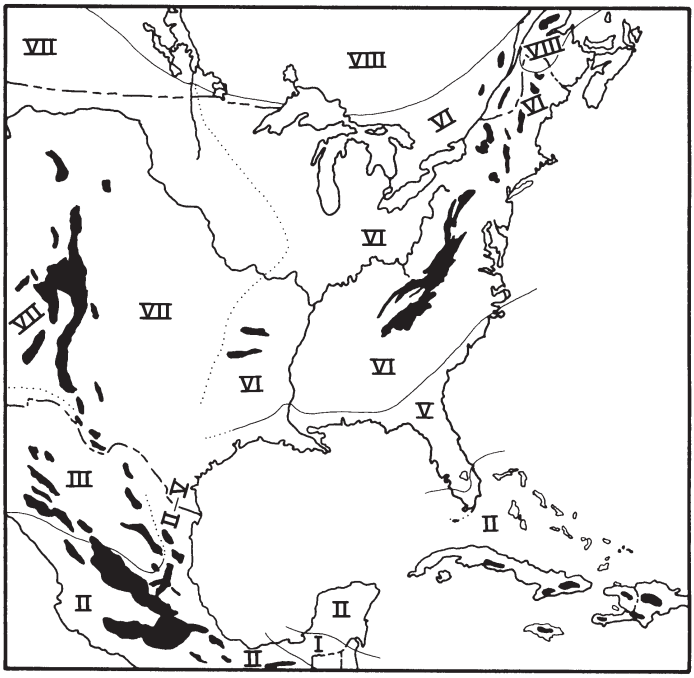


Figure 1: Bioclimatic Zones in Eastern North America.

The lines represent the approximate locations of transitions between the main bioclimatic zones in eastern North America, *sensu* Walter (1970, cf WALTER & BOX 1976), as interpreted by BOX (1988, 2002, and in press). Notation:

VIII = boreal climate, with boreal conifer forests as the zonal vegetation
VI = typical temperate climate, with summergreen deciduous forests as zonal vegetation
V = warm-temperate climate (= Ve), with potentially evergreen broad-leaved forests (zonal)
II = tropical summer-rain climate, with tropical raingreen (deciduous) vegetation types
VII = temperate continental climate, with grasslands as zonal vegetation.

Black areas represent mountains. Note that the Ve-VI boundary, between potentially summergreen and evergreen broad-leaved forests, occurs farther south than in East Asia and farther south than on most climate maps (e.g. Köppen). This is due to control of potential forest types by infrequent extreme low winter temperatures rather than mean temperatures (see BOX 1995a). As a result, the warm-temperate (Ve) region is rather narrow and confined to the southeastern coastal plain, leaving a relatively large interior region with potential for "warm-temperate deciduous" forests (see main text). The map is from BOX (1988).

as large and extending quite far south. This is due to the infrequent but quite low extreme temperatures in the southeastern USA (see Table 1), which preclude woody evergreens even though mean winter temperatures are distinctly higher than at the same latitudes in (evergreen) East Asia (see BOX 1995a, FUJIWARA & BOX 1994). The warm-temperate (potentially evergreen) region is restricted to the southeastern coastal plain (excluding subtropical south Florida), which is low-lying, geologically young, sandy, and one of the world's largest regions where the substrate does not match the climate.

Table 1: Winter Temperatures in the main Temperate Forest Regions of the Northern Hemisphere.

	East Asia	Eastern North America	Europe
Tmin	**low**	**higher**	**[low]**
(mean of coldest month)	-5º to -20ºC in north +3ºC at Shanghai	-5º to -10ºC in north +10ºC at same latitude	-5ºC in north [+5ºC at 44ºN]
Tabmin	**not much lower**	**suddenly much lower**	**[much lower]**
(absolute minimum)	-35º to -40ºC in north -12ºC at Shanghai	-35º to -40ºC in north -20ºC at same latitude	-35º to -40ºC in north [-15ºC at 44ºN]

Mainland East Asia has largely east-west mountains, while North America has north-south mountains and is open in the south much more to invasion by unusually cold air masses from the north. Whereas East Asia has a strong monsoon system that depresses winter temperatures in general, southeastern North America has a source of warm, wet air to its south in winter, namely the Gulf of Mexico. As a result, southeastern North America has higher mean winter temperatures (Tmin) but lower extremes (Tabmin) than does East Asia at the same latitude and comparable geographic position (e.g. elevation, proximity to coast). The result for vegetation is that especially southern Japan but also the East Asian mainland (eastern China) have evergreen broad-leaved forests at latitudes where southeastern North America still has deciduous forest (see BOX 1995a and map by Fujiwara, in FUJIWARA & BOX 1994, p. 305). The temperate region of Europe is at higher latitude, is not directly comparable, and is cooler and deciduous throughout.

North = 40º-45º N latitude in East Asia and eastern North America,
but 60º N in Europe (reference: Uppsala)
South = 30º N latitude (Shanghai) in East Asia and eastern North America,
but 44º N in Europe (reference: Avignon)

Temperatures are generalized over the respective regions, except for site values at Shanghai, Uppsala and Avignon.

The temperate zone has been divided classically into two subzones, called cool-temperate (nemoral, with cool summers) and warm-temperate (with mild winters). Indeed, eastern North America has various species with northern or southern ranges, such as sugar maple (*Acer saccharum*, northern) and southern red oak (*Quercus falcata*). In eastern North America, though, this two-part division leaves a large, subcontinental gap in the middle between the cooler summer of the north and the mild winters of the south. Many species ranges overlap in this area. As a result it seems better to recognize three subdivisions (see also Table 2):

- a cool-temperate zone mainly in New England, with cooler summers (due to higher latitude) and mixed forests involving both non-boreal (*Pinus strobus* and *P. resinosa*) and boreal (*Picea rubens*) conifers;
- a main, generally subcontinental 'typical temperate' zone, with four seasons of roughly equal expression and more completely deciduous forests (without conifers at maturity); and
- a warm-temperate zone with milder winters, quite warm-sultry summers, and the potential for evergreen broad-leaved forests, unless absolute minima are too cold or other factors intervene.

Warm-temperate deciduous forests, based on species compositions, can be seen as falling into parts of the warm-temperate zone but also extending into warmer parts of the typical-temperate zone.

Beech and Oak Species of North America

For better understanding, taxon names for North America follow long-established terminology (e.g. RADFORD et al. 1968). Beech in North America is represented by only two species: *Fagus grandifolia* in the east and the questionably distinct *F. mexicana* (cf LITTLE

Table 2: Zonation in Humid Temperate Eastern North America

Classic Division into 2 parts (e.g. Japan)			**Division into 3 parts** (better in eastern North America)	
Cooler summers in north (Tmax < 24ºC) "**cool-temperate**"	Summergreen forests, with non-boreal and a few boreal conifers		**Cool-Temperate**	Summergreen forests, with non-boreal and a few boreal conifers
		Subcontinental middle, with warm summers but still cold winters	**Typical Temperate**	Summergreen forests, with fewer conifers (mainly successional)
Milder winters in south (Tmin > 8ºC) "**warm-temperate**"	Evergreen broad-leaved forests, with some conifers + deciduous		Warm-Temperate Deciduous	Deciduous forests with southern species (conifers successional)
			Warm-Temperate	Evergreen broad-leaved forests (potentially), unless precluded by fire, substrate or topography

Cool-temperate climates have cooler summers and warm-temperate climates have milder winters. In eastern North America, however, this leaves a large gap in the subcontinental middle, roughly from New York to Tennessee to Missouri. Temperature data in eastern North America argue strongly for division into three parts, as shown above at right. In fact, infrequent extreme cold, plus substrate and topography, all intervene to preclude evergreen broad-leaved forests across much of the warm-temperate southeastern coastal plain (see Table 1 and main text). As a result, "warm-temperate deciduous" forests occur across much of the warm-temperate region, not only as successional stages but also as permanent vegetation (Box 2015). There is also evidence to support this three-part subzonation in East Asia (cf BOX & FUJIWARA 2012).

1965) in the Sierra Madre Oriental mountains of eastern Mexico. On the other hand, oaks in North America number over 200 species (MILLER & LAMB 1985, NIXON 2006). These include around 40 species in the east, about 30 species are deciduous; 2 species (*Q. nigra* and *Q. phellos*) are "tardily deciduous" (not losing their deciduous leaves until December); 2 species (*Q. laurifolia* and *Q. nigra*) can be called semi-evergreen (evergreen only in part of their range); and 6 species are evergreen (generally hard-coriaceous but sometimes truly sclero-phyllous, i.e. brittle).

Fagus species are, worldwide, generally considered rather demanding. In particular they appear to require continuous humidity and soil moisture, but also well drained, aerated soils. As a result, *Fagus* forests occur often on sites that are persistently humid but also have somewhat sandy or otherwise well drained substrates, as on slopes, especially in cloudy montane or subalpine belts. *Fagus* species often produce mono-dominant stands, sometimes over large areas. Many *Fagus* forests have relatively sparse understoreys.

Quercus, on the other hand, has many more species and some with wide ecological amplitudes. Most oaks require less moisture than does beech, but some can also tolerate consistently wet conditions, including temporary or even seasonal flooding (e.g. *Q. bicolor*, *Q. lyrata*, *Q. michauxii*, *Q. laurifolia*, *Q. nigra*). For oaks in North America, though, one must also recognize differences between:

- white oaks (subgenus *Leucobalanus*) and red oaks (*Erythrobalanus,* which occurs only in North America);
- northern and southern species – as well as species that span the full north-south range; and
- deciduous and evergreen species, as well as semi-evergreen and tardily deciduous species.

Oak species in eastern North America can be grouped roughly into four regional sets, plus wider-ranging species, as shown in Figure 2. Some of these species appear similar to some European species (BOX & MANTHEY 2005, 2006). For example, *Quercus macrocarpa* has a mainly northern-continental range (Great Lakes and Mississippi Valley but not east of the Appalachians), reminiscent of *Q. robur* in Europe, which extends eastward in Russia to the Volga River (see Figure 3). The widest range belongs perhaps to *Quercus alba*, which occurs from southern Canada to northern Florida and west to eastern Oklahoma and Texas. Projection of its climate space to Europe suggests the range of *Q. petraea*.

