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報　文

Evergreen Broad-Leaved Forests of the Southeastern United States: Preliminary Description*

アメリカ南東部の常緑広葉樹林 — 予報

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Synopsis

Despite a warm-temperate climate similar to that of southern Japan, the coastal plain of the southeastern USA is usually described as a region of mostly deciduous "Southern mixed hardwoods" forests. Evergreen broad-leaved canopy trees and some evergreen forest patches do remain, however, suggesting that evergreen broad-leaved forest may be the potential natural vegetation. Forests on sand and uplands would be dominated by evergreen *Quercus* species, while more mesomorphic "laurel forests" comparable to those of East Asia are generally restricted to more moist sites in depressions and floodplains. The evergreen *Quercus* region extends from the Atlantic coast as far west as central Texas, where low evergreen *Quercus-Juniperus* woodlands occur on dry limestone hills. Most American evergreen genera occur also in Japan. Interpretation of vegetation dynamics and potential natural vegetation is made more complicated in the southeastern USA, however, by the important role of recurring forest disturbance (fire, plus summer and winter storms). These American evergreen broad-leaved forests are being studied ecologically and phytosociologically for analysis of vegetation dynamics and comparison with similar forests in East Asia.

Introduction

The coastal plain of the southeastern United States of America, from southern Virginia to Texas, has sometimes been viewed, in global perspective, as a region of potential evergreen broad-leaved forest, comparable to that of East Asia (e. g. Schmithüsen 1976, Ovington 1983). Although evergreen broad-leaved tree species do occur, this region has generally not been recognized as potentially evergreen broad-leaved forest by most Americans (e. g. Braun 1950, Daubenmire 1978, Vankat 1978, Chabot and Mooney 1985, Barbour and Billings 1988) and some others (e. g. Knapp 1965), who have described the region

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variously as "Southern mixed hardwoods" (Quarterman and Keever 1962, Monk 1965), southern oak-hickory-pine forest (Küchler 1964), "Southern pine forest" (e. g. Eyre 1968), or "warm-temperate mixed forest" (Lieth 1974). This apparent confusion has perhaps two main causes:

1. the longstanding dominance of much of the region by secondary deciduous forests and by successional and/or disclimax pine forests; and
2. the low-lying mosaic topography of white sand, smaller areas of silt or clay, plus limestone in Florida, much of which is too wet or too dry or too nutrient-poor to permit full expression of a "zonal" vegetation.

Evergreen broad-leaved forests are usually seen as comprising small, scattered stands on appropriate substrates (e. g. Olson 1983), usually within a matrix of extensive, substrate-induced pine flatwoods (maintained by fire), deciduous forests, a variety of wetland types (e. g. Penfound 1952), and various scrub types on some of the poorest soils (e. g. Wells 1942, Wharton 1978, Soil Conservation Service 1978, Christensen 1988). Climate may also play some more subtle role in the importance of deciduous trees in this apparently warm-temperate climatic region.

It is relatively difficult to get descriptive papers published in American biological journals. As a result, there has been little progress in the description of Southern vegetation types or regions (as opposed to statistical treatments of particular stands) for over 20 years, except in the books on North American vegetation which began to appear in 1978 (e. g. Daubenmire 1978, Barbour and Billings 1988). These books also, however, tend to emphasize evolutionary and ecophysiological aspects rather than vegetation classification or regionalization. Phytosociology was flirted with briefly by the Americans but has now all but disappeared, being generally considered to be "classification for the sake of classification." Although "the South" (i. e. the southeastern region from Maryland to Texas and inland to Kentucky and Arkansas) always appears as a separate natural region in national or continental-scale treatments of vegetation, papers and monographs treating the climate, soils, or vegetation of the South as a regional unit have hardly appeared at all. The Association of Southeastern Biologists is currently producing two volumes on "Southeastern Ecosystems", but the proposed tables of contents which have appeared so far (e. g. Martin 1985) have not included an evergreen broad-leaved forest region.

As a region, the American South is usually described as having a warm-temperate climate, i. e. Köppen's Cfa (e. g. Trewartha 1980) or type V of Walter and Lieth (1960-67), as distinct from the more "typical temperate" climate (Walter's type VI, Köppen's Df) in the northeastern USA. The South also stands out clearly on maps of dominant soil types, being mainly a region of red-yellow podzolic clays (now badly eroded), except over the broad, young coastal plain, which is mostly white sand – though sometimes only a thin layer over red clay or limestone. The eastern deciduous forest region of North America also seems to segregate into distinct northern and southern regions (e. g. Knapp 1965, Daubenmire 1978), but this leaves the South as still mainly a region of deciduous forests until one nears the coast of the Atlantic Ocean or Gulf of Mexico. This seems to be a result of the distinctly continental climate of eastern North America, which can have relatively high mean temperatures in winter but then sudden nighttime minima as low as -15℃ (absolute minima around -20℃) as far south as northern Georgia to northern Texas (Box 1988). The evergreen broad-leaved forests characteristic of humid

warm-temperate climates on other continents are present in the southeastern USA, at least now, only as small remnants in narrow strips along the Atlantic and Gulf coasts.

In theory, at least in East Asia, secondary forests in the evergreen broad-leaved forest region are commonly deciduous and may persist for many years but, if left undisturbed long enough (and if the substrate has not been impoverished too much), will eventually succeed to evergreen broad-leaved forests as the potential natural vegetation (e. g. Miyawaki 1984). Although the southeastern USA has only about 50-70% as much precipitation as corresponding areas in Japan (and thus has more frequent and more damaging droughts), we believe that an evergreen broad-leaved forest, a bit more xeromorphic than the Japanese "laurel forest", may also be the true potential natural vegetation of the coastal portion of the southeastern USA, where topography and substrates permit. Others have also reported scattered evergreen broad-leaved forests from inland sites (e. g. Laessle and Monk 1961, Wharton 1978), as well as more localized evergreen hammocks (i. e. topographically induced forest islands). Furthermore, it is now widely believed that low nutrient levels favor evergreen plants over deciduous ones, an idea which may have originated in the poorer soils of the southeastern coastal plain (Monk 1966). This hypothesis, however, conflicts with the prevailing American view that "Southern mixed hardwoods", mainly a mixture of deciduous and evergreen *Quercus* species, *Carya* (Juglandaceae), *Fagus grandifolia, Magnolia* spp., and *Pinus* spp., is the potential climax forest type on the southeastern coastal plain (cf. Quarterman and Keever 1962, Küchler 1964, Monk 1965, Daubenmire 1978).

We believe that a region of potentially evergreen broad-leaved forest extends from southeasternmost Virginia to the eastern part of the "hill country" of central Texas, in a coastal strip gradually widening to the south, as shown very generally in Figure 1. *Quercus virginiana* spans this entire range (but also extends further inland than does the potential for a fully evergreen forest). Although *Qu. virginiana* also occurs in south Florida, that region is subtropical (slight if any winter frost) and is not included in this study, which focuses on the warm-temperate zone. It is the purpose of this paper to describe the main taxa and vegetation types of this potential evergreen broad-leaved forest region and how they correspond to environmental conditions and to similar vegetation types in Japan and continental East Asia.

