Vegetation of the Longleaf Pine Region of the West Gulf Coastal Plain

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ABSTRACT

For nearly 20 years we have been studying the Big Thicket of southeast Texas as an example of the vegetation of the western Gulf Coastal Plain. Most of this area is covered by closed forests which vary in structure and species composition along a soil texture gradient. Longleaf pine is a distinctive element, but it is dominant in only a few of the identifiable vegetation types in the region. New ordination analysis confirms western Gulf vegetation patterns and their relationship to soil texture. However, soil phosphorus and nitrogen availability, as well as moisture, may be important in explaining changes in forest composition and structure along the soil texture gradient. The strong relationship between vegetation and soil properties suggests that fire interacts with edaphic factors in influencing the landscape distribution and species composition of plant community types.

Longleaf pine in the Big Thicket is dominant on level-to-gently rolling hilltops with sandy surface soils and on some low flat sites. It also occurs in upland stands with other pines, oaks, and hickories characteristic of dry, nutrient-poor sites. Frequently, understory vegetation is dense. It has been suggested that in the past many of these forests were open savannas with a longleaf pine canopy and a grassy groundcover. Stand history data from one oak-hickory-pine stand do indeed suggest that longleaf pine was more important prior to logging early in the century. However, these data also show that several species of oaks also occurred frequently in the presettlement forest.

INTRODUCTION

Several papers have appeared in recent years which review and synthesize literature about the vegetation of the southeastern Coastal Plain (Christensen 1981, 1988, Frost et al. 1986, Bridges and Orzell 1989, Platt and Schwartz 1990, Myers 1990, Ware et al. 1993). These reviews have mostly emphasized basic similarities in vegetation patterns throughout the Coastal Plain, with particular emphasis on sites east of the Mississippi River. As information accumulates from different localities, however, it is becoming increasingly apparent that significant, geographically related, variation does occur within this region (see also Peet and Allard, 1993). In particular, Coastal Plain vegetation west of the Mississippi River differs from Coastal Plain vegetation farther to the east (Harper 1920, Marks and Harcombe 1981, Bridges 1988, Bridges and Orzell 1989). Thus, an overview of the vegetation focusing primarily on the western Coastal Plain is in order.

Because this Proceedings is concerned with conservation and management of the "longleaf pine ecosystem," we will consider only that part of the west Gulf Coastal Plain which encompasses

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the natural range of longleaf pine (*Pinus palustris*). This area stretches from the western edge of the Mississippi River bottomland forests in Louisiana almost to the Trinity River in Texas (see maps in Wahlenberg 1946, Allred and Mitchell 1955, Little 1971, Bridges and Orzell 1989, and Ware et al. 1993). The southwestern boundary, in Hardin County, TX, coincides rather precisely with the boundary between the Beaumont and Montgomery geologic formations. The northern boundary, which runs through southern Angelina, San Augustine and Sabine Counties, TX, and through Sabine, Natchitoches, Bienville and Jackson parishes, LA, also coincides with a geologic boundary; longleaf pine and associated outer Coastal Plain vegetation are restricted largely to sedimentary surfaces of Miocene age or younger (Bridges and Orzell 1989). The southern boundary, in Jefferson and Orange Counties, TX, and in Calcasieu, Allen, and Evangeline Parishes, LA, is marked by a transition from forests and savannas, including plant communities with longleaf pine, to coastal prairies and marshes (Allred and Mitchell 1955, Marks and Harcombe 1981, Diamond et al. 1987, Bridges 1988, Bridges and Orzell 1989).

Our discussion of the vegetation of the longleaf pine section of the west Gulf Coast will proceed as follows: first, we review the major types of plant communities of the longleaf pine region of the west Gulf Coastal Plain; second, we consider relationships between vegetation and environment, focusing on gradual changes in plant communities and tree species abundances across important environmental gradients; third, we focus on the herbaceous communities of longleaf pine savanna, a vegetation type particularly threatened in the west Gulf Coast (Bridges and Orzell 1989); fourth, we consider how vegetation presently existing in the west Gulf Coast may differ from vegetation of the presettlement landscape.

REGIONAL SETTING

Climate and geology of the area under consideration are summarized by Marks and Harcombe (1981), and Bridges and Orzell (1989). Here we present only briefly a few facts directly relevant to the present discussion.

The climate of the longleaf pine area of the west Gulf Coast is humid subtropical, with abundant rainfall. Precipitation is generally well distributed throughout the year, though intervals of drought may be more prevalent during spring (i.e. mid March through mid-June; M. Olson and W.J. Platt, unpublished data from Pineville, LA). Summer rainfall is associated primarily with convectional thunderstorms, which are also associated with lightning and lightning-induced ground fires (Komarek 1968). Such fires are thought to have occurred frequently in the presettlement landscape, with important consequences for vegetation composition and landscape patterns (Greene 1931, Wahlenberg 1946, Frost et al. 1986, Bridges and Orzell 1989).

The west Gulf Coastal Plain is underlain by a series of former marine terraces, most of which date to the Pleistocene (Bernard & Leblanc 1965). The youngest surface, deposited within the Recent geological period, is occupied by coastal prairies and marshes. In general, the age of the surface is positively correlated with its distance from the coast, elevation, drainage, and the amount of dissection, all of which can have important effects on vegetation. Inland from the oldest Pleistocene Terraces, exposed strata date from the Miocene Period. These older surfaces tend to be well drained and highly dissected, though under some conditions (e.g., the tuffaceous sandstone of the Catahoula Formation; see Bridges and Orzell 1989) drainage may be limited and unusual plant communities may be found.

A number of authors have mapped the vegetation of all or part of the longleaf pine section of the west Gulf Coastal Plain. Early authors mapped most of the area as longleaf pine forest (Bray 1901, 1906, Harper 1920, Tharp 1926, Brown 1945, Allred and Mitchell 1955) or "southern evergreen forest" (Braun 1950), perhaps because they could personally remember a time when most of the landscape was indeed covered with longleaf pine. Later authors, especially those ecologists more concerned with potential or "climax" vegetation than with vegetation actually existing over most of the landscape, mapped the area as "southern mixed hardwood forest" (Quarterman and Keever 1962, Kuchler 1964), beech-magnolia forest (Delcourt and Delcourt 1977), and deciduous dicotyledonous-evergreen dicotyledonous-coniferous forest (Greller 1989). Foresters and range managers, who were already beginning to convert large sections of the landscape into loblolly and slash pine plantations, mapped the vegetation as "longleaf-slash pine forest" (Nelson and Zilgitt 1969) and "longleaf-slash-bluestem range" (Lewis 1974). In the last few years, conservationists, convinced of the past importance of longleaf pine and associated herbaceous-dominated understory communities, again have begun to map the regional vegetation as longleaf pine forest (Arnold 1978) or longleaf pine savanna (Frost et al. 1986, Bridges and Orzell 1989, Ware et al. 1993).

PLANT COMMUNITIES

Plant communities in the longleaf pine region of the west Gulf Coast have been described or classified by many authors, (e.g., Bray 1901, 1906, Gow 1904, Harper 1920, Tharp 1926, 1939, Penfound 1944, Brown 1944, 1945, Allred and Mitchell 1955, Watson 1975, Ajilvsgi 1979, Mohler 1979, Marks and Harcombe 1981, Ward 1984, 1986, Nixon 1985, Matos and Rudolph 1985, Diamond et al. 1987, Bridges 1988, Bridges and Orzell 1989). Instead of reiterating the details of all of these nomenclatural systems, we will attempt to provide an overview of the major vegetation types, indicating, where possible, differences among authors in classification and subdivision.

Beginning with the earliest studies, plant ecologists working in the longleaf pine region of the west Gulf Coastal Plain have appreciated the general relationships between plant communities and the habitats in which they occur (Gow 1904, Harper 1920, Tharpe 1926, 1939). A basic observation is that communities tend to occur at different points along a broad topographic-soils gradient, from dry, often infertile, uplands to moist or wet, usually more fertile, bottomland habitats (Tharp 1926, Marks and Harcombe 1981, Matos and Rudolph 1985, Nixon 1985, Bridges 1988). In the following brief overview of the major terrestrial plant communities, we will begin with the characteristic communities of dry upland sites and then discuss the communities of moist and wet habitats. With a few exceptions, species names follow Correll and Johnston (1970).