Figure 2: Regional Affinities of Major *Quercus* Forest Species in Eastern North America

North	*Quercus rubra*, *Q. macrocarpa*, *Q. coccinea*	**North**
		↓
Appalachians	*Quercus prinus* [*Q. velutina*]	↓
		Quercus alba, *Q. velutina* [*Q. rubra*, *Q. macrocarpa*]
Midwest	*Quercus stellata*, *Q. marilandica*	↓
		↓
South	*Quercus falcata*, *Q. nigra* + evergreen *Q. virginiana*, *Q. laurifolia*, *Q. hemisphaerica*	**South**

Quercus rubra and *Q. macrocarpa* are more important in the north but do extend far south. *Q. velutina* also has a wide north-south range but is more important on drier, often upslope sites, as in the Appalachians (and further west). *Quercus alba* spans the full north-south range, from southern Canada to central Florida; its range also extends westward to (Missouri and eastern Oklahoma. It is probably the most common and important oak throughout eastern North America. *Quercus stellata* and *Q. marilandica*, with thicker leaves, occur in the east but are more common and become co-dominant in the drier Midwest. *Quercus falcata* and *Q. nigra* are true southern species, occurring commonly in often mixed-oak upland southern forests. The evergreen oaks are found naturally only on the sandy southeastern coastal plain, from southeasternmost Virginia to Texas. *Quercus virginiana* is the potential dominant of upland forests across the southern coastal plain (where not precluded by fire, soil or topography – in most places) as well as in maritime forests (on sand). *Quercus laurifolia* is a bottomland oak, often dominant in floodplains (with *Q. nigra*). *Quercus hemisphaerica* is a colonizer, abundant and forming secondary forests after fire or land abandonment but dying out after about 100 years (replaced usually by *Q. virginiana*, if no fire).

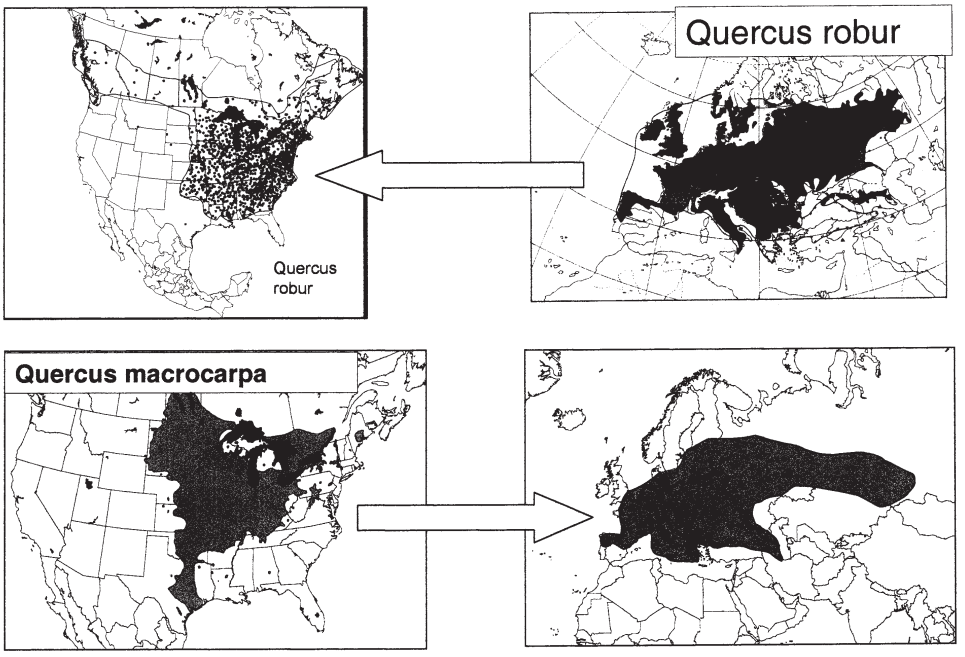


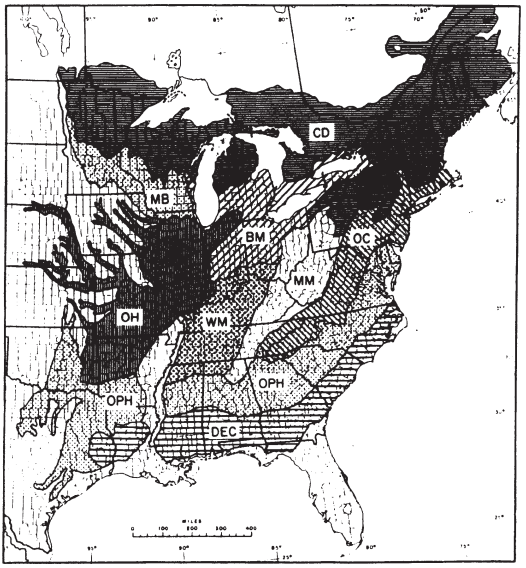
Figure 3: Northern-Continental Ranges of *Quercus robur* and *Quercus macrocarpa*.

The ranges of *Q. robur* (Europe) and *Q. macrocarpa* (North America) are mapped on their home continent, and their climate spaces are then projected to the other continent (cf BOX & MANTHEY 2006). Dots represent climate stations (enclosing curves and final graphic drawn by Manthey). Both species show generally northern distributions that extend well into highly continental interior areas but also southward to some extent. *Q. macrocarpa* seems to be the North American species most similar to *Q. robur*, perhaps a so-called vicariant species. Interesting to note is that *Q. robur* is also projected to fill the southeastern US area not occupied by *Q. macrocarpa* and to extend all across the continent in the north, something that no native, truly temperate-zone tree species does.

Main Forest Types of Eastern North America

The main forest types of the deciduous region of eastern North America were identified by Lucy BRAUN (1950), and these regions are still used (see Figure 4). Detail for the northern and southern transitions was added by GRELLER (1980, 1989), based partly on the concept of "Southern Mixed Hardwoods" forest (QUARTERMAN & KEEVER 1962). Beech-magnolia forests were recognized as a type by DELCOURT & DELCOURT (1974, 1977), and live oak-magnolia forests were identified as an association by DAUBENMIRE (1990). Some other types of evergreen broad-leaved forest and woods across the southeastern coastal plain were described by BOX & FUJIWARA (1988), including topography-dependent situations. These ideas are combined in the regional organization of main forest types shown in Table 3, which includes the Braun types by name as well as transitional and topographically determined situ-ations on the southeastern coastal plain.

Forest types of Eastern North America (from Lucy Braun 1950, modified by Greller 1980)



CD = Conifer-Deciduous Mixed Forest

MM = Mixed Mesophytic Forest (many species, no dominant)

WM = Western Mesophytic Forest (*Quercus* + co-dominants)

OC = Appalachian Oak-Chestnut Forest (*Quercus-Castanea*)

BM = Beech-Maple Forest (*Fagus grandifolia-Acer saccharum*)

MB = Maple-Basswood Forest (*Acer saccharum -Tilia*)

OH = Oak-Hickory Forest (*Quercus-Carya*)

OPH = Oak-Pine-Hickory Forest (pine largely successional)

DEC = Deciduous-Evergreen-Conifer Forest ("Southern Mixed Hardwoods")

Figure 4: Main Forest Types of Eastern North America.

Forests co-dominated by deciduous *Quercus* species occur primarily in the regions WM, OC, OH and OPH; both deciduous and evergreen oaks may co-dominate in the DEC region, with evergreen *Quercus virginiana* a potential mono-dominant in uplands and on coastal dunes, and evergreen *Q. laurifolia* a potential mono-dominant in many floodplain forests. Beech (*Fagus grandifolia*) forests occur primarily in the BM region, but beech can also be an important canopy component in the WM, MB, OPH and DEC regions. *Quercus rubra* and *Fagus grandifolia* also extend into some mixed forests of the CD region.

Tabel 3: Main Forest Types of Eastern North America

Sub-Boreal Mixed Forest	Northern broad-leaved deciduous trees (*Acer*, *Betula*, etc.) + temperate conifers (*Pinus strobus*, *P. resinosa*) + boreal conifers (*Picea rubens*, *P. glauca*, *Abies balsamea*)
Deciduous Forests	Northern Hardwood [Mixed] Forest (*Acer saccharum*, *Betula* spp, ***Fagus***, etc. + *Pinus strobus*)
	Beech-Maple Forest (***Fagus*** *grandifolia* + *Acer saccharum*)
	Maple-Basswood Forest (*Acer saccharum* + *Tilia americana*)
	Mixed Mesophytic Forest (*Fraxinus, Tilia, Liriodendron*, etc. (no clear dominant, ***Quercus*** less importamt)
	Western Mesophytic Forest (***Quercus*** + *Fraxinus, Tilia, Liriodendron, Acer*)
	Appalachian **Oak-Chestnut** Forest (***Quercus*** + *Castanea*) (eliminated by chestnut blight: became mixed *Quercus* forest)

Table 3: continuation

	Piedmont **Oak-Hickory** Forest (***Quercus*** + *Carya*) (with Pinus important in successional stages)
	Mid-western **Oak-Hickory** Forests (***Quercus*** + *Carya*) (S: mainly *Q. stellata* + *Q. marilandica,* N: *Q. macrocarpa*)
Deciduous-Evergreen Transition	"Southern Mixed Hardwoods" Forest (Quarterman & Keever) (southern deciduous + few evergreen broad-leaved trees)
Topogenic:	Bottomland forests, especially ***Quercus*** *michauxii,* ***Quercus*** *nigra*
Warm-Temperate region (potentially evergreen broad-leaved forests)	**Beech**-Magnolia Forest – "climatic climax" but rare ***(Fagus*** *grandifolia + Magnolia grandiflora)*
	Upland **Live Oak**-Magnolia Forest ***(Quercus*** *virginiana, Magnolia grandiflora)*
Topogenic:	Bottomland forests, especially ***Quercus*** *laurifolia,* ***Quercus*** *nigra* Laurophyll forests in moist depressions *(Persea, Magnolia virginiana, Gordonia)*
	Maritime **Live Oak** Forest on coastlines (***Quercus*** *virginiana*) Sandhill **Oakwoods:** evergreen ***(Quercus*** *virginiana,* ***Quercus*** *geminata)* deciduous ***(Quercus*** *laevis, with Pinus palustris*