Sites and Methods

Data collection involved sampling the vegetation of as many sites as possible across the region of potential evergreen broad-leaved forests. Study sites were chosen on the basis of having evergreen broad-leaved tree species in the canopy, but some successional or other apparently related forest types were included also. Data collection has so far involved three surveys (1986, 1987, and 1988) by the two authors, plus more localized surveys by the first author. It is very difficult to find examples of mature evergreen broad-leaved forest, since the USA does not have any tradition of shrine or temple forests comparable to those of East Asia. Thirty forest samples (relevés) are used in this study, ranging from the South Carolina coast to central Texas. Locations of study sites and a very general outline of the potential extent of evergreen broad-leaved forests are shown in Figure 1. At this time, no data are available for the region spanning coastal Alabama, Mississippi, and Louisiana, due to the low-lying topography and greater importance of wetlands, plus early destruction of the few upland evergreen forests. Data

collection continues.

Locations of relevé sites, some environmental attributes, and description of the current vegetation type are summarized in Table 1.

All vegetation sampling was done by the method of Braun-Blanquet relevés (see Braun-Blanquet 1964, Miyawaki 1969, Westhoff and van der Maarel 1973, or Mueller-Dombois and Ellenberg 1974), using the quantitative scale and refinements described by Fujiwara (1987). This methodology was chosen because it is:

— well designed for extensive vegetation sampling in limited amounts of time;
— well known to both authors (especially KF, with 20 years of experience); and
— is probably the only methodology sufficiently standardized to provide a reliable basis for comparisons of different regions, especially on different continents.

True phytosociological analysis requires the accumulation of many relevés and is by no means the only objective of this study. The Braun-Blanquet field methodology, however, is a very appropriate and convenient method for this type of ongoing geographic study. It may also permit formal phytosociological analysis and direct comparisons with data from evergreen broad-leaved forests in Japan (e. g. Miyawaki 1980-88, Fujiwara 1981-86) and other areas (e. g. China, southern Europe) at a later time.

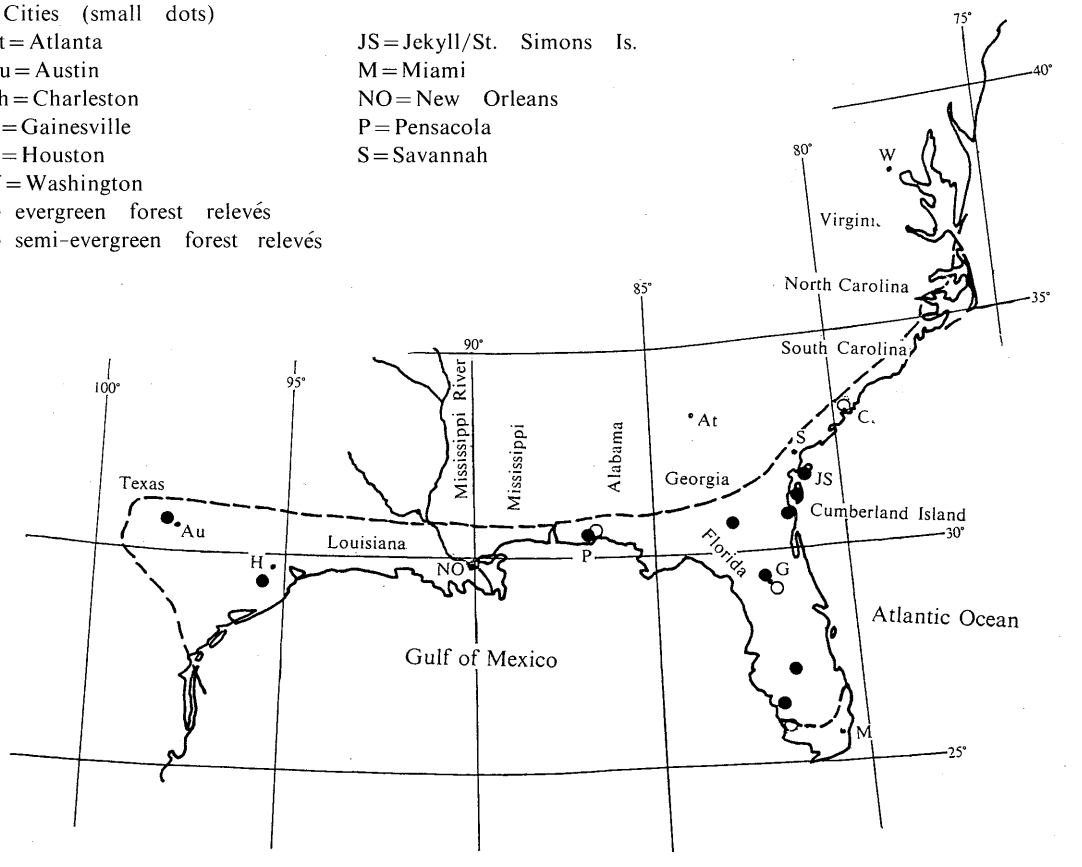

Fig. 1 Locations of Evergreen Broad-Leaved and Related Forest Relevés in the Warm-Temperate Southeastern United States (1986-88).

	Veg. Height	Canopy Cover	Vegetation	No. Spp.	Substrate
South Carolina					
Charleston (20km NW)	22	80	Semi-EG mixed hardwood forest	28	sandy
Georgia					
St. Simons Island	25	70	*Pinus*-EG *Quercus* forest	20	sand
	19	80	EG *Quercus virginiana* forest	22	sand
	25	80	EG *Quercus* forest, EG understoreys	24	sandy with humus
	30	85	EG *Quercus* forest, EG understoreys	20	gray sand with humus
Cumberland Island	22	60	EG *Quercus* forest, EG understoreys	(13)	sand
	16	60	EG *Quercus-Serenoa* forests (x2)	(7)	dunes (lee side)
	22-24	50-70	EG *Quercus-Lyonia* forests (x2)	(15)	sand
	20	80	EG *Persea-Pinus* littoral belt	(8)	mud over sand
	23-24	70-80	EG *Quercus-Magnolia* forests (x2)	(11-19)	sand with humus
Lake Louise (Valdosta)	18	75	EG *Persea-Magnolia* bay forest	18	mud (wet to hydric)
Florida					
Fort George Island	27	80	EG *Quercus* forest, EG understoreys	31	sandy
Gainesville (NW)	18	70	*Pinus* forest, deciduous understorey	27	limestone
	22	80	Semi-EG *Carya-Quercus-Pinus* forest	33	limestone
	36	85	EG *Quercus-Magnolia* forest, with *Ostrya*	30	sandy, near pond
Paynes Prairie	22	80	*Liquidambar* forest (deciduous)	49	karst terrace (hilly)
	24	70	*Ulmus-Liq.-Carya* forest (deciduous)	46	karst terrace (hilly)
Highlands Hammock	25	75	EG *Quercus-Sabal* forest with deciduous trees	24	humus over limestone
Myakka River St. Park	22	70	EG *Quercus* forest with palm understoreys	18	mud (summerwet)
Corkscrew Swamp Sanctuary	24	70	*Taxodium-Persea* swamp forest	34	standing water, mud
Pensacola (Naval Oaks)	12	80	EG *Quercus* low forest, EG understorey	18	old dunes (seaward)
	18	75	EG *Quercus* forest, EG understorey	22	white sand (flat)
	22	75	EG *Quercus-Magnolia* forest, with *Carya*	25	slight depression, sandy
Pensacola (Univ. W Fla.)	25	40(80)	Semi-EG *Pinus-Quercus* forest	32	sand with litter
Texas					
Brazos Bend State Park	20	80	EG *Quercus* forest, *Ilex* understorey	28	sandy levee
Austin (west)	16	60	EG *Quercus-Juniperus* woodland	36	brown soil on limestone
	8	60	EG *Quercus-Juniperus* scrub	29	limestone ridgetop