Dry Upland Forests and Savannas

Dry upland forests and savannas occur on sandy, excessively drained soils on stream terraces, moderately to excessively drained ridgetops, plateaus and dry upper slopes (Marks and Harcombe 1981, Bridges and Orzell 1989, Nixon 1985). In general, these habitats occur more commonly on the older geologic surfaces [Willis (Williana in Louisana), Fleming and Catahoula Formations] in the northern half of our study region (see also discussion under presettlement vegetation). Dry upland plant communities are invariably dominated by pines, oaks, or mixtures of the two. Longleaf pine (*Pinus palustris*) is a characteristic, but not necessarily dominant, species on most of these sites.

Very dry upland habitats created by deep sand deposits of old stream terraces are characteristically dominated by bluejack oak (*Quercus incana*), sand post oak (*Q. margaretta*), and hickories (*Carya texana, C. tomentosa*). Longleaf (*Pinus palustris*) and loblolly (*P. taeda*) pines typically occur as scattered trees emerging over the shorter oaks. Communities of this sort are termed sandhill pine forests by Marks and Harcombe (1981), oak-farkleberry sandylands by Ajilvsgi (1979) (though some aspects of her description may perhaps apply instead to the somewhat moister oak-pine forests discussed below), and xeric stream terrace sand ridge savanna by Bridges and Orzell (1989). Despite their use of the term savanna to describe this community, Bridges and Orzell (1989, p. 250) acknowledge that "the herbaceous cover is usually sparse, with considerable exposed sand and lichen cover." Except for the absence of turkey oak (*Q. laevis*) and wiregrass (*Aristida stricta*) these very dry forests are similar in species composition and structure to longleaf pine-turkey oak sandhill forests described by Christensen (1988) for the east Gulf Coast.

These sandhill pine forests represent the driest of the upland forests. With decreasing aridity (i.e., slightly less excessive drainage or slightly finer textured soils) bluejack and sand-post oak decline in importance and pines become more important. Early workers classified these slightly less xeric upland forests as longleaf pine forests (Bray 1901, 1906, Tharp 1926, 1939) or "pine uplands" (Gow 1904) because "dominance in the forest must be credited preeminently to *Pinus palustris*, which formerly occupied vast stretches of territory to the almost total exclusion, not only of all other trees, but of shrubby and herbaceous vegetation as well" (Tharp 1926, p. 22). Today, longleaf pine is still the dominant species on many dry upland sites (Marks and Harcombe 1981, Matos and Rudolph 1985, Ward 1986). Other species of pines and oaks may also be important in some locations (Marks and Harcombe 1981, Ward 1984, Nixon 1985). Upland stands dominated almost exclusively by oaks (principally *Q. stellata*) and hickories (especially *Carya texana*) have also been described (e.g., Marietta 1979, Marietta and Nixon 1983, Ward 1984).

Nixon (1985) groups the pine-dominated forests with the oak-hickory forests and the oak-pine mixtures, and describes them all simply as "dry upland communities". Marks and Harcombe (1981), however, distinguish two types of dry upland forests: (1) upland pine forests, dominated by longleaf pine, occurring on ridges and plateaus, and (2) upper-slope pine oak forests, occurring on dry uplands, dominated by pine-oak mixtures.

Though these two forest types were distinguished by Marks and Harcombe (1981) on the basis of topography and soils as well as by species composition, more recent analysis (see below) suggests that the relationship between upland forest vegetation composition and environmental factors is not as straightforward as was originally thought. It may be safest at present simply to recognize the existence of a gradient in dry upland vegetation from pine- to oak-dominated without necessarily associating this compositional gradient directly with topography or other environmental features.

Marks and Harcombe (1981) and Nixon (1985) tend to refer to dry upland vegetation of the west Gulf Coast as "forest" because most upland sites are presently dominated by relatively closed stands of trees with a well-developed woody understory (see Marks and Harcombe 1981, Ward 1984, and Bridges and Orzell 1989 for lists of common understory shrubs and hardwood trees characteristic of dry forests). In contrast, several authors (Watson 1975, Ajilvsji 1979, Diamond et al. 1987, Bridges 1988, Bridges and Orzell 1989) classify these communities as longleaf pine savannas because frequent natural burning may at one time have maintained an herbaceous-dominated understory (Frost et al. 1986, Ware et al. 1993, Bridges and Orzell 1989). This use of the term "savanna" is mostly restricted to the western Gulf; farther east, the term is generally reserved for mesic or wet sites with unusually low tree densities. At present, dry upland savanna vegetation in the western Gulf Coast is quite scarce and is restricted to areas managed with prescribed burning (Diamond et al. 1987, Bridges 1988, Bridges and Orzell 1989).

Wetland Pine Savannas

Wetland pine savannas (Marks and Harcombe 1981) [also "pine flats" of Gow (1904), "longleaf-black gum savannas" of Ajilvsgi (1979), "longleaf pine-rhynchospera series" of Diamond et al. 1987, "wetland longleaf pine savannas" of Bridges and Orzell (1989)] tend to occur mostly south of the upland pine forests, on the younger Bentley and Montgomery geologic surfaces (Intermediate Terraces in Louisiana), closer to the Gulf of Mexico (Gow 1904, Marks and Harcombe 1981, Bridges and Orzell 1989; see also discussion below of presettlement vegetation patterns). These surfaces are characterized by poorly drained soils and a seasonally high water table (Bridges and Orzell 1989). Wetland pine savannas also occur as inclusions within upland pine forests wherever drainage is limited (Streng 1979, Streng and Harcombe 1982, Marietta and Nixon 1984). Bridges and Orzell (1989) distinguish these smaller upland inclusions as hillside seepage herb bogs/seepage slopes (these are also referred to as pitcher plant bogs by Nixon and Ward 1986, and as Bogs—*Sphagnum-Rhynchospora* series by Diamond et al. 1987). Both types of wetland savannas are characterized by a diverse herbaceous layer, often dominated by sedges (principally species of *Rhynchospora* and *Scleria*), grasses (*Andropogon* spp., *Schizachyrium* spp., *Aristida* spp., *Muhlenbergia* spp., and, in Louisiana, *Ctenium aromaticum*) and composites (Streng 1979, Nixon and Ward 1986, Allen and Parris 1988, MacRoberts and MacRoberts 1990, 1991, Hermann in press). Bridges and Orzell (1989) suggest that bogs may differ from wetland savannas in herbaceous species composition (see below), though this has not yet been thoroughly quantified. However, the high relative importance of pitcher plants (*Sarracenia alata*), other carnivorous plants, and *Sphagnum*, does appear to distinguish bogs from savannas, at least in the west Gulf Coast (Folkerts 1982, Rebertus and Barker 1984, Allen and Parris 1988, Bridges and Orzell 1989, Hermann, in press).

Most authors agree that a combination of poorly drained soils and a history of more or less frequent burning is responsible for the existence of wetland pine savannas (Watson 1975, Marks and Harcombe 1981, Bridges and Orzell 1989), though Streng and Harcombe (1982) found that soil factors alone appeared to be sufficient to explain an east Texas wetland savanna. Long-unburned savannas may develop an understory dominated by wetland shrubs, including sweet bay (*Magnolia virginiana*), gallberry holly (*Ilex coriacea*), titi (*Cyrilla racemiflora*) and blackgum (*Nyssa sylvatica*). With prolonged fire suppression, these areas may possibly be converted to baygalls (see below).