The classic description of deciduous forest types and regions in eastern North America was given by BRAUN (1950). For the subsequent additions, especially in the warm-temperate region, see main text. Contributions by *Fagus* and *Quercus* species are shown in boldface type (live oak = evergreen *Quercus virginiana*)

Northern Forests

The treatment by Braun showed a Maple-Basswood region (MB: *Acer saccharum-Tilia*) in the western Great Lakes area and a Beech-Maple region (BM: *Fagus-Acer saccharum*) further east – but no region where *Fagus* alone should be dominant. On the other hand, relevés (see Table 4) and some literature suggest that a more complete list of (deciduous) forest types in the north should include:

- *Fagus-Acer* forests, in the Beech-Maple region
- *Quercus* forests (especially *Q. rubra*) with significant *Fagus* in the canopy or understorey
- some localized *Fagus* forests, dominated overwhelmingly by beech (in particular situations)
- *Tsuga* stands (usually small) with *Fagus* as a consistent companion or subdominant species
- *Fagus* woods on older, stabilized coastal dunes (sometimes mixed with oaks)

Some examples of northern beech forests have been described by GRELLER (1989).

An example of a forest dominated by *Fagus* is shown in Relevé 1, from near Québec city. Such forests can be quite shady, and the overall species richness may not be high. Even so, in this example one can see good regeneration of both *Fagus* and *Acer* species. Also common

Table 4: Relevé-Based Suggestions of *Fagus* Forest Types and other Importance in Eastern North America

Type	Cover	Locations	Comments	Richness	Relevés
North					
Fagus forest	5	SE Canada-New England	Less *Acer*, little *Quercus*	21-26	2 Qué, Mass
Fagus-Acer saccharum	3-4	Ontario-New York	Cf Beech-Maple region (Braun)	19-36	3 Ont, NY, Pa
Fagus-Quercus rubra	3	Ontario-New England	Also *Acer*, often other oaks	36-37	2 Ont, Mass
"Carolinian" forest	3	southern Ontario	*Liriodendron*, other "southern" spp.	69	1 Ont
South (interior)					
Fagus-Quercus forest	3	Southern piedmont	With *Q. alba*, *Q. rubra*, *Carya*	37-59	3 NC, Ga
Southern *Fagus* forest	4	(isolated/scattered)	Old growth, with *Liriodendron*, *Q. rubra*	43	1 Ga
Special Situations					
"Beech Gaps"	5	Exposed mtn. slopes	Mono-dominant, may be stunted	27	1 NC
Coastal dunes	4	Barrier islands, on old dunes	Not > 20m; few oaks, maybe *Q. virginiana*	22	1 NC
Coastal floodplains	4	(isolated/scattered)	Flood terraces, + *Liquidambar*, *Liriodendron*	54-55	2 NC
Warm-Temperate (coastal plain)					
Fagus-Magnolia grandiflora	4-3	(isolated/scattered)	Fire-protected sites, to 40m tall, some rich	29-63	7 La, Fla
Southern Mixed Hardwoods	[3]	Scattered throughout	*Fagus* mainly in seral oak-pine understoreys	49	1 Miss
Mexico					
Fagus forests		Sierra Madre Oriental	Montane belts, on slopes	--	- ---

Most of these *Fagus* (beech) forest types were already recognized in literature, but some are suggested from relevé data, mainly from the Eastern North American Vegetation Survey (see MIYAWAKI et al., 1994). *Fagus*-dominated forests do occur in eastern North America but do not cover large areas. Mono-dominant *Fagus* stands occur especially in certain topographic situations, such as humid but well drained mountain slopes, as also in parts of China. The unusual beech floodplain forest on the North Carolina coastal plain was documented by NELSON and TREIBER (1977).

throughout the northern "beech-maple" and "northern hardwoods" regions are *Quercus rubra* forests, usually with *Fagus*. An example is shown in Relevé 2, from near the coast of Maine. Here there is little apparent regeneration by the oaks, but there is a significant *Fagus* understorey and overall diversity is higher. One wonders if such forests will develop eventually into *Fagus* forests.

Relevé 1: *Fagus grandifolia* Forest in Québec

QUEBEC LAC ST-AUGUSTIN Low undulating, W of Cap-Rouge (site #2: Fagus) 27.6.88

	T1	22m	80%	Elevation: 50m	
	T2	15m	30%		
	S	5m	20%		
	H	.8m	20%	30m x 30m	Personnel: AM et al.,MG,EB
T1:	5.5 Fagus grandifolia			1.1 Quercus rubra	1.1 Acer saccharum
	1.1 Acer rubrum				
T2:	3.3 Fagus grandifolia			+ Acer rubrum	
S:	2.2 Fagus grandifolia			+ Acer saccharum	+ Viburnum alnifolium
H:	1.2 Acer saccharum			+ Fagus grandifolia	+ Quercus rubra
	1.3 Clintonia borealis			1.2 Maianthemum canadense	1.2 Dryopteris spinulosa
	+ Aralia nudicaulis			+.2 Dennstaedtia punctilobula	+.2 Epifagus virginiana
	+ Erythronium americanum			+ Hieracium maculatum	+ Medeola virginiana
	+ Mitchella repens			+.2 Prenanthes altissima	+ Streptopus roseus
	+ Trillium erectum			+ Trillium undulatum	+.2 Lycopodium lucidulum
	+.2 Carex arctata			+.2 Carex novae-angliae	+.2 Carex communis
	+ Danthonia spicata			+ Brachyelytrum erectum	+.2 Gramineae sp.

Total number of species counted: 25

Relevé 2: *Quercus rubra* (red oak) Forest in Maine

MAINE FRANKLIN E on hwy 182 (N of Bar Harbor), on dry moder 24.9.89

	T1	27m	70%	Elevation: 70m Slope: 23° to SW	
	T2	12m	20%		
	S	5m	30%		
	H	.6m	35%		
	M		20%	20m x 30m	Personnel: MG,FL,AM,EB et al.
T1:	4.4 Quercus rubra			1.1 Betula papyrifera	1.1 Populus grandidentata
	1.1 **Pinus resinosa**				
T2:	2.2 Fagus grandifolia			1.2 Acer rubrum	1.2 **Picea rubens**
S:	2.3 Fagus grandifolia			2.2 Acer pensylvanicum	1.2 Acer rubrum
	1.1 **Picea rubens**			1.1 Hamamelis virginiana	1.2 Viburnum rafinesquianum
	+ Quercus rubra			+ **Pinus strobus**	+ Corylus cornuta
	+ Diervilla lonicera			+ **Tsuga canadensis**	+.2 Vaccinium angustiflium
	+ Ilex verticillata			+ Viburnum cassinoides	+ Amelanchier sp.
H:	3.3 Gaultheria procumbens			2.2 Aralia nudicaulis	1.2 Viburnum rafinesquianum
	1.2 Oryzopsis sp.			+ Quercus rubra	+ **Pinus resinosa**
	+ Acer rubrum			+.2 **Pinus strobus**	+ **Thuja occidentalis**
	+ Aster acuminatus			+ Aster macrophyllus	+ Maianthemum canadense
	+ Trientalis borealis			+ Cyprepedium acaule	+ Polypodium virginianum
	+ Solidago sp.			+.2 Carex sp.	+ Orchidaceae sp.
M:	2.3 Dicranum montanum			1.2 Leucobryum glaucum	1.2 Dicranum scoparium
	1.3 Dicranum sp.			1.2 Dicranum "small"	1.3 Eurynchium sp.
	+.2 Polytrichum sp.			+.3 Hepaticae "small" #1	+ Hepaticae "small" #2
	1.2 Cladonia squamosa			+.2 Cladonia coniocrea	

Boldface = evergreen species Total number of species counted: 42

In areas with warmer summers (more continental or further south), *Fagus* may be mixed also with tall *Liriodendron tulipifera*, as in the so-called "Carolinian forests" of southern Ontario. *Fagus*, often mixed with *Quercus*, may also form stands on stable, old but undulating coastal dunes, as for example on Long Island (New York) and the Outer Banks of North Carolina. Finally, *Fagus grandifolia* may also occur (e.g. southern Indiana) as "wet beeches" in what are essentially flatwoods, i.e. woods on low-lying, flat areas with seasonally high groundwater if not actual flooding during extended periods in winter or early spring. This locally known phenomenon seems not to be well known in the scientific literature.

Appalachian Forests – Mainly Oak

In the Appalachians the windward west side is wetter and the leeward east side drier, with only about 700-1000mm of precipitation per year. Braun's original description recognized two forest regions: Mixed Mesophytic Forest (MM) on the west side, with little representation by Fagaceae; and Appalachian Oak-Chestnut Forest (OC: *Quercus-Castanea*) on the east side. The mesophytic forests are tall and species-rich, co-dominated in individual stands by up to 10 straight-growing canopy trees such as *Liriodendron tulipifera*, *Liquidambar styraciflua*, *Fraxinus* spp., *Tilia* spp., and *Acer saccharum*, with little *Fagus* or *Quercus*. Some of these forests, in especially humid concavities called "coves", may reach 40m or more in height.

The characteristic oak forests of the Appalachians are found on the drier east side (and were the basis for local furniture industries). When *Castanea dentata* disappeared in the earlier 1900s, its place was taken especially by *Quercus prinus*, the most representative oak of dry upland sites. The composition of a typical Appalachian *Quercus prinus* forest is shown in Relevé 3, from a steep upper slope in north Georgia. This stand is very species-rich and shows some regeneration by the canopy oaks, as is common on drier upland sites. Although it is not in this stand, the wide-ranging *Q. velutina* also appears commonly in most Appalachian oak forests.