Table 1. Forests Sampled in the Region of Potential Evergreen Broad-Leaved Forests in the Southeastern USA.

Thirty forests were sampled, from the South Carolina coast near Charleston (see also Figure 1) to the eastern edge of the dry, limestone "Hill Country" of central Texas, just west of Austin. Most sites were selected on the basis of having evergreen broad-leaved trees in the canopy, but a few successional or edaphic types are also included. Vegetation (canopy) height is given in meters and canopy cover as a percentage. (At Pensacola, the 80 in parentheses represents the cover of the second tree layer, which is more closed.) Value ranges are given where similar relevés have been grouped (see Cumberland Island). Numbers of species in the Cumberland Island relevés are given in parentheses because sampling was done in winter, when some species may have been overlooked.

Vegetation Composition

Most of the important evergreen broad-leaved tree or other arborescent species of the warm-temperate southeastern USA are from genera which also occur in evergreen forests in East Asia, including Japan (e. g. Gray 1846, Miyawaki 1967, Graham 1972, Good 1974, Numata 1974, Missouri Botanical Garden 1983). Not all of the important evergreen broad-leaved genera from warm-temperate Japan, however, occur also in the southeastern USA, as shown in Table 2. Many important Japanese evergreen genera not occurring in the (drier) southeastern USA are of the more mesophyllic "laurel forest" type, e. g. *Neolitsea, Camellia, Aucuba.* The important Asian Fagaceae *Castanopsis* and *Pasania* (= *Lithocarpus*) also do not occur in the southeastern USA, though each genus has one or more species in California. *Cinnamomum camphora* has become naturalized as far north as southern Georgia, and several *Ligustrum* species have successfully invaded deciduous forest areas as far north as southern Virginia (Mellinger 1984, Jones and Coile 1988, Radford et al. 1968). Some arborescent Japanese genera missing in eastern North America are successfully cultivated, including *Camellia, Cleyera, Citrus, Eriobotrya,* and *Podocarpus.*

The most important evergreen broad-leaved tree genus in the southeastern USA is *Quercus* (oak), with at least six evergreen species, several other forms (e. g. *Qu. virginiana* var. *maritima*), and many hybrids. *Quercus virginiana,* the character tree of the South. with its spreading crown and long lifespan (to 400 years), spans the entire potential evergreen forest region, from coastal Virginia to the limestone hills of central Texas, where it grows in low woodlands densely mixed with *Juniperus ashei. Qu. geminata* is a usually shorter, more sclerophyllous but otherwise very similar species which grows mainly on sand, while *Qu. fusiformis* is a short, smaller-leaved but similar species from the limestone area of central Texas (and on into northern Mexico). *Qu. laurifolia* is a straight-growing, more mesomorphic, shorter-lived tree growing on more moist substrates (e. g. bottomlands or sand with high groundwater), while *Qu. hemisphaerica* is its similar but more spreading upland counterpart. Both species occur further inland (e. g. Jones and Coile 1988) and are the main potential dominants of inland evergreen broad-leaved forests. *Qu. myrtifolia* is a short, sclerophyllous tree of sandy coastal areas. All of these evergreen oaks, like most temperate-zone evergreens, are seasonal evergreens (not evergrowing), i. e. they exchange old leaves for new ones all at the same time, in the early springtime. As a result, some species may appear leafless for up to 2-3 weeks, especially *Qu. geminata* and *Qu. laurifolia* (which is in fact only semi-evergreen in more northern areas). In addition to these evergreen species, several other *Quercus* species may be "tardily deciduous" or even nearly evergreen in more southern areas, notably *Qu. nigra, Qu. phellos, Qu. chapmanii,* and *Qu. incana. Qu. minima* is an evergreen sclerophyllous shrub on sandy areas subject to burning (Kurz and Godfrey 1982). Unfortunately, the taxonomy of evergreen *Quercus* species has not been unified across the whole southeastern USA, and some important species such as *Qu. hemisphaerica* and *Qu. geminata* are not recognized in some floristic manuals.

The second important group of evergreen broad-leaved trees in the southeastern USA is the so-called "bay" species: *Persea* (red bay, 3 spp.), *Magnolia virginiana* (sweet bay), and *Gordonia lasianthus* (loblolly bay), which is very similar to *Schima* in appearance. (*Gordonia* does not occur in Japan but is in China.) Bay species all have somewhat aromatic, laurel-like leaves, hence the name "bay" (an English common name for *Laurus*

Family	Japanese genera	Species in southeastern USA
LAURACEAE	*Persea*	*Persea borbonia, P. palustris*
	Litsea	
	Neolitsea	
	Cinnamomum	*(Cinnamomum camphora)*
	Actinodaphne	
FAGACEAE	*Quercus*	*Quercus virginiana, Qu. laurifolia, Qu. hemisphaerica, Qu. myrtifolia, Qu. geminata, Qu. fusiformis* (+hybrids)
	Castanopsis	
	Pasania	
THEACEAE	*Schima*	
	(in China)	*Gordonia lasianthus*
	Camellia	
	Cleyera	
	Eurya	
	Ternstroemia	
MAGNOLIACEAE	*Magnolia*	*Magnolia grandiflora, M. virginiana*
	Michelia	
	Illicium	2 shrub spp.
MYRSINACEAE	*Ardisia*	*Ardisia escallonioides*
	Maesa	
	Myrsine	*Rapanea* (= *Myrsine*) *punctata*
ROSACEAE	*Prunus*	*Prunus caroliniana*
	Rhaphiolepis	
	Photinia	
	Eriobotrya	
OLEACEAE	*Osmanthus*	*Osmanthus americanus*
	Ligustrum	*(Ligustrum sinense,* et al.)
SYMPLOCACEAE	*Symplocos*	*Symplocos tinctoria*
AQUIFOLIACEAE	*Ilex*	*Ilex opaca, I. vomitoria, I. cassine, I. myrtifolia*
MYRICACEAE	*Myrica*	*Myrica cerifera, M. inodora*
ERICACEAE	*Vaccinium*	*Vaccinium arboreum*
	(deciduous)	*Lyonia ferruginea*
EUPHORBIACEAE	*Daphniphyllum*	
RUTACEAE	*Citrus*	(various spp. cultivated)
	Murraya	
	Skimmia	
CELASTRACEAE	*Euonymus*	*Euonymus americanus*
ELAEOCARPACEAE	*Elaeocarpus*	
SAPOTACEAE		*Bumelia tenax, B. lanuginosa*
CYRILLACEAE		*Cliftonia monophylla*
		Cyrilla racemiflora

Table 2. Main Evergreen Broad-Leaved Tree Genera in Warm-Temperate Japan and their Evergreen Tree Counterparts in the Southeastern USA.