Mesic Upland Forests

Mesic upland forests occur on well-drained to somewhat poorly drained loamy soils, frequently occupying gentle slopes or steep bluffs between dry uplands and bottomlands (Marks and Harcombe 1981, Matos and Rudolph 1985, Nixon 1985, Ward 1986). Nixon (1985) classified the vegetation of these sites simply as mesic upland communities. Marks and Harcombe (1981) and Bridges (1988) recognized finer moisture-related subdivisions. The midslope oak pine forest of Marks and Harcombe (1981) is characterized by the codominance of loblolly pine (*Pinus taeda*), shortleaf pine (*P. echinata*), southern red oak (*Quercus falcata*), and white oak (*Q. alba*). Other important trees include sweetgum (*Liquidambar styraciflua*) and blackgum (*Nyssa sylvatica*). Bridges (1988) recognizes a "mixed evergreen-deciduous forest" that may be derived from either wetland pine savanna or from heavily cutover mesic forest (see below) as a result of fire suppression or logging. This same sort of community is referred to by Diamond et al. (1987) as loblolly pine-oak forest. The lower slope hardwood pine forest (Marks and Harcombe 1981) [also referred to as beech-magnolia forest-hardwood slope forest (Bridges 1988) and beech-magnolia-loblolly slopes (Ajilsvsgi 1979)] is characterized by beech (*Fagus grandifolia*), southern magnolia (*Magnolia grandiflora*), and American holly (*Ilex opaca*). Loblolly pine is often important, as are a wide variety of other hardwoods. This type occurs throughout the Coastal Plain. In a more general context, it has been referred to variously as beech-magnolia forest (Kurz 1944, Blaisdell et al. 1973, Delcourt and Delcourt 1977), southern mixed hardwoods forest (Quarterman and Keever 1962) and decidous broadleaved dicotyledonous-evergreen broadleaved dicotyledenous-neadleleaved coniferous forest (Greller 1989). Beech-magnolia forests of the west Gulf Coast are similar to forests of this type occurring farther to the east, though some common species east of the Mississippi (e.g. *Pinus glabra, Liriodendron tulipifera, Oxydendron arboreum, Osmanthus americanus*) are absent westward.

Christensen (1988) refers only briefly to mesic upland forests, grouping them together as upland hardwood forests. He acknowledges that "there are considerable variations in community structure and composition within particular regions related to gradients of moisture and nutrient availability" (p. 335) but does not explicitly make finer distinctions.

Wet Forests

Early writers tended to group all wetland forests together as "swamps" (Gow 1904, Tharp 1926). However, more recent treatments have described a number of different types of wet forests. Marks and Harcombe (1981), for example, recognized three types, including floodplain hardwood pine forest, floodplain hardwood forest, and swamp-cypress tupelo forest. Floodplain hardwood pine forest occurs in active floodplains of smaller streams. Beech, magnolia, loblolly pine, water oak (*Q. nigra*), blackgum, and sweetgum are important trees in this community. Floodplain hardwood forest occurs in floodplains of major rivers. It is distinguished by the absence of pine, stronger dominance of water oak and sweetgum canopy trees, and a dense midstory of ironwood (*Carpinus caroliniana*). Other important trees include basket oak (*Quercus michauxii Nutt*), blackgum, water hickory (*Carya aquatica*), red maple (*Acer rubrum*) and cherrybark oak (*Q. pagoda* Raf.). Swamp cypress tupelo forests occur in deeper backswamps, sloughs, oxbows and other depressions and along inlets of the major rivers. They are dominated by cypress (*Taxodium distichum*) and tupelo (*Nyssa aquatica*). Characteristic understory trees and shrubs include water ash (*Fraxinus caroliniana*), water elm (*Planera aquatica*), and buttonbush (*Cephalanthus occidentalis*). Other authors have described a similar range of bottomland forests, though with slightly different boundaries along the moisture/flooding gradient (Ajilsvgi 1979, Mohler 1979, Diamond et al. 1987, Bridges and Orzell 1989, Nixon 1985). Mohler (1979) also recognizes a wide variety of subtypes or "noda" within each major forest type.

Baygalls

Baygalls [also bay-gallberry holly bogs of Ajilsvgi 1979] are shrub-dominated wetland communities characterized by *Cyrilla racemiflora, Ilex coriacea*, and sometimes *Myrica cerifera* (Marks and Harcombe 1981). Except for laurel oak (*Quercus laurifolia*), canopy dominants are similiar to those described for Nixon's (1985) wet creekside community (see above). Baygalls are commonly found in depressions and poorly-developed drainages in upland habitats where water stands for much of the year. Christensen (1988) grouped baygalls with bay forests and bayheads. In our treatment they include some forest communities of acid backswamps and seeps along the floodplains of less energetic creeks and rivers. These communities might be grouped with an acid swamp subtype of river floodplain forest, were they to occur in a region with many nutrient- and sediment-poor, but tannin-rich, blackwater rivers. Large blackwater rivers are rare in the western Gulf Region, although they may have been more common before widespread forest cutting. Several evergreen shrubs typical of eastern bay forests and shrub bogs (e.g. *Ilex myrtifolia, Lyonia lucida*, and *Gordonia lasianthus*) are absent from Texas baygalls.

GRADIENT ANALYSIS OF BIG THICKET WOODY VEGETATION

Basic relationships between environmental gradients and plant communities have long been appreciated by plant ecologists of the west Gulf Coast [see especially Tharp's (1926) description of the gradient in topography and soils between upland pine forests and swamp cypress forests]. Only recently, however, have ecologists working in this part of the country begun to develop statistical models to express these relationships in a quantitative fashion. Such models make it easier to visualize the gradual changes in vegetation composition which occur along environmental gradients, and tend to reduce the need for multiple community names to describe subtle changes in vegetation composition.

Over the past decade, several studies of west Gulf Coast vegetation have used ordination techniques (see ter Braak 1987 for an especially lucid treatment of this rather complicated subject) to objectively arrange stands on the basis of species composition and/or to test for effects of environmental variability on vegetation composition (Mohler 1979, Marks and Harcombe 1981, Ward 1986, Nixon et al. 1987). The study by Marks and Harcombe (1981) of forest vegetation in the Big Thicket area of southeast Texas is still the most comprehensive. These authors used indirect ordination to assess their ideas about plant community types and to search for relationships between forest vegetation and important environmental factors such as soil texture (which they assumed to be a surrogate for soil moisture), soil organic matter, and soil fertility. Results of their analyses were consistent with previous observations (Tharp 1926). Specifically, the arrangement of stands on the first axis corresponded to the gradient from dry upland communities to wetland communities discussed in the previous section. Surface soil texture (percent sand in the upper 15 cm of the soil column) was the most important environmental variable. A second axis separated baygalls from other wetlands. This second pattern was harder to explain, but it appeared to be primarily related to certain aspects of soil fertility (pH and calcium concentration).

For this paper, we repeated the analysis of Big Thicket woody vegetation using detrended canonical correspondence analysis (DCCA; ter Braak 1987), a more powerful direct approach than the correspondence analysis (CA) employed by Marks and Harcombe (1981). Since a strong correlation between soil texture and vegetation change was identified in the earlier work, we constrained our first DCCA axis by this environmental variable. In so doing, we accomplished two objectives. First, we directly tested variation in stand composition and abundances of individual species vs soil texture simply by examining the site scores and species scores for this first axis. And second, we statistically accounted for the variation associated with this particular environmental gradient on the first, or direct, ordination axis, leaving the remaining variation in vegetation composition for the second and higher axes. By then examining vegetation changes along these "unconstrained" axes, we could determine whether any meaningful patterns emerged that were not related to soil texture.

In addition to the 54 stands sampled by Marks and Harcombe (1981), the new direct ordination analysis also included data from 20 more upland stands in the Big Thicket National Preserve and nearby Nature Conservancy lands (Liu 1992). Also, our input data (i.e the tree data for each species in each stand) consisted of the logarithm of tree density (where a tree is defined as any stem greater than 4.5 cm dbh) rather than tree basal area. The choice of density and of the log transformation were based partly on statistical criteria which we need not discuss here (however, see Knox and Peet 1989, Knox in press). The essential idea is that the log of density tends to weight species most heavily that have many tree-sized stems . Thus, stand position along an ordination axis will be dependent to a large extent on numerically dominant species.

As expected, the first DCCA axis confirms a strong relationship between soil texture and Big Thicket forest vegetation (Fig.1a). This axis, constrained to be related to percent sand in the surface soils, accounts for about 70% of the variation summarized by the first axis of an unconstrained, indirect ordination of the same vegetation data and performed with a closely related technique (eigenvalues: 0.424 and 0.605 respectively). In addition to demonstrating once again the strength of the soil-texture vegetation relationship, the first DCCA axis also illustrates the confounded effects of topography and soils on Big Thicket forest communities. From left side to right, this axis shows the transition from dry upland communities located on sandy soils through mesic forests located on intermediate-textured soils to wet bottomland communities occurring on clay-rich soils. Characteristic species of these different forest types are shown in the plot of species scores across the first two axes (Fig.2). Dry upland species (e.g., *Quercus incana, Carya texana*) are found on the lefthand, or "sandy," side of the first axis; species such as beech and magnolia, typical of mesic sites, are found on intermediate textured soils towards the center of the first axis; and species typical of floodplains (e.g., *Quercus lyrata, Carya aquatica*) or other wet sites are found on the righthand or "clay-rich" side of the first axis.