Less dry forests in the Appalachians may include significant amounts of *Fagus*, but pure beech stands are limited mainly to two topographic situations: "beech gaps" in concave situations between other slopes, and dense low scrub on especially windy locations (as at Craggy Gardens, in N Carolina).

Relevé 3: Appalachian *Quercus prinus* Forest in North Georgia

GEORGIA FLOYD SPRINGS Johns Mountain, steep upper slope (Chattahoochee Nat. Forest) 21.10.89

T1 20m 70%	Elevation: 340m	Slope: 30° to NW	
T2 10m 30%			
S 4m 30%			
H .5m 30%	40mx20m		Personnel: ENAVS team
T1: 4.4 Quercus prinus	1.1 Quercus rubra		1.1 Fraxinus americana
1.1 Carya glabra	1.1 Carya ovata		1.1 **Pinus virginiana**
T2: 2.3 Quercus prinus	2.2 Acer rubrum		2.3 Cornus florida
S: 3.3 Acer rubrum	2.2 Cornus florida		1.2 Nyssa sylvatica
+.2 Quercus rubra	+ Fraxinus americana		+ **Pinus virginiana**
+ Quercus alba	+ Amelanchier laevis		+ Prunus serotina
+ Ceanothus americanus	+ Philadelphus hirsutus		+ Ulmus alata
+ Vaccinium stamineum	+ Viburnum acerifolium		+ Viburnum rufidulum
H: 1.2 Quercus prinus	+ Ceanothus americanus		1.2 Asplenium platyneuron
1.2 Solidago porteri	1.2 Monarda fistulosa		1.2 Carex pensylvanica
1.2 Vitis rotundifolia	+.2 Panicum scoparium		+.2 Dioscorea villosa
+.2 Polypodium polypodioides	+ Woodsia obtusa		+ Uvularia perfoliata
+ Smilax glauca	+ Parthenocissus quinquefolia		+ Anisostichus capreolata
+ Campsis radicans	+ Coreopsis major		+ Solanum americanum
+ Houstonia purpurea	+ Thalictrum thalictroides		+ Heuchera americana
+ Spigelia marilandica	+ Campanula divaricata		+ Cheilanthes lanosa
+ Phlox divaricata	+ Antennaria plantaginifolia		+ Phlox amoena
+ Desmodium rotundifolium	+ Lysimachia quadrifolia		+ Vernonia noveboracensis
+ **Chimaphila maculata**	+ Vicia caroliniana		+ Hystrix patula
+ Lespedeza hirta	+ Viola palmata		+ Acalypha rhomboidea
+ Galium sp. ("pratense")	+ Penstemon sp.		+ Scutellaria sp.
+ Sanicula sp.	+ Aster sp. (white flower)		+ Aster sp.
+ Senecio "small"	+ Galium "four leaves"		+ Oxalis sp.
+ Arabis sp.	+ Viola sp.		+ Desmodium sp. #1
+ Desmodium sp. #2	+ Trifolium sp.		+ Panicum "narrow"
+ Festuca sp.	+ Gramineae sp. #1		+ Gramineae sp. #2

Boldface = evergreen species — Total number of species counted: 70

Midwestern Forests – also Mainly Oak

In addition to the Maple-Basswood region, BRAUN (1950) also recognized an Oak-Hickory Forest region (OH) covering much of Illinois, Missouri and Arkansas, plus eastern Oklahoma

and Texas. In this drier area, the oakwoods are usually not taller than about 15m and are co-dominated by just two species, *Quercus stellata* and *Q. marilandica*. Both occur throughout the deciduous forest region but are more xeromorphic (e.g. thicker leaves) and dominate only in the west. *Carya* is only a subordinate element. These oakwoods have been summarized in BRYANT et al. (1993; cf BRUNER 1931, KÜCHLER 1964). Woodland mosaics called "cross timbers" represent the transition to the Great Plains grasslands (DYKSTERHUIS 1948).

Forests of the Interior South

This region includes the southern piedmont, from Maryland to Georgia, and its counterpart west of the Appalachians (Kentucky and Tennessee, plus northern Alabama and Mississippi), but not the coastal plain, which is treated in the next section. The region has a typical temperate (VI) climate that becomes "warm-temperate deciduous" (VI-Ve) to the south. The piedmont in particular has gently rolling terrain and reddish clay soils formed during earlier warm-temperate or subtropical conditions. These soils were described as somewhat stratified before plowing and are thus sometimes called podzolic, although most of the A-horizon is now in the Atlantic Ocean or Gulf of Mexico.

BRAUN (1950) recognized two main forest regions: a Western Mesophytic Forest region (WM), along a gradient of increasing dryness westward from the humid Appalachians; and an Oak-Pine-Hickory Forest region (OPH) over most of the piedmont. The WM region covers most of Kentucky and Tennessee and involves still species-rich forests that include significant *Quercus*, usually co-dominating with several other canopy trees, such as *Liriodendron*. The OPH region includes the classic oak-hickory forests (*Quercus-Carya*) of the piedmont, which do not always have so much *Carya* (cf WARE 1992). Pines are common in these forests but are successional and do disappear in older stands. The northern boundary of some "southern pines" such as *Pinus taeda* occurs in Tennessee and was attributed to cold soil in winter, which hinders water uptake by evergreens (HOCKER 1956).

The most characteristic southern forest is the Piedmont oak-hickory forest, an example of which is shown as Relevé 4, from central North Carolina (see also BOX 2015). This stand shows moderate species richness and the typical oak dominance (with some regeneration) in this drier, leeward piedmont area of the Carolinas. Other dry-site species are also apparent, including *Oxydendrum arboreum* (Ericaceae) and *Viburnum* spp., but there is little *Fagus*. In less dry areas, *Fagus* commonly forms a distinct understorey in oak forests over much of the southern piedmont. This becomes apparent in winter, since *Fagus* keeps its dead, brown leaves all winter (marcescence). This has been interpreted as protection against browsing by deer. Again here, one wonders if beech is the potential dominant of such forests at maturity.

Especially in the Carolinas and Georgia, the boundary between the coastal plain and the piedmont is marked by the "fall line" (first impassible rapids encountered by colonists) and by "sandhills" (old, stable dunes now far from their original coastline locations). The sand may have a good humic content or be quite white and sterile. The only trees that grow on the sterile sands are short, deciduous *Quercus laevis* (called 'turkey oak' because the leaves, seen at a distance, suggest flying turkeys); evergreen *Quercus geminata* (similar to *Q. virginiana* but shorter and with true sclerophylls); and the main sandhill pine *Pinus palustris*. The relative topographic positions of these species are illustrated by WHARTON (1978).

Forests of the Southeastern Coastal Plain

The southeastern coastal plain extends from Maryland and Delaware through the Carolinas and Georgia to Florida, and westward to coastal Texas. The climate is warm-temperate

Relevé 4: Piedmont Oak-Hickory Forest in Central North Carolina

NORTH CAROLINA Duke Forest, Korstian (Wooden Bridge Rd), typical upland (kaolinite) 15.6.88

T1 30m 70%	Elevation: 190m		
T2 15m 30%			
S 6m 20%			
H .5m 35%	30mx40m	Personnel: ENAVS team	
T1:	4.3 Quercus alba	2.2 Carya tomentosa	1.2 Quercus rubra
	1.1 Quercus coccinea	1.1 Liriodendron tulipifera	
T2:	3.3 Oxydendrum arboreum	2.2 Acer rubrum	1.2 Cornus florida
	1.1 Juniperus virginiana	+ Fraxinus sp.	
S:	2.3 Acer rubrum	1.2 Cornus florida	2.3 Viburnum acerifolium
	2.2 Viburnum rafinesquianum	1.2 Carya ovata	1.2 Nyssa sylvatica
	+.2 Quercus rubra	+ Liriodendron tulipifera	+.2 Carya glabra
	+ Quercus velutina	+ Diospyros virginiana	+ **Euonymus americanus**
	+ Prunus serotina	+.2 Sassafras albidum	+ Chionanthus virginicus
	+.2 Ilex montana	+ Viburnum pruniflium	+ **Lonicera sempervirens**
	+ Vitis rotundifolia		
H:	2.3 Viburnum acerifolium	1.2 Vaccinium stamineum	1.2 **Euonymus americanus**
	+.2 Carya glabra	+.2 Quercus velutina	+.2 Prunus serotina
	+.2 **Lonicera sempervirens**	1.2 Vitis rotundifolia	1.2 **Chimaphila maculata**
	+ Fagus grandifolia	+.2 Carya tomentosa	+ Carya ovalis
	+ Quercus phellos?	+ Ostrya virginiana	+.2 Vaccinium vacillans
	+ Viburnum rufidulum	+.2 Parthenocissus quinquefolia	+ Smilax glauca
	+ Aureolaria virginica	+.2 Desmodium nudiflorum	+.2 Euphorbia corollata
	+ Potentilla simplex	+.2 Polygonatum biflorum	+ **Tipularia discolor**
	+ Uvularia perfoliata	+ Hieracium sp.	+ Carex sp. #1
	+ Carex sp. #2		

Boldface = evergreen species Total number of species counted: 45

and the vegetation potentially evergreen broad-leaved forest. Such moisture-demanding forests are restricted to small areas, though, due to the mostly sand substrates and the fact that much of the region is covered by pine savannas that are caught in a fire cycle and burn frequently. The vegetation of the coastal plain is in fact a mosaic, due to the further complications of low-lying topography, with rapid vertical changes from wet in depressions (1m or less) to dry (on slightly higher sand) (cf WELLS 1942, WHARTON 1978, CHRISTENSEN 1988).