Quercus is the most important evergreen broad-leaved tree genus in the warm-temperate southeastern USA, but other important East Asian genera also occur, including some non-native taxa which have become successfully naturalized (names given in parentheses, e. g. *Ligustrum*). Almost all of the American evergreen tree genera also occur in Japan. Note, however, some synonyms: *Persea* is also called *Machilus, Pasania*=*Lithocarpus,* and *Myrsine* is *Rapanaea* (Brockman 1986). Terminology follows Hayashi (1985) and Miyawaki et al. (1983) in Japan and mainly Kurz and Godfrey (1982), Jones and Coile (1988), and Correl and Johnston (1970) in the USA, plus Radford et al. (1968) and Brockman (1986).

nobilis, used in cooking). The bay species generally require more moist habitats, including periodically flooded sites, and often occur together in "bays" (bay forests or "bayheads") at the edge of shallow ponds or partly peat-filled depressions, which are common on the Atlantic coastal plain (i. e. "Carolina bays" or "pocosins", e. g. Sharitz and Gibbons 1982). *Persea* is represented by the more widespread *P. borbonia* (red bay), *P. palustris* (swamp red bay, which grows only in wetlands), and *P. humilis* (silkbay, a shrub of white-sand areas in northeastern Florida only) (Kurz and Godfrey 1982).

Another important evergreen broad-leaved tree is *Magnolia grandiflora,* with its large, fragrant flowers and large sclerophylls (making it unlike the more mesophyllous "laurel forest" species, despite a preference for moist sites). *M. grandiflora* tolerates the low nighttime winter temperatures of the piedmont area, but its natural range is restricted to the milder coastal plain. It grows straight but slowly in forests and can become a canopy co-dominant in depressions and other moist areas, usually with evergreen *Quercus* but also with deciduous *Fagus grandifolia* on certain moist, relatively fertile sites (Nesom and Treiber 1977, White 1987).

Ilex (holly) species can be important companions on a wide variety of sites. Large-sclerophyll *Ilex opaca* (cf. *I. cornuta)* can approach canopy co-dominance on moist coastal sandy soils (but also occurs as an understorey species in deciduous forests as far north as Massachusetts). Small-leaved *I. vomitoria* (cf. *I. crenata* leaves) is a consistently important understorey tree from Virginia to central Texas. It was an early source of "yaupon tea" for European settlers (as was *I. paraguayensis* in Argentina).

Two evergreen Ericaceae, *Vaccinium arboreum* and *Lyonia ferruginea,* are important understorey trees and can dominate the tree understorey in humid coastal *Quercus* forests. *Lyonia lucida* can be an important evergreen shrub in moist areas. (*Lyonia* occurs in Japan but only as deciduous *L. ovalifolia* var. *elliptica* in temperate deciduous forests.)

Myrica cerifera is a consistently important large shrub or arborescent characteristic of forest edges and understoreys with high groundwater. *M. inodora* is similar but much less common and has no fragrance. *Osmanthus americanus* (with entire leaves) and *Symplocos tinctoria* (cf. *S. glauca*) are similar to their Japanese counterparts, occurring as understorey companions in richer forest.

Bumelia lanuginosa and *B. tenax* (Sapotaceae, not in Japan) occur patchily as understorey trees in lowland forests from coastal South Carolina to eastern Texas and Oklahoma. *Cliftonia monophylla* and *Cyrilla racemiflora* (Cyrillaceae, not in Japan) form dense thickets in wet to hydric situations, usually along streams, from the Atlantic coast to coastal eastern Texas. *Cyr. racemiflora* is semi-evergreen in most of the southeastern USA but also occurs (with larger, truly evergreen leaves) in montane forests on some Caribbean islands (e. g. White 1963).

Two other types of evergreen tree, palms and pines, are also very important in the evergreen vegetation of the warm-temperate southeastern USA. Palms are represented by *Sabal palmetto* trees (to 15-18m) and by usually trunkless *S. minor, S. etonia,* and *Serenoa repens,* any of which may be called a "palmetto". *Sabal palmetto* can be a companion or dominant in the understorey tree layer or can occur also as scattered, trunkless individuals. *Serenoa,* on the other hand, rarely forms an erect trunk but can form impenetrable thickets by means of long, horizontal, partly underground "trunks" and colonial growth, especially on sand with high groundwater.

At least eight species of *Pinus* can be important over the southeastern coastal plain,

Forest Type	Habitat	Main Woody Taxa (evergreen unless noted) Canopy	Understorey(s)
Evergreen Oak Forests			
-Maritime oak forest	dunes	*Quercus virginiana, Qu. geminata* (with *Magnolia grandiflora*)	*Serenoa repens, Myrica cerifera, Ilex vomitoria, Juniperus*
-Coastal oak forest	coastal sands (flat)	*Qu. virginiana, Qu. laurifolia, Qu. hemisphaerica (Magnolia grandifl., Carya)*	*Persea borbonia, Lyonia ferruginea, Vaccinium arboreum, Serenoa repens*
-Mesophytic forest	moist depressions	*Qu. laurifolia, Qu. virginiana, Magnolia grandiflora (Carya glabra)*	*Ilex opaca, Persea borbonia, Lyonia, Vaccinium arboreum, Osmanthus, Serenoa repens*
-Oak-palm forest (transition to subtropical)	mesic /wet	*Qu. virginiana., Qu. laurifolia, Qu. hemisphaerica, Sabal palmetto*	*Sabal palmetto, Serenoa repens, Persea (Ulmus, Acer, Carya)*
-Upland oak forest	mesic/ subhumid	*Qu. virginiana., Qu. hemisphaerica (Carya?, Magnolia?)*	*Ilex vomitoria, Persea borbonia, Magnolia virginiana, Carya*
Xeric Oak Woodlands	subhumid	*Qu. virginiana., Qu. geminata, (Qu. fusiformis,) Juniperus*	*Ilex vomitoria, Rhus* spp., *Juniperus,* Rosaceae (Rhamnaceae)
Evergreen Bay Forests	wet depressions	*Magnolia virginiana, Persea* spp, *Gordonia lasianthus (Nyssa biflora, Taxodium)*	*Persea, Gordonia, Ilex, Lyonia, Nyssa, Myrica, Rhododendron, Acer rubrum*
Floodplain Forests	floodplains (briefly flooded)	*Qu. laurifolia., Qu. michauxii, Magnolia virginiana, Acer rubrum, Liquidambar, Pinus, Liriodendron*	*Ilex opaca, Acer rubrum, Magnolia virginiana, Persea, Liquidambar, Ulmus (Sabal)*
Swamp Forests	hydric	*Taxodium* spp., *Nyssa biflora*	*Nyssa, Persea, Magnolia virginiana, Acer rubrum, Fraxinus, Myrica*