Examining plots of species scores across the first ordination axis provides some indication of the effect of the soil texture gradient on changes in the abundance of individual species across this gradient. However, it is easier to visualize such changes by plotting directly some measure of the abundance of a species across the entire gradient. Examples of such plots are shown in Fig.3. Each plot shows the density of one common species in each stand (indicated at the location of the stand in the ordination space defined by the first two axes). Focusing on the first axis, it is apparent that species characteristic of upland sites are more abundant (i.e., occur at higher density) towards the high-sand end of the gradient, species characteristic of bottomland sites are more abundant towards the high-clay end of the gradient, and species characteristic of mesic sites are more abundant on medium-textured soils towards the center of the gradient. Shortleaf pine is slightly more restricted to very sandy soils than longleaf pine. Additional plots of the same kind are shown in Fig.4 for common species of oaks. This latter figure shows clearly that the various species of oaks are distributed differently across the soil texture gradient. Note that two of the common oak species, post oak and especially bluejack oak, are more restricted to very sandy soils than is longleaf pine.

Turning now to vegetation patterns not associated with soil texture (i.e., those appearing on the unconstrained axes of the DCCA ordination), we observe that the second DCCA axis is particularly interesting. In contrast to the second axis of the Marks and Harcombe (1981) CA ordination, which distinguished baygalls from other wetland forests, the new DCCA second axis represents a gradient among upland sites on the "sandy" end of the first axis. On one end of this second gradient (i.e., the lower end of the vertical axis in Fig.1) are stands dominated by mixtures of oaks and pines (see also Figs.2-3). These stands are also characterized by numerous shrub species including *Cornus florida* and *Ilex vomitoria*.

On the other end of this same gradient (i.e. the upper side of axis 2 in Fig.1) are stands more strongly dominated by longleaf or shortleaf pine, with fewer oaks, loblolly pines and shrubs (*Q. marilandica*, blackjack oak, seems to be an exception here). Thus, the second axis appears to represent a gradient from stands which Marks and Harcombe (1981) refer to as upper slope pine oak to stands which they would classify as upland pine. Focusing on the upland sites and re-ordinating only those stands with greater than 50 percent sand in surface soils, the pattern appears much the same as before (Fig. 5). Sand content remains significantly associated with differences in tree species composition (p = 0.001, by a randomization test). When the Marks-Harcombe (1981) community names are superimposed on this new ordination (Fig. 5), sandhill stands with abundant bluejack oak continue to form a tight cluster, but there is no clear

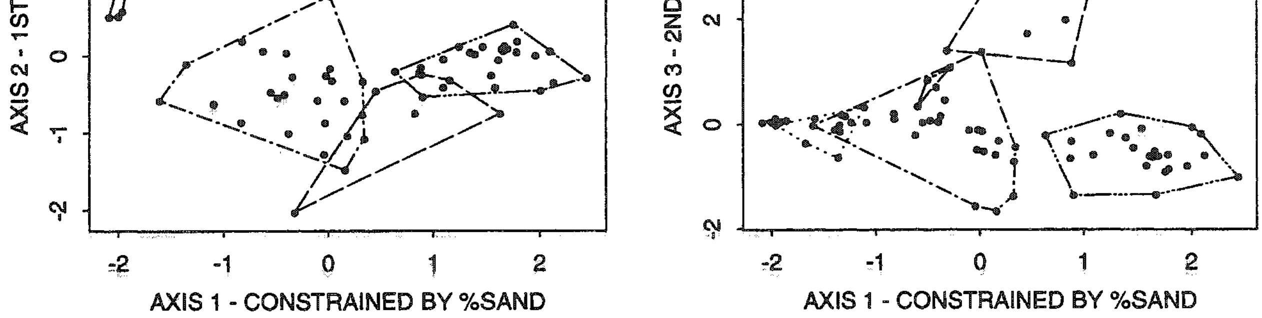

Figure 1. Distribution of Big Thicket forest stands across (A) the first and second axes, and (B) the first and third axes of a detrended canonical correspondence analysis (DCCA) ordination. Detrending was done using second order polynomials. On the first axis, stand scores were alternately calculated from a linear regression on percent sand-sized particles in the upper 15 cm of soil and from a weighted average of species scores, repeated until convergence. Subsequent axes maximize dispersion of species scores, in an unconstrained fashion, after removing any linear and quadratic dependence on earlier axes.

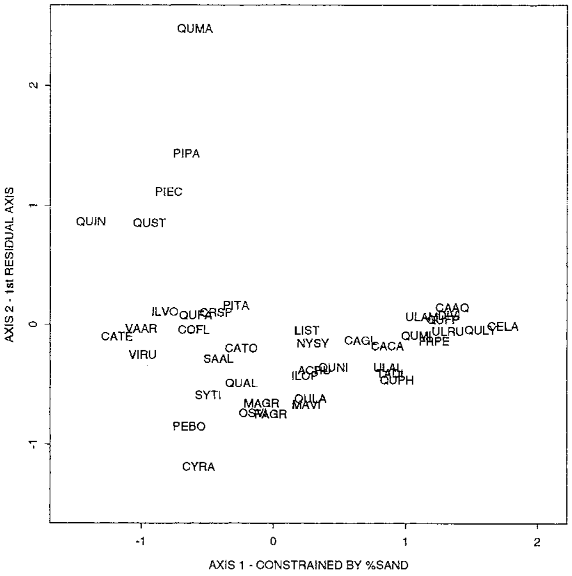

Figure 2. Distribution of Big Thicket tree species across the first and second axes of a DCCA ordination. (Stand scores from this same ordination appear in Figure 1.) Species abbreviations were formed from scientific names (see Appendix I).

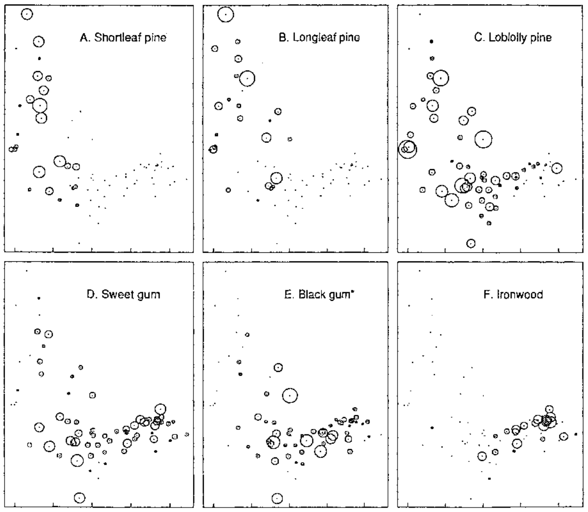

Figure 3. Abundances of the six most common Big Thicket tree species (excluding oaks) in each stand. Circle area is proportional to density of tree-sized stems in the stand at that location in the plane defined by the first two axes of a DCCA ordination (see Figure 1A). For visual reference, circles were superimposed on dots showing the distribution of all stands in the DCCA ordination. The sequence of panels runs from species restricted to sandy uplands (A) to those of floodplains and wetter mesic forests (F)

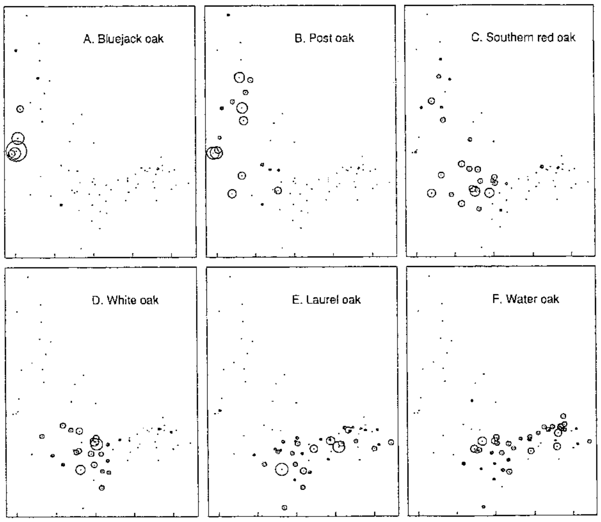

Figure 4. Abundances of the six most common oak species, plotted as per Figure 3.

separation of upland pine and upper slope pine oak types. However, composition of shrub layer and herbaceous communities may support a more refined classification of these upland forests than is readily apparent from the overstory (see below).