The amplification by GRELLER (1980) of Braun's original regionalization called most of the coastal plain the Deciduous-Evergreen-Conifer Forest (DEC) region (see Figure 4). At least four types of forest involving *Fagus* or *Quercus* can be recognized:

- *Fagus-Magnolia* grandiflora forests
- a *Quercus virginiana-Magnolia grandiflora* forest association
- "Southern Mixed Hardwoods" forests (varying mixes of deciduous and evergreen trees)
- "bottomland" forests in the broad floodplains and their adjacent, broader lowlands.

Other types include the wide expanses of pine savannas and woodlands, controlled by frequent ground fires that do not damage the pines but maintain a fire-tolerant ground layer (largely palmettos) and keep out more sensitive trees, such as oaks and beech.

Beech-magnolia forest (*Fagus grandifolia-Magnolia grandiflora*) was recognized as the climatic potential vegetation of the coastal plain (DELCOURT & DELCOURT 1974, 1977) but occurs only in small areas that are protected from fire. The example shown as Relevé 5 is from the loop of a protecting river, in Louisiana (WHITE 1987). The trees grow very straight and can reach 40m in height, but the total number of species is often not high. Regeneration of beech and magnolia is reduced in this case by the dense shrub layer of evergreen *Illicium floridanum*, which produces an aromatic oil and may have allelopathic effects. Species-rich beech-magnolia forests, with additional canopy trees, occur especially in "steepheads"

Relevé 5: Tall Beech-Magnolia Forest in Louisiana

LOUISIANA HAMMOND Zemurray Estate, on loess 27.10.89

	T1 40m 80%	Elevation: 40m			
	T2 20m 20%				
	S 5m 60%				
	H .2m 10%	30mx30m		Personnel: KF	
T1:	4.4 Fagus grandifolia	2.2 **Magnolia grandiflora**		2.2 Liquidambar styraciflua	
	2.1 Quercus alba	1.1 Quercus michauxii		+ Quercus nigra	
	+ **Pinus glabra**				
T2:	1.1 **Magnolia grandiflora**	1.1 Quercus michauxii		1.2 Halesia diptera	
	1.2 Carpinus caroliniana	1.2 Symplocos tinctoria		+ Nyssa sylvatica	
S:	3.4 **Illicium floridanum**	2.2 Symplocos tinctoria		1.1 Fagus grandifolia	
	1.2 **Magnolia grandiflora**	1.2 Halesia diptera		1.2 Carpinus caroliniana	
	1.1 **Prunus caroliniana**	+.2 **Ilex vomitoria**		+ **Magnolia virginiana**	
	+ Hamamelis virginiana	+.2 Trichomanes petersii		+ Smilax smallii	
H:	2.2 **Illicium floridanum**	2.2 Carex sp.		1.2 Hexastylis arifolia	
	1.2 Chasmanthium sessiliflorum	+ **Pinus glabra**		+ Carpinus caroliniana	
	+.2 Symplocos tinctoria	+ Smilax smallii		+ Erythrina herbacea	
	+ **Mitchella repens**	+.2 Epifagus virginiana		+.2 Anisostichus capreolata	
	+ Rhus radicans	+ Vaccinium tenellum		+ **Ligustrum sinense**	
	+ Elephantopus tomentosus	+ Smilax rotundifolia		+ Smilax glauca	
	+ Smilax sp.	+ Vitis sp.		+ Panicum sp.	
	+.2 Liliaceae sp.				

Boldface = evergreen species Total number of species counted: 35

Relevé 6: *Quercus virginiana-Magnolia grandiflora* Forest in South Georgia

GEORGIA VALDOSTA Dudley Hammock (military), on mesic, humic sand 22.10.90

	T1 26m 85%	Elevation: 135m			
	T2 16m 30%				
	S 7m 60%				
	H .3m 2%	20m x 30m		Personnel: KF,DH,EB	
T1:	4.4 **Quercus virginiana**	3.3 Quercus nigra		2.2 **Pinus glabra**	
	1.1 Carya glabra	+.2 **Tillandsia usneoides** (ep)		+.2 Polypodium polypodioides	
T2:	3.3 **Magolia grandiflora**	2.2 Quercus nigra		1.2 **Pinus glabra**	
	1.2 Carya glabra	1.1 Quercus alba		1.1 Nyssa biflora	
	1.2 **Tillandsia usneoides**	1.2 Polypodium polypodioides (ep)			
S:	3.3 **Lyonia ferruginea**	3.3 **Vaccinium elliottii**		2.2 **Pinus glabra**	
	2.2 **Vaccinium arboreum**	2.3 **Serenoa repens**		1.2 Quercus nigra	
	1.1 **Osmanthus americanus**	1.2 Vaccinium corymbosum		1.2 Gaylussacia frondosa	
	+ Quercus michauxii	+ **Quercus hemisphaerica**		+ Carya tomentosa	
	+ Liquidambar styraciflua	+ Nyssa biflora		+ Acer rubrum	
	+ **Ilex opaca**	+.2 Vaccinium stamineum		+.2 Vitis rotundifolia	
	1.1 **Tillandsia usneoides**	+.2 Polypodium polypodioides			
H:	1.2 **Quercus virginiana**	1.2 Quercus nigra		+ **Pinus glabra**	
	+ **Ilex opaca**	+.2 **Quercus hemisphaerica**		+ **Persea palustris**	
	+.2 **Lyonia lucida**	1.2 **Mitchella repens**		+.2 Vitis rotundifolia	
	+ **Gelsemium sempervirens**	+ **Smilax bona-nox**		+ Pteridium aquilinum	
	+.2 Uniola laxa	+ Scleria triglomerata			

Boldface = evergreen species Total number of species counted: 32

(slightly upslope, concave seepage areas) (see BOX 2015, Table 12; DELCOURT & DELCOURT 1977).

A potentially more widespread forest type over the broad humic-sand uplands, as well as on stabilized coastal dunes, was recognized by DAUBENMIRE (1990) as the *Quercus virginiana-Magnolia grandiflora* association (see example in Relevé 6). Both co-dominant species have somewhat harder but shade-tolerant evergreen 'lauro-sclerophylls', grow slowly, and tolerate infrequent short-term exposures to temperatures a bit below the usual -15ºC limit for broad-leaved evergreens (cf WOODWARD 1987, BOX 1995a, 1997). These live-oak forests typically have slightly open canopies that may include deciduous *Carya glabra* and are usually festooned with epiphytic *Tillandsia usneoides* (Bromeliaceae). Branches may also be covered with epiphytic *Polypodium polypodioides*. Live-oak forests are usually not species-rich but usually do show continuous regeneration by *Quercus virginiana*. All across the South

these forests have a quite consistent composition that includes mostly evergreen Ericaceae (*Lyonia*, *Vaccinium*, *Gaylussacia*), *Osmanthus americanus* (Theaceae), palmettos (*Sabal*, *Serenoa*), *Ilex opaca*, *Persea borbonia*, and deciduous *Quercus* spp. Many stands have been initiated, after burning or other land abandonment, by the evergreen colonizer *Quercus hemisphaerica*, which has a shorter lifespan of about 100 years and is replaced eventually by *Q. virginiana*. Live-oak forests become simpler westward and can be especially species-poor on coastal dunes and along the Texas coastal plain.

Relevé 7: Mesophytic *Quercus* Forest ("Southern Mixed Hardwoods") in NW Florida

FLORIDA CHATTAHOOCHEE Torreya State Park, Bluffs Trail (lower slope) 24.10.89

T1 38m 80%
T2 14m 30%
S 6m 60%
H .8m 50%

Elevation: 40m Slope: 5° to SE

20m x 35m

Personnel: KF,EB

T1:	3.3 Quercus rubra	2.2 Quercus nigra	3.3 **Pinus taeda**
	2.2 Fraxinus americana	2.2 Liriodendron tulipifera	1.1 **Pinus glabra**
	1.1 Liquidambar styraciflua	1.1 Carya tomentosa	1.2 Quercus alba
	1.2 Vitis rotundifolia	1.2 Tillandsia usneoides (ep)	
T2:	2.2 Quercus rubra	2.2 Quercus nigra	2.2 Carpinus caroliniana
	2.2 Cornus florida	2.2 Halesia diptera	1.1 **Magnolia grandiflora**
	1.1 Juglans nigra	1.1 Fraxinus americana	1.1 Liriodendron tulipifera
	1.1 Ulmus alata	1.1 **Pinus taeda**	+ **Pinus glabra**
	+ Tilia heterophylla	+ Prunus serotina	1.2 Anisostichus capreolata
	1.2 Parthenocissus quinquefolia	1.2 Rhus radicans	1.2 Tillandsia usneoides
S:	2.2 **Magnolia grandiflora**	2.2 Ulmus alata	2.2 Halesia diptera
	2.2 Arundinaria gigantea	1.2 Cornus florida	1.2 **Ilex opaca**
	1.2 Viburnum dentatum	+ Prunus serotina	+ Ostrya virginiana
	+ Acer barbatum	+ Callicarpa americana	+ Torreya taxifolia
	+ **Myrica cerifera**	+ Viburnum rufidulum	+.2 Vitis rotundifolia
	+ **Smilax bona-nox**	+ Hydrangea quercifolia	+ Mikania cordifolia
	+.2 Cornus sp. (small shrub)	+ Crataegus sp.	+ Clematis sp.
H:	2.3 **Sabal minor** (palm)	2.2 Uniola laxa	2.2 Panicum commutatum
	1.2 Dicliptera halei	1.2 Sanicula canadensis	+ Prunus serotina
	1.2 Anisostichus capreolata	1.2 Oplismenus setarius	+.2 Vitis rotundifolia
	+ Parthenocissus quinquefolia	+.2 Rhus radicans	+ Acer barbatum
	+ Mikania cordifolia	1.2 Carex sp. (short)	1.2 Carex sp. (medium)
	+ Celtis laevigata	+ **Euonymus americanus**	+ **Lonicera sempervirens**
	+ Smilax rotundifolia	+ Campsis radicans	+ Cocculus carolinus
	+ Polystichum acrostichoides	+ Elephantopus tomentosus	+ Asplenium platyneuron
	+ Eupatorium rugosum	+ Galium uniflorum	+.2 **Mitchella repens**
	+.2 **Tovara virginiana**	+ Lithospermum tuberosum	+.2 Selaginella apoda
	+ Quercus sp. (seedling)	+ Clematis sp.	+ Desmodium sp.
	+ Tradescantia sp.	+ Oxalis sp.	+ Carex sp. (long)