Table 3. Main Evergreen Broad-Leaved Forest Types of the Southeastern United States (warm-temperate zone, excluding subtropical south Florida)

All taxa listed are evergreen except the following: *Carya, Nyssa, Taxodium, Ulmus, Acer, Liquidambar, Fraxinus,* and most *Rhus,* Rosaceae, and Rhamnaceae species.

all so-called "hard pines", with 2-3 needles per fascicle and potentially rapid growth. Pines may persist indefinitely on poor, mineral soils, but *P. taeda, P. glabra,* and *P. serotina* can also grow and may persist on relatively moist, organic-rich sites, including periodically flooded sites.

Potentially dominant deciduous trees include *Taxodium* (a conifer, similar to *Metasequoia*) and *Nyssa aquatica* and *N. sylvatica* var. *biflora* (=*N. biflora,* Nyssaceae), all of which grow in swamps and other wet to hydric situations. The most important deciduous co-dominants of more upland forests are typically *Quercus* and *Carya* (Juglandaceae) species and *Liquidambar styraciflua* (Hamamelidaceae), a mainly successional tree common also in some mountain areas of eastern Mexico.

Finally, many woody vines and a few epiphytes are also important, especially evergreen *Smilax* (Liliaceae) and deciduous *Vitis* species, plus the picturesque, gray "Spanish moss" (*Tillandsia usneoides,* Bromeliaceae) which hangs from many trees throughout the region.

Vegetation Types

In the southeastern USA, secondary succession normally proceeds from grassy pine savannas to pine forests to mixed forests (deciduous forest with persisting canopy pines) and eventually to deciduous forests, generally dominated by deciduous *Quercus* and *Carya* spp., with *Liquidambar, Fagus,* etc. on particular sites (e. g. Braun 1950, Knapp 1965, Daubenmire 1978). On the coastal plain, however, with its milder winters, evergreen broad-leaved trees such as evergreen *Quercus* spp. plus *Magnolia,* etc. may grow up slowly under the deciduous (or pine) canopy until they reach canopy height and can compete directly for dominance. Evergreen broad-leaved trees have the advantage of a permanent foliage cover combined with tolerance to partly shady conditions, which gives them a competitive advantage against both (light-demanding) pines and deciduous trees (which must produce new leaves in spring). Where soil, lack of disturbance (by fire, storms, cutting, etc.), and other factors permit, the secondary deciduous forest of the southeastern warm-temperate region can eventually succeed to an evergreen broad-leaved forest climax (potential natural vegetation), as happens in warm-temperate Japan, China, the Mediterranean region, etc.

Although we suggest a more important role for evergreen broad-leaved forests than do some other authors, we find basically the same five types of warm-temperate forests recognized by others, as summarized in Table 3. The difference lies in the evergreen *Quercus* forests, which are the most important geographically and which are divided into five sub-types.

The Maritime oak forest (Figure 2)* occurs on dunes closest to the shoreline, especially on the barrier islands along the Gulf and Atlantic coasts, and corresponds to the "salt-spray climax" of Wells (1939) and Bourdeau and Oosting (1959). It is dominated by *Quercus virginiana* and/or *Qu. geminata,* has the fewest species, but typically has a dense understorey of *Serenoa repens* and a variety of vines, including *Anisostichus capreolata* (Bignoniaceae) as well as *Smilax* and *Vitis* species.

The Coastal oak forest occurs on flatter sandy terrain near the coast and differs from the maritime oak forest by having more species, both in the canopy (e. g. *Qu.*

*All photographs were taken by the second author.

Fig. 2. A maritime evergreen *Quercus* forest (20m, 80% canopy cover) with mainly *Serenoa repens* understorey, on old dunes on the inland side of Jekyll Island along the Georgia coast. The canopy at this site contains only *Qu. virginiana,* plus *Vitis* spp. and epiphytic *Polypodium polypodioides* and *Tillandsia usneoides* ("Spanish moss"). This relatively simple type of evergreen *Quercus* forest represents the 'salt-spray climax' of Well (1939) and was found on essentially all the barrier islands from southern Virginia to Texas before being cut for shipbuilding, settlement, or tourism development. A relevé for a similar but more diverse site, with *Magnolia grandiflora* etc., is given in Table 4.

laurifolia, Qu. hemisphaerica, Magnolia grandiflora) and in the understoreys (e. g. *Persea borbonia, Vaccinium arboreum, Lyonia ferruginea).* On the other hand, this type could be considered simply as transitional between the more austere maritime forest and the Mesophytic evergreen oak forest (see sample relevé in Table 4), which occurs patchily in moist depressions and includes at least *Magnolia grandiflora* as a canopy co-dominant with the evergreen *Quercus* species. Large individuals of *Ilex opaca, Osmanthus americanus,* etc. may also occur in this type.

The evergreen Oak-palm forest (see Figure 3) could also be treated as transitional, namely between the warm-temperate evergreen oak forests and the subtropical forests of south Florida. The oak-palm forest is best developed in south-central Florida and contains a well developed palm subcanopy (*Sabal palmetto*) and palmetto ground layer (*Serenoa repens*). This leaves only the Upland evergreen oak forest (inland), which corresponds to the area of the "Southern mixed hardwoods" across the upland portions of the lower coastal plain and which will be discussed later.

The Xeric oak woodlands can be divided into eastern types on sand and a western

Fig. 3. An evergreen *Quercus* stand with extremely well developed *Sabal palmetto* tree understorey and ground layer, on mud over limestone (partly inundated), in the Big Hammock at Highlands Hammock State Park (interior south-central Florida). This location at 27° N latitude is in the transition zone between warm-temperate and subtropical forests and is characterized by increased importance of palms. Dominant species include evergreen *Qu. hemisphaerica* and *Qu. virginiana,* accompanied on moist sites by deciduous *Carya, Ulmus, Celtis,* and/or *Liquidambar.*