The third ordination axis (see Fig. 1b) turns out to be very similar to the old second axis of the CA ordination run by Marks and Harcombe (1981). Just as was the case with the CA second axis, the DCCA third axis primarily distinguishes baygalls from

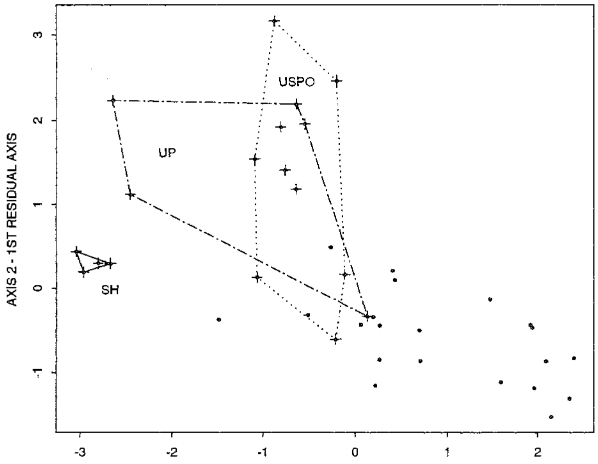

Figure 5. Distribution of Big Thicket forest stands having greater than 50 percent sand in surface soils, across the first two axes of a separate DCCA ordination of this subset. + = stands assigned to one of three Marks and Harcombe (1981) types of dry upland forest, before reclassifying the combined data set. SH = Sandhill; UP = Upland Pine; USPO = Upper Slope Pine Oak.

mesic upland forests and other wet forests. None of these three groups are important longleaf pine habitats, so they were not split out for separate analysis in this study.

Causes of gradient patterns

In his review of the vegetation of the southeastern Coastal Plain, Christensen (1988, p. 351) remarked that "I have discussed the foregoing relationships between vegetation and environmental gradients as though we really understand the mechanisms underlying these relations. Nothing could be further from the truth." We must now make a similar admission. Originally, soil texture was interpreted as a straightforward indicator of soil moisture availability, and it was assumed therefore that changes in soil moisture availability must underly observed changes in plant species composition across the first ordination axis (Marks and Harcombe 1981). It turns out, however, that the assumption that percent sand is a simple surrogate for available soil moisture is incorrect. When texture is converted to an estimate of moisture retained in freely draining soils at moderate soil water potentials using the formula of Gupta and Larson (1979), the relationship between percent sand and moisture appears to be unimodal (Fig.6). Soils with high clay content are as likely as very sandy soils to experience physiological drought, a conclusion which is consistent with the observation by Streng et al. (1989) of drought-related mortality among tree seedlings in a floodplain site underlain by a heavy clay soil.

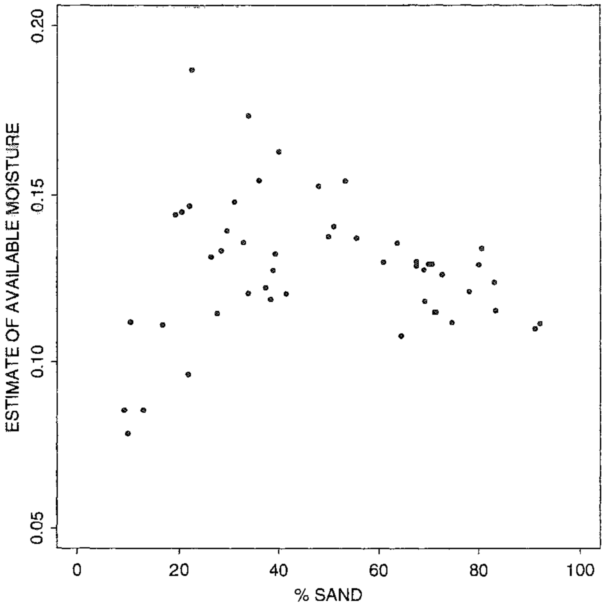

Figure 6. Relation between percent soil sand and retained plant-available moisture for Big Thicket soils, estimated using the formula of Gupta and Larson (1979).

If percent sand is not a simple surrogate for soil moisture, why is there such a strong relationship between this variable and tree species composition? Perhaps because sand content is a good indicator for a number of interrelated factors. For example, soil texture may covary with soil depth as well as with topography, and these latter two factors may influence soil moisture more strongly than does soil texture. Soil texture also appears to covary with nitrogen and phosphorus availability (Walbridge and Knox, unpublished data), and recent experiments suggest that both of these nutrients may be limiting to seedling growth in intact plugs of some Big Thicket soils (Knox and Harcombe, unpublished data).

Another possible covariate of soil texture is fire frequency. Because finer-textured soils retain more total moisture nearer the surface, these soils are likely to take longer to dry out after rains resulting in a reduced probability of burning. Thus, fire frequency probably is highest in upland habitats and decreases downslope (Platt and Schwartz 1990). Since southeastern trees differ in their tolerance to burning (Garren 1943, Wahlenberg 1946, Komarek 1983), differing fire-return intervals and burning intensities along the soil texture/topography gradient may partially account for the variation in tree species composition along this gradient (Platt and Schwartz 1990).

Concerning the second axis, which separates longleaf pine from mixtures of pines and oaks, we can offer several plausible explanations. One possibility is topographic effects on site moisture. Stands dominated by longleaf may occur in upland habitats on sandy soils, while stands dominated by oaks and pines may occur on equally sandy sites, but on gentler or lower slopes. Another possible explanation for the second axis is some aspect of soil fertility not correlated with soil texture. For example, because fire is known to volatilize nitrogen and mineralize phosphorus, sites with different burning histories may differ in availability of these important plant nutrients, even if they do not differ in soil texture. Of course, fire also may directly affect forest composition, and there is no reason to believe that fire frequency always is directly correlated with soil texture or topography (e.g. upland sites surrounded by natural firebreaks may burn less frequently than more extensive upland areas). A final possibility is that the second axis is not even truly independent of soil texture but rather represents a non-linear response of the vegetation to subtle changes in texture on very sandy sites.

HERBACEOUS COMMUNITIES OF LONGLEAF PINE SAVANNAS

Our discussion of west Gulf Coastal Plain plant communities has focused on woody plants (i.e. trees and shrubs). There are two reasons for this. First, because data on herbaceous plants are more difficult to collect, quantitative data on herbaceous plants are not available for many types of habitats and communities. Second, most of the landscape in the southeastern Coastal Plain is dominated at present by woody plants, and it is sensible to focus an analysis on dominant species. However, herbaceous communities were probably once much more widespread than they are now (Frost et al. 1986, Bridges and Orzell 1989, Ware et al. in press), and so the few remaining examples, and the species that occur in them (including many rare and local plants), are of considerable interest to conservationists (Bridges and Orzell 1989).

In the section above on vegetation classification, we recognized the existence of two different types of longleaf pine savannas: upland pine and wetland pine. In a recent paper, Bridges and Orzell (1989) subdivided each of these broad types into a number of different communities (or "subtypes"), distinguished primarily on the basis of herbaceous species composition. The four subtypes of upland pine savannas included (1) typic upland longleaf pine savanna, (2) xeric longleaf pine savanna/sandhill woodland-barrens, (3) xeric stream terrace sand ridge, and (4) dry rocky longleaf pine savanna. In terms of our previous discussion of dry upland communities, these herbaceous communities fall primarily along the gradient between upland pine forests and xeric sandhill forests. Because Bridges and Orzell (1989) based their community designations on qualitative surveys rather than quantitative sampling, it is difficult to be specific about differences in species dominance among these communities. The same species of dominant grasses (i.e. *Schizachyrium scoparium, S. tenerum, Sporobolus junceus, Andropogon ternarius, Dichanthelium dichotomum, D. oligosanthes*) occur in all the subtypes, but with lower frequency and cover in subtypes 3 and 4. The major differences are in the characteristic herbaceous species (defined in terms of percent of sites in which a species was present). An abbreviated list of characteristic species of each subtype, abstracted from Bridges and Orzell (1989; their Table 3), is presented as Table 1. Many of the species on this list are restricted to the west Gulf Coastal Plain. The subtype with fewest west-Gulf endemics is typical upland longleaf pine savanna. It is interesting to note that most of the

Table 1. Percent frequency of characteristic herbaceous species of upland longleaf pine savanna subtypes 1-4. (Abstracted from Bridges and Orzell 1989).