Boldface = evergreen species

Total number of species counted: 65

The potential "climax on the southeastern coastal plain" was declared by QUARTERMAN and KEEVER (1962) to be Southern Mixed Hardwoods, a mixed-canopy forest involving broad-leaved evergreen and deciduous trees plus some conifers. Such forests may have much deciduous *Quercus* and some *Fagus* but can be quite variable in their actual composition. The authors identified 13 potentially co-occurring canopy species (see list in Table 5), including two *Carya* species, *Liquidambar styraciflua* (a classic warm-temperate deciduous species), *Nyssa sylvatica*, and evergreen *Magnolia grandiflora*. The deciduous oaks are *Quercus alba* (white oak), *Q. falcata* (southern red oak), and *Q. nigra*, a "tardily deciduous" species of immature upland woods as well as mature bottomland forests. The evergreen oaks are *Quercus laurifolia* (semi-evergreen further north) and the colonizer *Q. hemisphaerica*. The conifers are *Pinus taeda*, which is very light-demanding and thus successional, but also *Pinus glabra*, a shade-tolerant pine that indicates relatively mature forests. Also identified as common components were understorey trees *Ilex opaca* and *Vaccinium arboreum* (both evergreen) and *Cornus florida*. The example in Relevé 7 is from a lower slope in northwestern Florida, where a relict conifer *Torreya taxifolia* still has a small area. The stand is species-rich, has a well mixed canopy, and contains most of the requisite species, but it does not show obvious regeneration by the canopy trees. One wonders also why *Quercus virginiana* is absent from such forests. Stands of Southern Mixed Hardwoods have been described and analyzed from various locations (e.g. MONK 1965, WARE 1988, HARTNETT & KROFTA 1989, GIBSON 1992, WARE et al. 1993).

Table 5: Species of "Southern Mixed Hardwood" Forests

Fagus grandifolia	***Quercus laurifolia***
Quercus alba	***Quercus hemisphaerica***
Quercus falcata	***Magnolia grandiflora***
Quercus nigra	
Liquidambar styraciflua	+ ***Pinus glabra*** (shade-tolerant)
Carya tomentosa	+ ***Pinus taeda*** (light-demanding, thus successional)
Carya glabra	
Nyssa sylvatica	

Understorey trees: *Cornus florida,* ***Ilex opaca, Vaccinium arboreum***

Mixed-canopy forests called Southern Mixed Hardwoods were proposed by QUARTERMAN and KEEVER (1962) as the potential "climax in the southeastern coastal plain" of the USA (see main text). Included as potential components in this quite variable mix are both evergreen (in boldface) and deciduous broad-leaved tree species and two conifers; three understorey tree species are also expected consistently.

Relevé 8: *Quercus laurifolia* Floodplain Forest in Lower South Carolina

SOUTH CAROLINA JACKSONBORO Edisto Nature Trail: flat creek floodplain 18.10.90

	T1 30m 80%	Elevation: 40m		
	T2 20m 20%			
	S 6m 30%			
	H .8m 60%	15m x 25m	Personnel: KF,EB,ShM	
T1:	4.4 **Quercus laurifolia**	3.3 Carya aquatica	2.3 Carya glabra	
	1.1 Quercus phellos	1.1 Liquidambar styraciflua	1.1 Celtis laevigata	
	1.2 **Pinus taeda**	1.2 Berchemia scandens	1.2 Vitis rotundifolia	
	1.1 Vitis aestivalis			
T2:	2.2 **Quercus laurifolia**	1.1 Carya aquatica	2.2 Celtis laevigata	
	2.3 Berchemia scandens	1.2 Vitis rotundifolia	1.2 Vitis aestivalis	
	1.1 Quercus lyrata	1.1 Ulmus americana	1.2 Acer rubrum	
	1.1 Carpinus caroliniana	1.1 **Pinus glabra**	1.2 Rhus radicans	
	1.2 Campsis radicans			
S:	2.3 Sabal minor (Palmae)	1.2 Liquidambar styraciflua	1.2 Quercus lyrata	
	1.2 Myrica cerifera	1.2 Rhamnus caroliniana	+ **Pinus taeda**	
	+ Quercus phellos	+ Ulmus americana	+.2 Acer rubrum	
	+ **Ilex opaca**	+ **Ilex myrtifolia**	+ **Sabal palmetto**	
	1.1 Rhus radicans	1.2 **Lonicera japonica**	+ Diospyros virginiana	
	+ Hypericum hypericoides	+ Parthenocissus quinquefolia	+ Mikania scandens	
	+ Wisteria sinensis	+ Crataegus sp.		
H:	3.2 Tovara virginiana	3.3 Carex sp. (cyperoid)	2.2 Lonicera japonica	
	2.2 Rhus radicans	2.3 Leersia lenticularis	2.3 Oplismenus setarius	
	2.3 Uniola laxa	2.2 Carex debilis	2.3 Carex intumescens	
	2.3 Carex sp. (narrow)	2.2 Carex sp. (sketch)	1.1 Quercus phellos	
	1.1 Celtis laevigata	+ **Pinus taeda**	1.2 **Smilax bona-nox**	
	+ Berchemia scandens	+.2 Acer rubrum	+.2 **Sabal minor**	
	1.1 Ampelopsis arborea	1.2 Anisostichus capreolata	1.3 Mikania scandens	
	1.1 Aster linariifolius	1.2 Aster dumosus?	1.1 Boehmeria cylindrica	
	1.1 Fraxinus sp. (seedlings)	+ Crataegus sp.	1.2 Panicum (long lvs)	
	1.2 Panicum sp. (wide)	+ **Persea borbonia**	+.2 Ulmus alata	
	+.2 Vaccinium corymbosum	+ **Ligustrum obtusifolium**	+.2 Rubus trivialis	
	+.2 Smilax glauca	+.2 Asplenium platyneuron	+.2 Botrychium biternatum	
	+ **Gelsemium sempervirens**	+ Elephantopus tomentosus	+ Commelina communis	
	+ Hypericum hypericoides	+ Lobelia elongata	+ Lycopus rubellus	
	+.2 Matelea carolinensis	+.2 **Mitchella repens**	+.3 Onoclea sensibilis	
	+ Cirsium sp.	+ Desmodium sp. (narrow)	+ Desmodium (round)	
	+.2 Juncus sp.	+ Poa sp. (big)	+.2 Polygonum (white)	
	+ Ranunculus sp.	+ Labiatae sp.		

Boldface = evergreen species Total number of species counted: 72

Finally we come to the forests of the 'bottomlands', i.e. the broad, low-lying areas adjacent to actual floodplains (which may also be quite wide on the flat terrain). Various types of Southern Mixed Hardwoods may occur in bottomlands, but the most characteristic floodplain forests are dominated by *Quercus laurifolia*, often with *Q. nigra* (which may also dominate) and sometimes other oaks. Bottomland forests vary widely in species richness, from quite rich to quite simple, depending mainly on length of inundation periods. The example in Relevé 8 is quite species-rich but shows no obvious regeneration by *Q. laurifolia* (which may however require particular circumstances). Also in the canopy here are several (regenerating) species

characteristic of floodplains and other low-lying areas, including *Carya aquatica* (often in swamps), *Quercus phellos*, *Celtis laevigata*, and *Liquidambar styraciflua*; understorey *Q. lyrata* is also a floodplain species. An especially good example of a southern floodplain forest complex, with *Gleditsia* and a 30m canopy, can be seen near the Morris Bridge northeast of Tampa (Florida).

Mexican Beech Forests

In montane belts in the Sierra Madre Oriental of eastern Mexico there are forests that involve several of the same main summergreen tree genera as in the piedmont region of the eastern USA, especially *Liquidambar*, *Carya*, *Carpinus*, *Fagus* and *Quercus* (MIRANDA & SHARP 1950, RZEDOWSKI 1978, GRELLER 2000, VELÁZQUEZ et al. 2000). Some species are the same, such as *Cornus florida* in understoreys. There are too many *Quercus* species to treat here, and they occur in montane belts throughout the subtropical mountains of northern Mexico, especially further west (see VELÁZQUEZ et al. 2000). There are also *Fagus* forests (albeit over small areas), occurring often as pure stands on mid-slopes, as also in the subtropical mountains of China (see Figure 5; cf CAO et al. 1997, PETERS 1997; FUJIWARA et al. 2008). The beech is described as *Fagus mexicana* or as *F. grandifolia* ssp. *mexicana*, and is not so distinct from *Fagus grandifolia* further north. Its period of leaflessness in winter, though, is different, lasting only 2-3 weeks (see PETERS 1995).

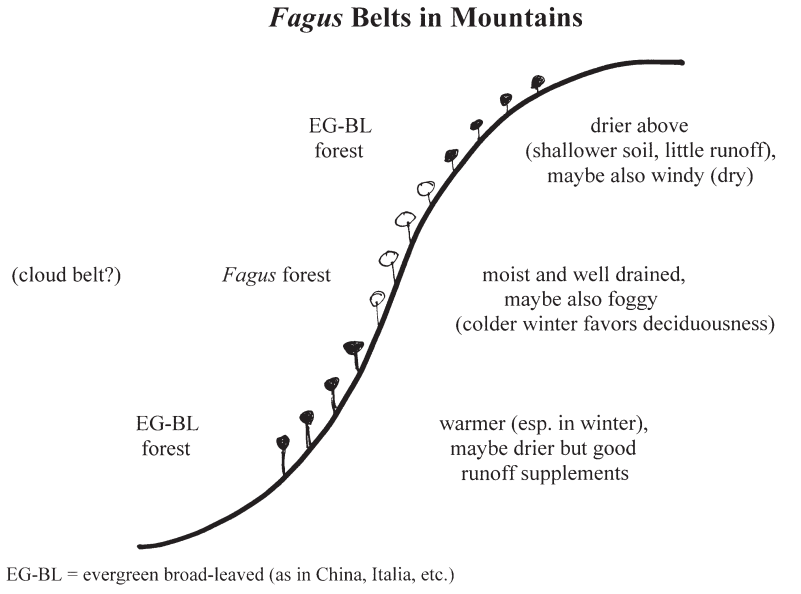


Figure 5: *Fagus* Belts in Mountains (as seen in China, Mexico and the southern Appalachians).