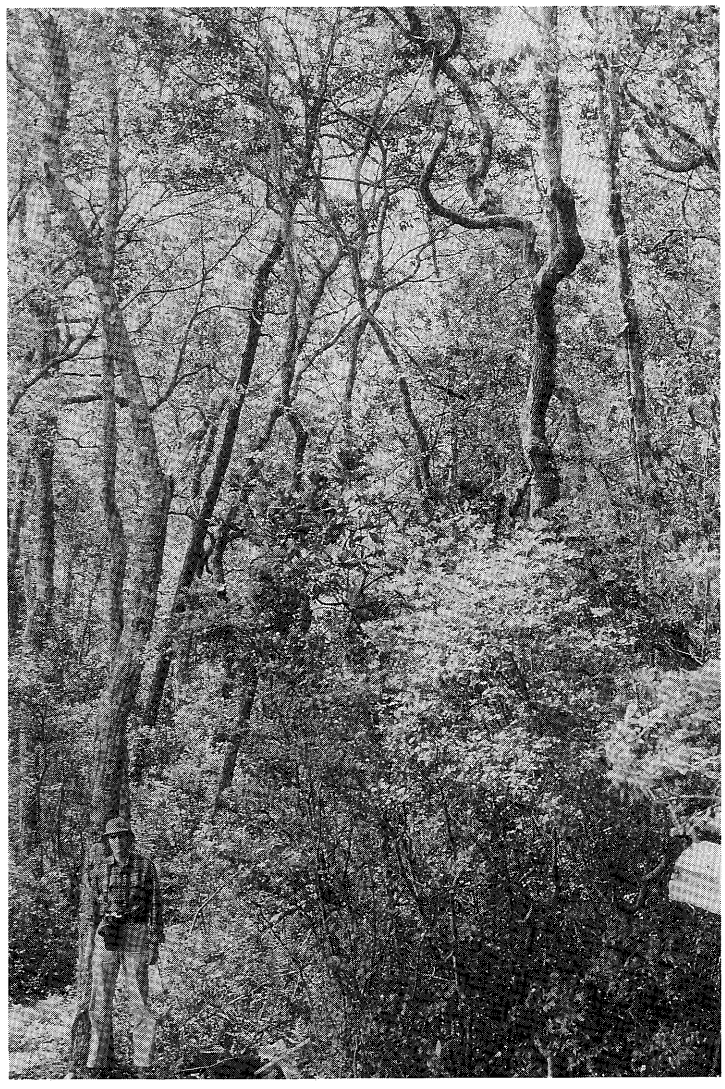

Fig. 5. An evergreen *Persea palustris–Magnolia virginiana* "bay forest", with *Gordonia lasianthus* as an understorey tree, at the Lake Louise preserve south of Valdosta (inland southernmost Georgia). This forest type is the most similar to East Asian "laurel forests" but occurs in the drier climate of the southeastern USA mainly in wetter large depressions (also called "bays"), often with a few centimeters of standing water. A relevé for this site is given in Table 5.

Fig. 4. (see previous page, below Fig. 3). A low *Quercus virginiana–Juniperus ashei* forest (16 m, 60% canopy cover) with *Juniperus* understorey, on brown soil over limestone, just west of Austin (central Texas). This site is near the dry western limit of *Quercus virginiana,* where its range overlaps with the similar but shorter, smaller-leaved *Qu. fusiformis.* The junipers are selectively cleared from such forests, leaving a picturesque, open *Quercus* parkland landscape which is used for cattle grazing.

type on the limestone hills of central Texas. The western type (see Figure 4) is short, somewhat open, and is dominated by *Qu. virginiana, Qu. fusiformis,* and *Juniperus ashei.* Eastern oak woodlands are dominated by *Qu. geminata* and *Qu. virginiana* plus scrubby deciduous oaks and Ericaceae. Both types commonly also contain *Ilex vomitoria* shrubs plus *Rhus* (e. g. *Rhus copallina)* and other shrubs. The western type represents the western (drier) limit of the evergreen *Quercus* region in the southeastern USA.

Evergreen bay forests (see Figure 5 and sample relevé in Table 5) are dominated by *Persea palustris* (or *P. borbonia*), *Magnolia virginiana,* and/or *Gordonia lasianthus,* etc. and occur

Table 4. Example of a Mesophytic Evergreen *Quercus-Magnolia* Forest, from the Naval Oaks Preserve in Pensacola (western Florida).

Date: 24.7. 1988

T_1	22m	75%
T_2	12m	30%
S	4m	40%
H	0.3m	40%

Elevation: 15m
Slope and aspect: 2° east
Substrate: 2 cm litter, 1 cm A, white sand with dirt
Micro-relief: very slight depression
Relevé dimensions: 15 × 15m
Relevé by: KF and EB

T_1:	3·2	*Magnolia grandiflora*	T_2: 2·1	*Magnolia grandiflora*
	3·3	*Carya glabra*	1·1	*Quercus virginiana*
	2·2	*Quercus hemisphaerica*	+·2	*Tillandsia usneoides*
	2·2	*Quercus virginiana*	+	*Vaccinium arboreum*
			+	*Juniperus silicicola*
			+	*Bumelia tenax*
S:	3·3	*Vaccinium arboreum*	+	*Magnolia grandiflora*
	2·3	*Serenoa repens*	+	*Osmanthus americanus*
	1·2	*Quercus virginiana*	+	*Juniperus silicicola*
	1·2	*Quercus hemisphaerica*	+	*Ilex vomitoria*
	1·2	*Persea borbonia*	+	*Asimina speciosa*
	1·2	*Vaccinium stamineum*	+	*Vitis rotundifolia*
	1·2	*Smilax* sp. (hastate)	+	*Smilax bona-nox*
	1·1	*Ipomoea sagittata*		
H:	2·2	*Ilex vomitoria* (seedlings)	1·1	*Persea borbonia*
	2·2	*Anisostichus capreolata*	+·2	*Smilax* (deciduous, cordate)
	1·3	*Carex* sp.1 (small, red stem)	+	*Rhus radicans*
	1·2	*Carex* sp.2 (large)	+	*Solidago* sp.
	1·2	*Quercus virginiana* (seedling)	+	*Panicum* sp.
	1·2	*Quercus hemisphaerica*		

Total number of species: 25

in moist to wet depressions of various kinds. This type corresponds most closely to the "laurel forests" of Japan and other parts of warm-temperate East Asia, even though these bay forests cannot occupy extensive upland areas in the (drier) southeastern USA. Some bay forests are closely associated with "pocosins" (Sharitz and Gibbons 1982) but lack the fire regime necessary for maintenance of a true pocosin (an *Ilex*-Ericaceae shrub bog, with or without an open overstorey of *Pinus serotina*). Bay forests are most common from North Carolina to western Florida and occur less frequently further west.

Table 5. Example of an Evergreen *Persea-Magnolia* "Bay Forest", at the Lake Louise preserve south of Valdosta (inland southernmost Georgia).