Species	Subtypes			
	1	2	3	4
Alophia drummondii	80	30	25	0
Aristida desmantha	0	10	100	0
Aristolochia reticulata	90	30	0	0
Aster linariifolius	80	0	0	100
Aureolaria pectinata	10	20	25	100
Berlandiera x *betonicifolia*	40	90	75	0
Bulbostylis ciliatifolia	20	100	100	0
Carex tenax	0	0	100	0
Cnidoscolus texanus	30	90	75	0
Cyperus grayioides	0	30	75	0
Dichanthelium dichotomum	50	100	100	0
Echinacea sanguinea	90	0	25	0
Euphorbia corollata	70	50	25	100
Froelichia floridana	10	90	75	0
Liatris squarrosa	60	0	0	100
Matelea cynanchoides	10	80	75	0
Paronychia drummondii	0	10	75	0
Pityopsis graminifolia	90	20	25	100
Polanisia erosa	0	0	100	0
Rhynchosia reniformis	90	10	25	0
Tradescantia reverchonii	20	80	75	0
Vernonia texana	80	20	25	100

non-endemics in this community are also characteristic of frequently burned, dry longleaf pine-dominated sites in other parts of the Coastal Plain (e.g., *Pityopsis graminifolia, Aster linariifolius, Galactia erecta, Rhynchosia reniformis;* see Platt et al. 1988, 1991, Peet and Allard, 1993, Streng et al. 1993).

In addition to distinguishing a number of different subtypes of dry upland longleaf pine savannas, Bridges and Orzell (1989) also recognized several subtypes of wetland pine savannas. Their distinction between upland herb bogs and low-elevation wetland savannas was discussed above. However, even within this latter category, they recognize several subtypes associated with differing moisture regimes and geologic formations. These include: (1) Beaumont Formation savannas, occurring on strongly pimple-mounded microtopography and containing species characteristic of calcareous, clayey soils, such as *Evolvulus sericeus, Gaura lindheimeri, Rhynchospora divergens* etc. (2) Montgomery Formation savannas, occurring on the slightly higher, better-drained soils of the Montgomery Formation, characterized by a "richer flora than subtype 1 (Beaumont Formation savannas) with more relation to bog flora", and (3) flat Bentley Formation savannas, occurring on surfaces yet again slightly higher and drier than the last, and containing more species of mesic savannas (e.g., *Ctenium aromaticum* and *Rhexia alifanus,* which are also common species of mesic flatwoods farther to the east; e.g., Platt et al. 1991; Peet and Allard, 1993; Streng et al. 1993).

The various subtypes of wetland savannas recognized by Bridges and Orzell (1989) occur along a north-south axis which crosses the major geological surfaces. However, savanna vegetation also varies from east to west within the west Gulf longleaf pine region. In particular, the Sabine River, which divides Texas from Louisana, appears to be an important geographical barrier, and many important species of Louisana savannas (e.g., *Ctenium aromaticum, Rhexia alifanus, Sabatia campanulata,* and *Hibiscus aculeatus*) fail to cross into Texas (Bridges and Orzell 1989).

PRESETTLEMENT VEGETATION

At present, much of the landscape of the longleaf pine section of the west Gulf coastal plain is covered by closed forests; savanna vegetation occurs only in a few small areas. A number of authors have suggested that the opposite situation prevailed in the presettlement forest; the landscape was mostly covered by longleaf pine savannas, and forests dominated by hardwoods or mixed loblolly-pine hardwoods were found only in restricted areas protected from frequent burning (Frost et al. 1986, Noss 1987, 1989, Bridges and Orzell 1989, Myers 1990, Ware et al. in press). According to these authors, most of the present-day upland forests were formerly longleaf pine savannas. If these authors are correct, the landscape of the southeastern United States has undergone a dramatic transformation over the last 100 to 200 years. In the present section, we attempt to test these suggestions by evaluating available evidence on the prevalence of various types of forests and savannas in the presettlement landscape. At least four kinds of evidence are available: (1) eyewitness accounts of original vegetation, (2) land survey data, (3) stand history reconstruction, and (4) early 20th century vegetation maps. Evidence from each of these kinds of data is considered below.

Early Descriptions

Unlike the Atlantic Coastal Plain, the west Gulf Coastal Plain was still largely uncut as late as the early 1900's, and many authors described the old-growth forests (e.g., Roberts 1881, Bray 1901, Gow 1904, Chapman 1909, Schwarz 1907, Foster et al. 1913, Harper 1920, Tharp 1926). These authors, without exception, described extensive open forests or savannas dominated by longleaf pine, often with a grass-dominated understory. Today, these extensive savannas and open forests do not exist in the west Gulf Coast.

Though longleaf pine savannas were once clearly much more prevalent than they are today, the early accounts are not quite so helpful in determining how prevalent they were. Some authors (e.g., Bray 1901, Schwarz 1907, Tharp 1926) stated categorically that virtually all upland sites within the range of longleaf pine once were dominated by monospecific stands of this species. Harper (1920) found that in the vicinity of Kountze, Hardin County, TX, "as in nearby parts of Louisana, *Pinus palustris* is practically the only tree on the uplands there." However, he also took note of the fact that E.N. Plank, in a previous description of Tyler County, TX, in the northern part of the longleaf pine region, failed to even "mention...the characteristic herbs of the pine forest, or even *Pinus palustris*, for that matter, which may indicate the presence of considerable areas of hardwood forests in the heart of the longleaf pine region." Gow (1904) observed that longleaf pine was almost always the dominant species in "pine flats" and "pine uplands" in southeast Texas, but that two species of oaks (post oak, *Q. stellata,* and blackjack oak, *Q. marylandica* (sic)) were "common" or "not uncommon" in the uplands, especially in the northern part of the longleaf pine range. These and other early observations (see Brown 1944 and Delcourt 1976 for reference to early accounts of Lousiana upland forests) suggest that at least in the more northerly upland areas, longleaf pine did occur in mixed stands with post oak, shortleaf pine or other dry forest tree species.

On the whole, these early accounts suggest that most upland sites may well have been occupied by longleaf pine, as many of them still are today. However, few of these sites still can be described structurally as savannas. Furthermore, it is not clear what was meant by "upland." Tharp (1926), for example, states that longleaf pine was the exclusive dominant on upland sites, but he also defines (p.26) a broad "hydrosere" (i.e. transition zone from wetland to upland) that clearly included dominants of mesic upland forests (e.g., *Magnolia grandiflora, Quercus alba, Q. stellata*) and he even shows a photograph of "a grove of *Fagus grandifolia* on a hillside, Polk County." As a consequence it is difficult to tell from these early descriptions alone how extensive such mesic forests were in the landscape.

Land Survey Data

Witness-tree data recorded during early land surveys represent another useful source of information for reconstructing presettlement forest composition (Bourdo 1956, Lorimer 1977). Two studies have used witness tree data to reconstruct presettlement vegetation of the longleaf pine region of the west Gulf Coast: Schafale and Harcombe (1983) for Hardin County, TX, and Delcourt (1976) for an area in NW Louisana spanning the present-day ecotone between forests containing longleaf pine and forests dominated entirely by shortleaf pine, oaks and hickories. Both papers provided maps of presettlement vegetation types within the study areas, thus simplifying the comparison with current vegetation.