Fagus species seem to need persistent humidity and moist soil but also drained, well aerated soil. This combination is often found especially on some mountain slopes, near the most frequent cloud levels, especially in humid-subtropical montane belts as in central to southern China. A similar situation appears to occur in the Sierra Madre Oriental of (subtropical) northeastern Mexico, which also has localized *Fagus* forests in montane belts (see PETERS 1995). In subtropical China, zonal evergreen broad-leaved forests usually cover larger areas both below and above the topographically limited *Fagus* forest stands.

Summary and Questions

In summary, it appears that American beech may not be so completely different from other beech species, even though it does not form mono-dominant forests over large areas. *Fagus grandifolia* can grow up under other trees but may enter relatively late into *Quercus* stands, due to dryness. The occurrence of the "wet beeches" on flat, seasonally inundated terrain does suggest that American beech, at least, may not require well aerated soil outside its growing season. Are there analogous "wet beeches" elsewhere? On some slopes American beech also shows behavior quite similar to that of other beech species, including the formation of small, topographically determined mono-dominant stands at mid-slope. The lack of *Fagus* in supposedly suitable areas of northern China was attributed by GUO and WERGER (2009) to springtime dryness, but this appears not to play any role in eastern North America.

For *Quercus* in eastern North America there are many more species, ecological types, forest types, and perhaps questions:

- What are the advantages of the "tardy deciduousness" of *Q. nigra* und *Q. phellos*?
- Are there similar patterns in other regions?
- How similar are apparently vicarious *Quercus* species in Europe and North America?
- Why has *Q. rubra* penetrated so successfully into European forests?

Other *Quercus*-related questions involve more general vegetation patterns. For example, are oak-forest stands with beech understoreys likely to develop into beech forests? And what are the advantages of the marcescence shown by *Fagus grandifolia* and by some but not all *Quercus* species? In southern Europe this has been linked to transitional submediterranean climates (SÁNCHEZ DE RIOS et al. 2009, cf GARCÍA-MIJANGOS et al. 2015).

A more global question concerns why deciduous forests go so far south in eastern North America. The infrequent incursions of unusually cold air and resulting low absolute minimum temperatures in the subcontinental southeastern USA would seem to explain this (BOX 1995a), and indeed climate-based global vegetation models show much better agreement with geographic patterns of temperate deciduous and evergreen broad-leaved forests when absolute minimum temperature is included (BOX 1995b). The relative advantages of evergreenness and deciduousness, in various climatic situations, have been considered by numerous authors (e.g. GIVNISH 2002, BOX 1997, DHAILA et al. 1995; cf HILDEBRAND-VOGEL 2002, VAN AUKEN et al. 1981, MOORE 1980, MONK 1966). Advantages of deciduousness include avoidance of seasonal cold or dryness; the possibility to evade late-summer drought (if enough reserves are stored); reduced water loss in the off-season, leaving more soil water for the next growing season; better tolerance of anaerobic soil (e.g. in floodplains, high groundwater); the generally softer leaves (malacophylls) of deciduous species, with higher photosynthesis and potential growth rates; and the fact that many malacophylls are more shade-tolerant and can grow up under the canopies of more light-demanding trees, including most conifers.

Disadvantages include the fact that deciduous species are "not present" at the start of the growing season and may lose their space to evergreens; must produce new leaves each year and thus do not use the whole growing season for photosynthesis and growth; generally need more water than do species with "harder" evergreen leaves (except laurophylls); generally require more nutrients (especially nitrogen) to build their leaves than do most evergreens; may lead to more nutrient loss from local ecosystems, since the softer leaves decompose faster; and usually have intermediate levels of shade tolerance and so may be replaced by highly shade-tolerant laurophyll species.

The location of the deciduous-evergreen transition in the southeastern USA lies suspiciously close, however, to several other boundaries:

- fall-line boundary between the coastal plain and piedmont topographies
- boundary between sand (coastal plain) and clay (piedmont) substrates
- 5ºC isotherm for mean minimum nighttime temperatures in January (cf GRELLER 1989), and
- boundary between potential litter-decomposition and litter-accumulation climates.

This last (BOX, unpublished map) is based on the climatic model for potential litter decomposition rates by MEENTEMEYER (1984) and suggests implications for soil organic content. One wonders what role these factors might play in placing the northern limit for potential evergreen broad-leaved forests, both now and in a global-warming future.

One final question remains, which seems not to have been raised frequently. On flat terrain between Tallahassee and Tampa in northwestern Florida, for example (but also further south), one can see, at least from the highway, surprisingly wide areas of deciduous forest. This is well south of the northern boundary of evergreen broad-leaved forests. Why do deciduous trees and forest stands reach so deep into this true warm-temperate, potentially evergreen zone of Florida? What advantage does deciduousness have here?

Acknowledgement: Many thanks to Kazue Fujiwara, who has helped with fieldwork and ideas over many years.

References

BOX, E. O. (1988): Some similarities in the climates and vegetations of central Honshu and central eastern North America. – Veröff. Geobot. Inst. ETH, Stiftung Rübel (Zürich) **98**: 141-168.

BOX, E. O. (1995a): Climatic relationships of the forests of East and South-East Asia. – In: Vegetation Science in Forestry: Global perspective based on forests ecosystems of East and southeast Asia (E. O. BOX et al., eds.), pp. 23-55. Kluwer Academic Publishers, Dordrecht.

BOX, E. O. (1995b): Global Potential Natural Vegetation: Dynamic Benchmark in the Era of Disruption. – In: Toward Global Planning of Sustainable Use of the Earth — Development of Global Eco-engineering (Sh. Murai, ed.), pp77-95. Elsevier, Amsterdam.

BOX, E. O. (1997): Bioclimatic Position of Evergreen Broad-Leaved Forests. – In: Island and High-Mountain Vegetation: Biodiversity, Bioclimate and Conservation, pp 17-38. Procs., annual IAVS meeting, Tenerife, April 1993. Universidad de La Laguna, Servicio de Publicaciones, Tenerife (Canary Islands, Spain).

BOX, E. O. (2002): Vegetation analogs and differences in the Northern and Southern Hemispheres: A global comparison. – Plant Ecology **163**: 139-154.

BOX, E. O. (2015): Warm-Temperate Deciduous Forests of Eastern North America. – In: Warm-Temperate Deciduous Forests around the Northern Hemisphere (E. O. BOX and K. FUJIWARA, eds.), pp 225-255. Geobotanical Studies. Springer-Verlag.

BOX, E. O. (in press). World Bioclimatic Zonation. – In: Vegetation Structure and Function at Multiple Spatial, Temporal and Conceptual Scales (E. O. Box, ed.). Springer-Verlag.

BOX, E. O. & K. FUJIWARA (1988): Evergreen broad-leaved forests of the southeastern United States: preliminary description. – Bull. Inst. Environm. Sci. Technol., Yokohama Natl. Univ. **15**: 71-93.

BOX, E. O. & K. FUJIWARA (2012): A comparative look at bioclimatic zonation, vegetation types, tree taxa and species richness in Northeast Asia. – Botanica Pacifica (Vladivostok) **1**: 5-12.

BOX, E. O. & K. FUJIWARA 2013 (2005): Vegetation Types and their Broad-Scale Distribution. – In: Vegetation Ecology (E. VAN DER MAAREL, ed.), 2nd ed., pp 455-485 (1st ed.: pp 106-128). Blackwell Scientific, Oxford.

BOX, E. O. & K. FUJIWARA (eds.) (2015): Warm-Temperate Deciduous Forests around the Northern Hemisphere. – Geobotanical Studies. Springer-Verlag. 292pp.

BOX, E. O. & M. MANTHEY (2005): Oak and other deciduous forest types of eastern North America and Europe. – Botanika Chronika (Greece) **18**(1): 51-62.

BOX, E. O. & M. MANTHEY (2006): Conservation of deciduous tree species in Europe: Projecting potential ranges and changes. – In: Nature Conservation: Concepts and Practice (D. GAFTA and J. AKEROYD, eds.), pp. 241-253. Springer-Verlag, Berlin.

BRAUN, E. L. (1950): Deciduous Forests of Eastern North America. Philadelphia: Blakiston 596 pp.

BRUNER, W. E. (1931): The vegetation of Oklahoma. – Ecol. Monogr. **1**: 101-188.

BRYANT, W. S., W. C. MCCOMB & J. S. FRALISH (1993): Oak-Hickory Forests (Western Mesophytic/Oak-Hickory Forests). – In: Biodiversity of the Southeastern United States: Upland Terrestrial Communities (W. H. MARTIN et al., eds.), pp 143-201. John Wiley & Sons, New York.

CAO K.-F., R. PETERS & R. A. A. Oldeman (1995): Climatic range and distribution of Chinese *Fagus* species. – J. Vegetation Science **6**: 317-324.

CHRISTENSEN, N. L. (1988) : Vegetation of the Southeastern Coastal Plain. – In: North American Terrestrial Vegetation (M. G. BARBOUR and W. D. BILLINGS, eds.), pp. 317-363. Cambridge University Press.

DAUBENMIRE, R. F. (1990): The *Magnolia grandiflora* - *Quercus virginiana* forest of Florida. – Amer. Midland Naturalist **123**: 331-347.

DELCOURT, H. R. & P. A. DELCOURT (1974): Primeval magnolia-holly-beech climax in Louisiana. – Ecology **55**: 638-644.

DELCOURT, H. R. & P. A. DELCOURT (1977): Presettlement magnolia-beech climax of the Gulf Coastal Plain: quantitative evidence from the Apalachicola River Bluffs, north-central Florida. – Ecology **58**: 1085-1093.