Location: Lake Louise boardwalk (Southern Georgia) Date: 15.4. 1987
(Valdosta State College research site)

T_1	18m	75%
T_2	9m	10%
S	3m	70%
H	0.5m	15%

Elevation: 60m
Slope and aspect: level
Substrate: mud, with 0–8 cm standing water
Micro-relief: next to pond, partly separated by small sill
Relevé dimensions: 10 x 10m (10 x 30m)
Relevé by: KF and EB

T_1:	3·3	*Persea palustris*	T_2:	1·2	*Gordonia lasianthus*
	1·2	*Magnolia virginiana*		1·2	*Persea palustris*
	1·1	*Nyssa sylvatica* var. *biflora*		+·2	*Magnolia virginiana*
	+	*Pinus serotina*		+·2	*Nyssa sylvatica* var. *biflora*
S:	3·3	*Ilex coriacea*		1·2	*Leucothoë axillaris* (fl)
	2·2	*Rhododendron viscosum*		+·2	*Vaccinium stamineum*
	2·2	*Lyonia lucida* (fl)		+·2	*Vaccinium atrococcum* (fr)
	1·2	*Magnolia virginiana*		+	*Viburnum cassinoides*
	1·2	*Clethra alnifolia* var. *tomentosa*		+	*Myrica cerifera*
	1·2	*Smilax laurifolia*		+	*Rhus radicans*
H:	2·2	*Persea palustris*		+·2	*Ilex coriacea*
	1·2	*Lyonia lucida*		+	*Viburnum cassinoides*
	1·2	*Woodwardia areolata*		+	*Rhus radicans*
	+·2	*Osmunda cinnamomea*			

Total number of species : 18

Floodplain forests of the southeastern coastal plain are typically only semi-evergreen, with evergreen *Qu. laurifolia* and *Magnolia virginiana* as important canopy species but usually with more deciduous canopy species, such as *Qu. michauxii* (swamp chestnut oak), *Qu. alba, Acer rubrum, Liquidambar styraciflua, Liriodendron tulipifera,* and *Nyssa sylvatica* var. *biflora.* Evergreen *Ilex opaca, Persea* spp., and *Magnolia virginiana* may be important in the subcanopy and tree understorey, while scattered *Pinus taeda* individuals may persist in the canopy (and grow to great size).

Swamp forests, as opposed to floodplain forests, are flooded for longer periods of the year and usually more deeply, either by standing or slowly moving water. True swamp forests are almost completely deciduous in the canopy, which is dominated by *Taxodium distichum* and/or *Nyssa* species. Smaller *T. ascendens* (also deciduous) grows mainly in shallow water at the edge of ponds.

Vegetation Dynamics

Most of the above-mentioned forest types are well recognized. The problem is with the hypothesized Upland Evergreen Oak Forest, which may once have extended over the broad upland area between the Atlantic coast and the Gulf of Mexico (covering roughly the southern half of Georgia and northern two-thirds of Florida, plus coastal strips along the Atlantic and the Gulf) but for which almost no representative stands remain. Canopy-size individuals of *Quercus virginiana* (Figure 6) and *Qu. hemisphaerica,* plus *Qu. laurifolia* and shorter *Qu. geminata,* can certainly be found across this region, especially in northern Florida. Apparently, even *Persea borbonia* (Figure 7) can grow to canopy proportions under favorable conditions. A canopy height of 20–25 meters for these upland oak forests seems typical, but individual evergreen oaks to 36 meters have been found. Nevertheless, examples of well developed Upland Evergreen Oak Forest are exceedingly rare. The best example we have sampled so far is near Gainesville (Florida) and occurs on a lower position in slightly undulating terrain. It has a canopy height of over 30 meters (which is unusually high), a canopy cover of 85%, and is surrounded by successional forest (i. e. deciduous or semi-evergreen) with large evergreen *Quercus* individuals. The main canopy dominant in this area seems to be *Quercus hemisphaerica* but with *Qu. virginiana* also (see Figure 8).

The relevés collected so far (Table 1) suggest three basic types of successional forest which might have evergreen potential. A pine-evergreen type occurs on sandy areas and contains mainly *Qu. virginiana, Qu. geminata,* and sometimes *Persea borbonia* and even *Magnolia virginiana* (higher groundwater) in the understorey, all of which are slow-growing and may remain shorter than the pines on poorer sites. Such sites may develop into peinotrophic, mixed evergreen woodlands (or forests) if left undisturbed, but examples illustrating this development are rare. A pine-deciduous successional type generally occurs on better soils and typically develops, over 50–75 years, into a deciduous forest. The third type is the "Southern mixed hardwoods" type, which may have some evergreen broad-leaved canopy trees.

Succession of these types into an Upland Evergreen Oak Forest depends on various factors. In the southeastern coastal plain, with its somewhat irregular precipitation and recurring droughts, its young sandy soils exacerbating climatic dryness, its low-lying topography,

Fig. 6. A remaining large individual tree of *Quercus virginiana* (with characteristic spreading crown form) in a semi-evergreen, secondary "Southern mixed hardwoods" forest near Charleston (coastal South Carolina). The presence of such large, long-lived evergreen oak trees in largely deciduous secondary forests strongly suggests the potential for an evergreen broad-leaved climax forest.

and with recurring disturbance by late-summer hurricanes and/or winter ice storms, catenal and historical factors become especially important. It is perhaps unrealistic to expect an unbroken belt of potential upland evergreen broad-leaved forest from the Atlantic coast to southeastern Texas. Evergreen broad-leaved forest should not be expected to occur in low-lying, saturated soil or on the driest and/or most nutrient-poor upland areas (which may support only dwarfed evergreen trees or more commonly deciduous *Quercus laevis* savannas). With continuing disturbances, faster-growing deciduous trees may maintain themselves quite well against potentially overshading but slower-growing broad-leaved evergreen trees, hence the concept of "Southern mixed hardwoods" as the potential climax forest type. Recurring disturbance has important implications for the concept of potential natural vegetation, which has largely ignored the role of disturbance. Without more data we cannot refute the view that "Southern mixed hardwoods" are the potential natural vegetation – but we believe it is still an open question.