Schafale and Harcombe (1983) used witness tree data to reconstruct 11 different presettlement vegetation types in Hardin County, including seven major types of forests or savannas. These types were mapped, and vegetation composition of each type was compared statistically to present-day vegetation types of the same area as described by Marks and Harcombe (1981). Two important results emerged from these analyses: (1) all of the current vegetation types could be recognized clearly in the presettlement data, including upland pine and the various mixed upland communities, and (2) these different vegetation types appeared to occupy roughly similar areas in the presettlement vegetation as they do at present. Upland pine (probably savanna, rather than forest, because of the low density of trees) occurred in a large area in central Hardin County. This is the area visited by Harper (1920) in 1918, where he observed examples of old-growth longleaf pine savannas. This area was also mapped as longleaf pine in the mid-1930's (Cruickshank and Eldridge 1939) and today would be classified as upland pine forest, some of it still dominated by longleaf.

In addition to this area of longleaf pine savanna, Schafale and Harcombe (1983) also reconstructed a sizable area of mixed oak-pine forest, distributed in a broad band from the northwestern to the southeastern part of the county. Important species included pine (today these are *P. echinata* and *P. taeda*), white oak, red oak, pin oak (*Q. laurifolia* and *Q. phellos*), sweetgum, blackgum, and magnolia. Some of this area may represent a broad ecotone with the loblolly pine-hardwood dominated forests to the southwest (see Gow 1904, Harper 1920), but at least part of it is well within the accepted boundary of the longleaf pine forest. These results show also that this mixed oak-pine community was an important component of the presettlement landscape well before any major effect of logging or fire suppression.

The other witness-tree study was Delcourt's (1976) reconstruction of presettlement vegetation of northwestern Louisana. She delineated four major types of vegetation in the presettlement forests of this area. The prevailing type over most of the landscape was upland pine forest. Though this forest type was strongly dominated by pine, it also included appreciable quantities of southern red oak, post oak and dogwood. Pines were not identified to species in the survey records, but Delcourt (1976) suggested, based on other evidence, that shortleaf pine was probably the dominant species in the northern part of her study area, while longleaf pine was dominant to the south. The presettlement distribution of oaks and hickories was unclear from her results, though it may be safe to assume that these species were associated mostly with the northern shortleaf pine forests, as they are today (Brown 1945).

A second important community type reconstructed by Delcourt (1976) was pine-oak flatwoods, which occurred in a broad band between wetland forest communities and the upland pine forests. Despite her use of the word "flatwoods", these transitional forests apparently were similar in species composition and structure to our mesic upland forests. Forests dominated by loblolly pine and mesophytic hardwoods may have occurred "on moist sites, near marais and streams", while pine-oak may have occurred on somewhat drier sites in the second bottoms of major rivers.

In addition to pine and pine-oak, Delcourt (1976) also reconstructed two wet forest types composed primarily of hardwoods, an "alluvial backswamp hardwoods community," which occurred on alluvial first bottoms of the study area, and a "tributary bottomland hardwoods community" which occurred along the smaller streams.

Considered together, the results of Delcourt (1976) and of Schafale and Harcombe (1983) are consistent with early observations that upland forests in the longleaf pine region of the West Gulf Coastal Plain were indeed dominated by longleaf pine. Low densities of pine trees in both studies also tend to confirm that these upland habitats were savannas (i.e. open woods) rather than closed forests. In contrast to the suggestions of some authors (Frost et al. 1986, Bridges 1988, Bridges and Orzell 1989), virtually all of the other forest communities recognizable in the current landscape also occurred in the presettlement landscape, mostly in the same sorts of places where they occur today. Some of these communities (e.g. mixed pine-oak or oak-pine forests occurring on midslope or upper slope topographic positions) may indeed be relatively more abundant now than they were in presettlement times (Ajilsvgi 1979, Bridges 1988, Bridges and Orzell 1989, W.J. Platt, personal observations), but this is difficult to confirm with existing data. Clearly, there is a need for additional geographically detailed studies of the sort reviewed in this section.

Stand history reconstruction

Yet another source of information on structure and composition of presettlement vegetation is stand history reconstruction (e.g., Henry and Swan 1974, Glitzenstein et al. 1986, Frelich and Lorimer 1991 and references therein). This method, which involves analysis of tree age distributions, growth patterns, and spatial distribution of stem ages, has been employed rarely in the southeast. However, one such study of an east Texas loblolly pine-hardwood forest (Glitzenstein et al. 1986) showed that many of the larger hardwoods were 100-250 years old. Clearly, this stand was not a longleaf pine savanna in recent times; it represented an example of one type of presettlement vegetation.

In addition to this study of a mesic east Texas forest, we have also been investigating the history of a dry upland forest in east Texas. The study site is located in the Turkey Creek Unit of the Big Thicket National Preserve, about 10 km southeast of Warren, Tyler County, TX. The site is 1.8 ha in area, and is located along a ridge and dry upper slope. Downslope, the stand is bounded by a narrow fringe of loblolly-pine dominated forest, grading rapidly into a baygall. Aside from the gradual decline in elevation from ridge top to slope bottom, the stand is homogenous topographically. Dominant canopy trees within the study site included loblolly pine, shortleaf pine, longleaf pine, southern red oak, post oak and hickories (*Carya texana* and *C. tomentosa*). In the summer of 1982, all woody stems in the study area greater than 2 cm dbh were identified, mapped and measured for diameter. All mapped stems of shortleaf and longleaf pine were subsequently cored and aged, as were substantial subsamples of loblolly pine and the two oak species.

Selected examples of ring-width records for old trees show obvious releases in 1929-1930 (Fig.7). Virtually all other old longleafs showed releases at this time, though sometimes not as strikingly. Since there are no other release peaks in the records, the stand must not have been logged before 1929-1930. Thus, we can assume that trees originating prior to around 1920 were at least small trees in the old-growth forest at the time of cutting.

The age structure data (Figs 8-9) demonstrate that oaks and longleaf pine were part of the forest vegetation long before logging, while shortleaf and loblolly pine may have entered the stand largely after logging. Also, regeneration of longleaf pine after logging was relatively minor compared to that of the four other species. Thus, logging and ensuing land use history (possibly including a reduced frequency of burning) may have favored oaks and other pines over longleaf pine. This is consistent with observations by Bray (1901) and others of scarcity of longleaf regeneration in many cutover stands.

The map of aged trees surviving from the virgin forest (i.e. trees older than 1920; Fig.10) shows some segregation of older oaks and pines. However, this was very subtle; the forest was not an obvious mosaic of two different forest types, nor was there any clear indication of a downslope transition from pines to oaks. These observations are consis-

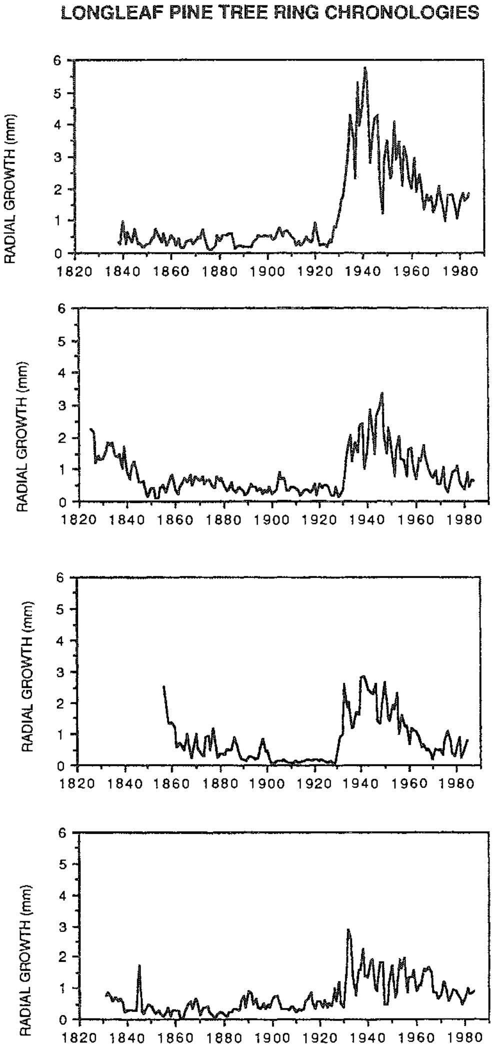

Figure 7. Representative tree-ring chronologies for longleaf pine at the Turkey Creek study site.

tent with the survey-record studies (Delcourt 1976, Schafale and Harcombe 1983) and other studies of mature hardwood- dominated forests (Marks and Harcombe 1981, Marietta and Nixon 1983, Ward 1984) in suggesting that post oak and southern red oak did occur with some frequency, at least in some of the more northerly longleaf pine stands.