DHAILA, S., S. P. SINGH, G. C. S. NEGI & Y. S. RAWAT (1995): Shoot-growth phenology of co-existing evergreen and deciduous species in an oak forest. – Ecological Research **10**: 151-159.

DYKSTERHUIS, E. J. (1948): The vegetation of the western cross timbers. – Ecol. Monogr. **18** :27-376.

FUJIWARA, K. & E. O. BOX (1994): Evergreen Broad-Leaved Forests of the Southeastern United States. – In: Vegetation in Eastern North America (A. MIYAWAKI et al., eds.), pp 273-312. Tokyo University Press.

FUJIWARA, K., YOU H.-M., TANG Q., A. HARADA, WANG ZH.-X. & WANG LIN (2008): Deciduous *Quercus* and *Fagus* Forests in Asia. In: Integrated Vegetation Mapping of Asia (K. Fujiwara, leader), pp 111-129. – Report to Japan Society for Promotion of Science.

GARCÍA-MIJANOS, I., J. A. CAMPOS, I. BIURRUN, M. HERRERA & J. LOIDI (2015): Marcescent forests of the Iberian Peninsula: floristic and climatic characterization. – In: Warm-Temperate Deciduous Forests around the Northern Hemisphere (E. O. BOX and K. FUJIWARA, eds.), pp 119-138. Springer-Verlag.

GIBSON, D. J. (1992): Vegetation-environment relationships in a Southern Mixed Hardwood forest. – Castanea **57**: 174-189.

GIVNISH, T. J. (2002): Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. – Silva Fennica **36**: 703-743.

GRELLER, A. M. (1980): Correlation of some climatic statistics with distribution of broadleaved forest zones in Florida, USA. – Bull. Torrey Botan. Club **107**: 189-219.

GRELLER, A. M. (1988): Deciduous Forest. – In: North American Terrestrial Vegetation (M. G. BARBOUR and W. D. BILLINGS, eds.), pp. 287-316. Cambridge University Press.

GRELLER, A. M. (1989): Correlation of warmth and temperateness with the distributional limits of zonal forests in eastern North America. – Bull. Torrey Botan. Club **116**: 145-163.

GRELLER, A. M. (1990): Comparison of humid forest zones in eastern Mexico and southeastern United States. – Bull. Torrey Botan. Club **117**(4): 382-396.

GRELLER, A. M. (2003): A review of the temperate broad-leaved evergreen forest zone of southeastern North America: floristic affinities and arborescent vegetation types. – Botanical Review **69**(3): 269-299.

GUO K. & M. J. A. WERGER (2009): Warum die chinesischen Buchenarten subtropisch und nicht temperat verbreitet sind. – Ber. Reinh. Tüxen Ges. **21**: 104-110.

HARTNETT, D. C. & D. M. KROFTA (1989.): Fifty-five years of post-fire succession in a southern mixed hardwood forest. – Bull. Torrey Bot. Club **116**: 107-113.

HILDEBRAND-VOGEL, R. (2002): Structure and dynamics of southern Chilean natural forests with special reference to the relation of evergreen versus deciduous elements. – Folia Geobotanica **37**: 107-128.

HOCKER, H. W. (1956): Certain aspects of climate as related to the distribution of Loblolly Pine (*Pinus*

taeda). – Ecology **37**: 824-834.
KIRA, T. (1949): Nippon-no shinrin-tai [Forest zones in Japan]. – Ringy Kaisetsu **17**: 105-141 (in Japanese).
KIRA, T. (1977): A Climatological Interpretation of Japanese Vegetation Zones. – In: Vegetation Science and Environmental Protection (A. Miyawaki, ed.), pp. 21-30. Maruzen, Tokyo.
KIRA, T. (1991): Forest ecosystems of East and Southeast Asia in a global perspective. – Ecol. Research (Japan) **6**: 185-200.
KLÖTZLI, F. (1988): On the global position of the evergreen broad-leaved (non-ombrophilous) forest in the subtropical and temperate zones. In: Contributions to Knowledge of the Flora and Vegetation of Central Japan (A. MIYAWAKI and E. LANDOLT, eds.). – Veröff. Geobot. Inst. ETH, Stiftung Rübel (Zürich) **98**: 169-196.
KÜCHLER, A. W. (1964): Potential Natural Vegetation of the Conterminous United States. – Amer. Geographical Soc., special publ. no. 36. New York.
LITTLE, E. L., jr. (1965): Mexican beech, a variety of *Fagus grandifolia*. – Castanea **30**: 167-170.
MEENTEMEYER, V. (1984): The geography of organic decomposition rates. – Annals Assn. Amer. Geographers **74**(4): 551-560.
MILLER, H. & S. LAMB (1985): Oaks of North America. – Naturegraph, Happy Camp (California). 327pp.
MIRANDA, F. & A. J. SHARP (1950): Characteristics of the vegetation in certain temperate regions of eastern Mexico. – Ecology **31**(3): 313-333.
MONK, C. D. (1965): Southern mixed hardwood forest of north-central Florida. – Ecol. Monogr. **35**: 335-354.
MONK, C. D. (1966): An ecological significance of evergreenness. – Ecology **47**: 504-505.
MOORE, P. (1980): The advantages of being evergreen. – Nature **285**: 535.
NESOM, G. L. & M. TREIBER (1977): Beech-mixed hardwoods communities: a topo-edaphic climax on the North Carolina coastal plain. – Castanea **42**:119-140.
NIXON, K. C. (2006): Global and Neotropical Distribution and Diversity of Oak (genus *Quercus*) and Oak Forests. – In: Ecology and Conservation of Neotropical Montane Oak Forests (M. KAPELLE, ed.), pp 3-13. Springer.
PETERS, R. (1995): Architecture and Development of Mexican Beech Forest. – In: Vegetation Science in Forestry: Global perspective based on forests ecosystems of East and Southeast Asia (E. O. Box et al., eds.), pp. 325-343. Kluwer, Dordrecht.
PETERS, R. (1997): Beech Forests. Kluwer, Dordrecht. 169pp.
QUARTERMAN, E. & CH. KEEVER (1962): Southern mixed hardwood forest: climax in the southeastern coastal plain, USA. – Ecol. Monogr. **32**: 167-185.
RADFORD, A. E., H. E. AHLES & C. R. BELL (1968): Manual of the Vascular Flora of the Carolina*s*. – University of North Carolina Press, Chapell Hill. 1184 pp.
RZEDOWSKI, J. (1978): Vegetación de México. – Limusa, Mexico (city). 432pp.
SÁNCHEZ DE DIOS, R., M. BENITO-GARZÓN & H. SAINZ-OLLERO (2009): Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. – Plant Ecology **204**: 189-205.
SCHMITHÜSEN, J. (ed.) (1976): Atlas zur Biogeographie. – Meyers Großer Physischer Weltatlas, vol. 3. Mannheim/Wien/Zürich: Bibliographisches Institut. 80 pp.
TAGAWA, H. (1997): Worldwide distribution of evergreen lucidophyll oak-laurel forests. – Tropics (Japan) **6**: 295-316.
TROLL, C. (1948): Der asymmetrische Aufbau der Vegetationszonen und Vegetationsstufen auf der Nord- und Südhalbkugel. – Jahresbericht Geobot. Inst. Rübel (1947): 46-83.
TROLL, C. (1961): Klima und Pflanzenkleid der Erde, in dreidimensionaler Sicht. – Die Naturwiss. **48**: 332-348.
VAN AUKEN, O. W., A. L. FORD & J. L. ALLEN (1981): An ecological comparison of upland deciduous and evergreen forests of central Texas. – Amer. J. Bot. **68**(9): 1249-1256.
VELÁZQUEZ, A., V. M. TOLEDO & I. LUNA (2000): Mexican Temperate Vegetation. – In: North American Terrestrial Vegetation, 2nd edition (M. G. BARBOUR and W. D. BILLINGS, eds.), pp 573-592. Cambridge University Press.
WALTER, H. (1954): Klimax und zonale Vegetation. – Angewandte Pflanzensoziologie **1**: 144-150.
WALTER, H. (1968): Die Vegetation der Erde in öko-physiologischer Betrachtung. Vol. II: Die

gemä igten und arktischen Zonen. – VEB Gustav-Fischer-Verlag, Jena. 1002 pp.
WALTER, H. (1970, 1977): Vegetation und Klimazonen. – Verlag Eugen Ulmer, Stuttgart. 382 pp (3rd edition: 309 pp).
WALTER, H. (1976): Die ökologischen Systeme der Kontinente (Biogeosphäre). – Gustav-Fischer-Verlag, Stuttgart. 131 pp (see English summary in Vegetatio **32**: 72-81).
WARE, S. (1988): Ordination of Quarterman and Keever's original Southern Mixed Hardwoods forest. – Castanea **53**: 197-206.
WARE, S. (1992): Where are all the hickories in the piedmont oak-hickory forest? – Castanea **57**: 4-12.
WARE, S., C. FROST & P. D. DOERR (1993): Southern Mixed Hardwood Forest: the Former Longleaf Pine Forest. – In: Biodiversity of the Southeastern United States:Lowland Terrestrial Communities (W. H. MARTIN et al., eds), pp. 447-493. New York: Wiley.
WELLS, B. W. (1942): Ecological problems of the southeastern United States coastal plain. – Botan. Review **8**: 533-561.
WHARTON, C. H. (1978): The Natural Environments of Georgia. – Ga. Dept. Nat. Resources, Atlanta. 228 pp.
WHITE, D. A. (1987): An American beech-dominated original growth forest in southeast Louisiana. – Bull. Torrey Botan. Club **114**: 127-133.
WOODWARD, I. (1987): Climate and Plant Distribution. – Cambridge University Press. 174 pp.

Authors address:

Prof. Dr. Elgene O. Box, University of Georgia, Geography Department, Athens, Georgia 30602- 2502, USA

E-Mail: boxeo@uga.edu