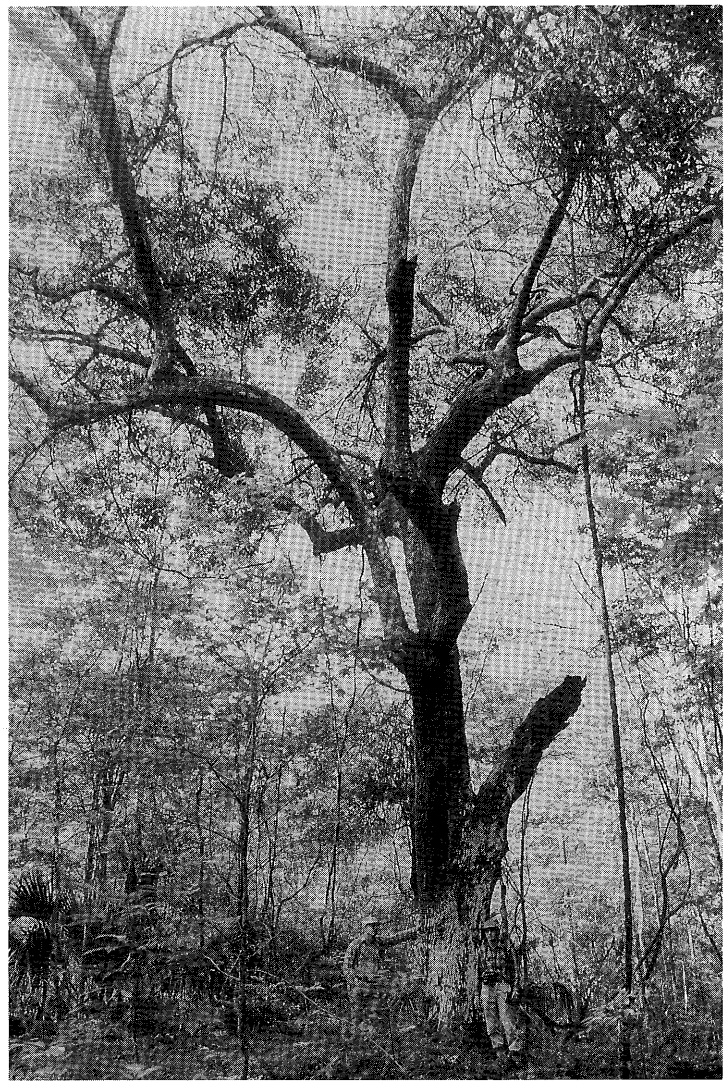

Fig. 7. Unusually large (20m) remaining *Persea borbonia* individual in an otherwise mainly deciduous but species-rich secondary forest at Paynes Prairie preserve near Gainesville (interior north-central Florida). The secondary forest is dominated by *Liquidambar styraciflua, Ulmus alata,* and *Carya glabra* (all deciduous) but also contains large, remaining individuals of *Quercus virginiana* (to 20m), *Qu. laurifolia* (to 25m), and *Qu. hemisphaerica* (to 22m). The potential natural vegetation seems to be a diverse evergreen broad-leaved forest of the upland type (mesic variant). This forest area was once part of a large cattle ranch.

Fig. 8. A semi-evergreen "Southern mixed hardwoods" stand with straight-growing, evergreen *Quercus hemisphaerica* in the canopy, at San Felasco Hammock preserve near Gainesville (interior north-central Florida). A nearby part of the same forest area (photograph not available) had a canopy dominated by *Qu. hemisphaerica* (30m, 85% canopy cover) but with many deciduous understorey trees, suggesting a successional status. The potential natural vegetation at this site seems to be a mosaic of typical and mesic variants of the upland type of evergreen *Quercus* forest.

Conclusion

The American South is now covered mainly by deciduous forests, pine plantations, or successional pine woods, even along most of the coastal plain. Even so, evergreen broad-leaved forests, especially with their romantic drapings of Spanish moss on spreading live oaks, were a distinctive feature of the coastal landscapes which were the historic origins of Southern culture. Such landscapes are preserved in some areas in the form of urban parks and squares (Figure 9) as well as in nature preserves and (less protected) state parks and hunting tracts. Southern culture is a product of the geographic juxtaposition of these exotic, evergreen coastal landscapes and the vast deciduous-forested interior into which settlers advanced. In this respect, Southern culture had somewhat similar origins as that of Japan, which also developed mainly in a region of evergreen broad-leaved forests.

Evergreen broad-leaved native trees are seen throughout the southeastern coastal plain, both as individual large trees (perhaps planted) and as apparently natural regeneration, perhaps especially on poorer soils (mainly *Quercus virginiana* and *Qu. geminata).* Other large evergreen broad-leaved trees can be found on more restricted sites. "Southern mixed hardwoods" seems a reasonable concept for interior parts of the coastal plain, where winters are colder. Evergreen broad-leaved forest, however, seems to be the potential natural vegetation, in the absence of recurring major disturbances, over much of the outer coastal plain, except in saturated lowlands (e. g. swamps and floodplains) including

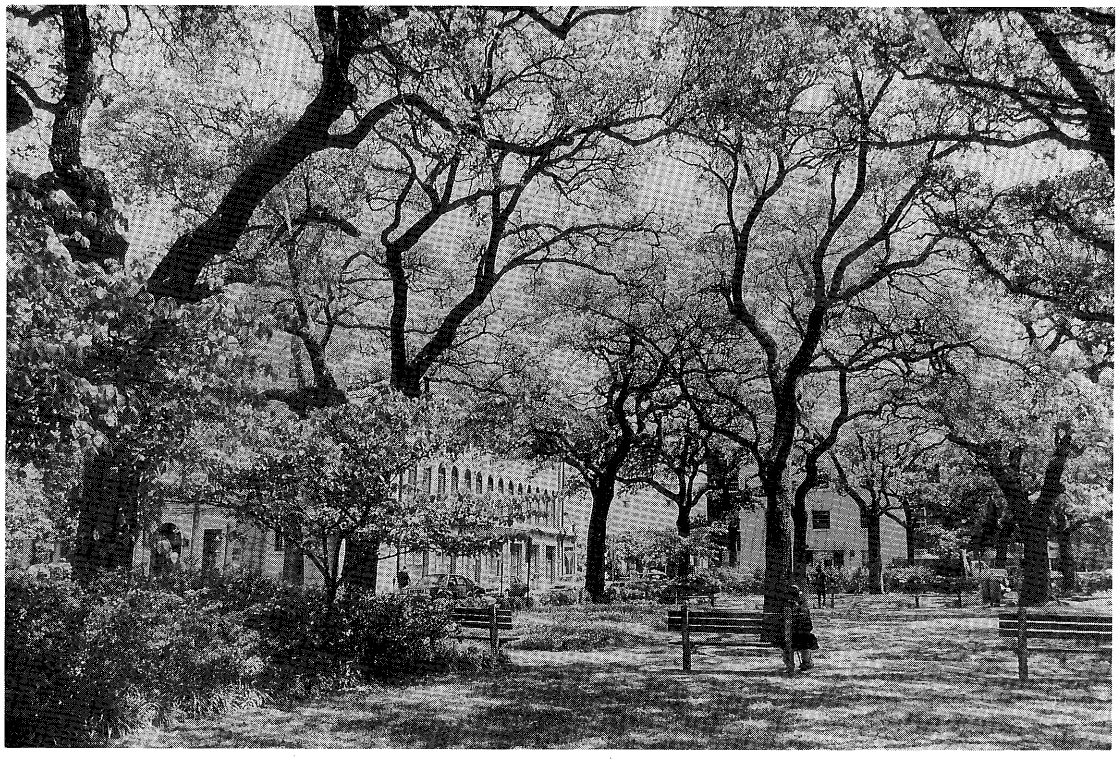

Fig. 9 A park-like city square with large evergreen *Quercus virginiana* trees, in Savannah (coastal Georgia). Such areas are common in the main cultural centers of the southeastern coastal region.

the extensive Mississippi River floodplain and delta, dominated mainly by *Salix* and *Celtis* species.

The eastern and southeastern USA provide interesting comparisons with Japan, due to similar latitude, climate, and vegetation. We hope to continue working in this region in order to develop date-bases which will permit more detailed analysis and comparison with other warm-temperate forest regions of the world.

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