Early vegetation maps

Early vegetation maps generated as part of the Southern Forest Survey Program (Cruickshank and Eldredge 1939) offer additional information that may help us to understand the presettlement landscape. However, these maps must be interpreted cautiously, because they were constructed after widespread logging of original forests had commenced and significant changes in vegetation may already have occurred.

The Texas map (Fig. 11) shows two significant things. First, of the area within the longleaf pine belt, half or less is mapped as longleaf pine, the rest being mostly bottomland hardwoods, loblolly hardwoods or oak-hickory. Second, the longleaf pine forest is divided up into patches by other vegetation. And, since this map was drawn at a scale of 1:2,000,000 it seems safe to assume that even within patches, inclusions of other types occurred.

This patchiness has interesting implications regarding fire frequency and spread. If the patches were isolated by broad stream bottoms or other wetlands which served as firebreaks, then patch size would have influenced fire frequency, and smaller patches might have escaped fire for considerable periods. The importance of patch size can be illustrated by considering the dependence of fire-frequency on patch size, given a known frequency of lightning-caused fires. Texas Forest Service records for 1963-1975 show approximately 1 lightning fire per 100,000 ha per year (Table 3 in Walker 1976). Since this averages over many vegetation types in a landscape largely devoid of large longleaf pines which may have functioned as lightning attractors (Platt et al. 1988), we take 1 fire per 10,000 ha per year as an upper limit for the fre-

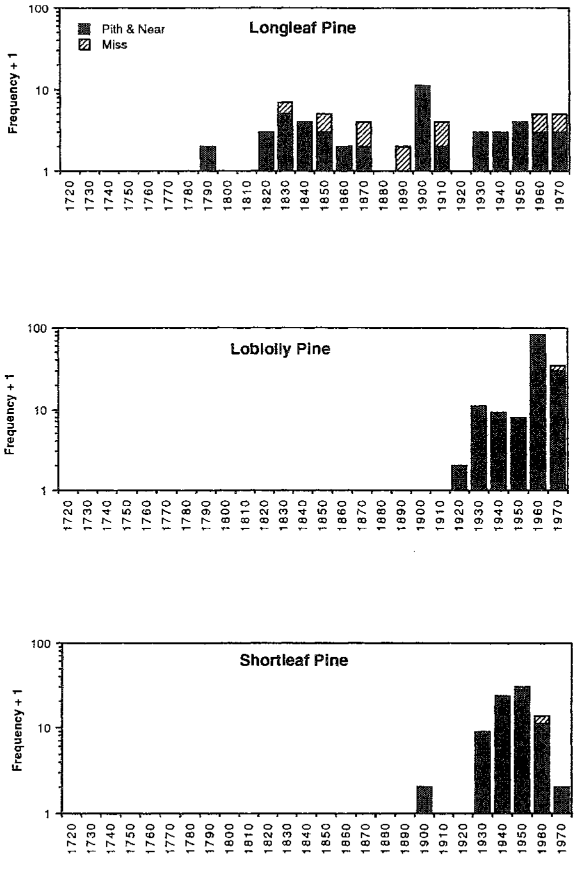

Figure 8. Pine age frequency distributions for the Turkey Creek study site. (Note that y axes are logarithmic.) Frequency is plotted as log (freq + 1). Age data were aggregated by decade. Ages were not corrected on trees for which the core did not include the pith ("near pith")

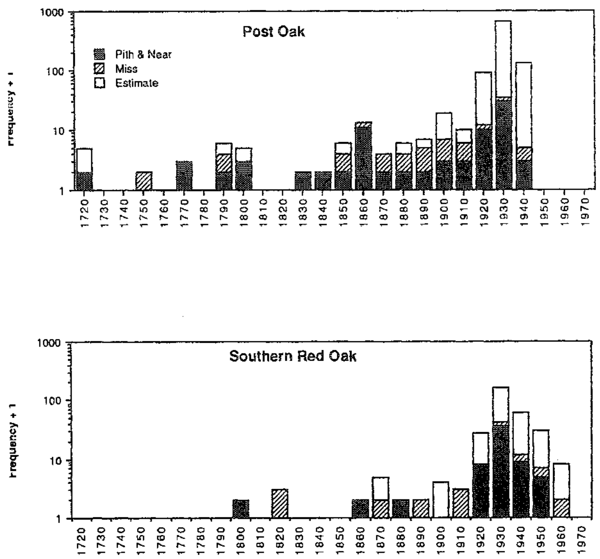

Figure 9. Oak age frequency distributions for the Turkey Creek study site. The oak age structures were based on random samples of trees in each of ten size classes. The percentage of trees cored varied by size class, with all or most trees cored in the larger size classes, and with much smaller percentages of smaller trees cored (this is because most smaller trees dated to logging in 1929-1930, and age structures for older trees were of greater interest). Ages were not corrected on trees for which the core did not include the pith ("near pith" or "missed"). The "estimated" data were generated by assuming that results from the random sample of trees which were cored applied to the size class as a whole (i.e. age structure data from each size class are scaled up to the number of trees in that size class, and then all size classes are plotted together).

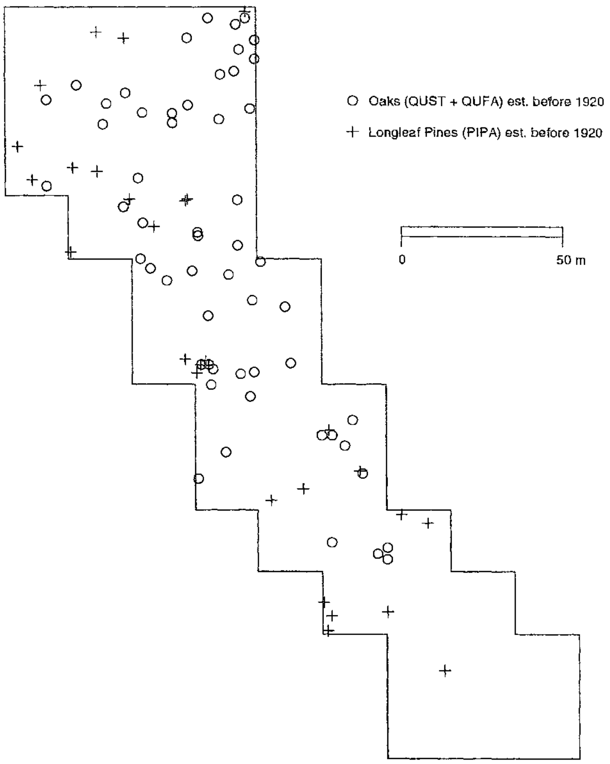

Figure 10. Map of stem locations for older oaks and longleaf pines in a mapped portion of the Turkey Creek study site.

quency of lightning fires in longleaf pine forests. We conclude, then, that patches > 10,000 ha would have burned as frequently as fuel accumulations would permit (probably 1-3 years; Christensen 1981), but that patches of 1,000 ha would have burned at only 10-year intervals on average. Median patch size for southeast Texas was 2800 ha median, so fire return interval would have been 3 years. However, nearly half the patches (42%) would have burned at intervals >5 years, and 29% of the patches would have burned at intervals >10 years.

The distribution of patches of longleaf pine forest across the landscape (Fig. 11) also illustrates the importance of physiography in determining the distribution of vegetation. The longleaf pine forests are clearly segregated into two geographically distinct units, the northern pine ridges and the southern pine flats. These correspond quite well to the two major subdivisions of longleaf pine dominated vegetation in the region (i.e. upland pine vs. pine savanna wetlands; Marks and Harcombe 1981, Bridges and Orzell 1989, also see the first section of this paper). The two subtypes are separated by a band about 15 miles wide on the Willis Geologic Formation. This strong relationship with physiography has been recognized historically as an important determinant of the vegetation (Gow 1904, Brown 1944). Brown (1944) notes, for example, a striking change in the vegetation in the vicinity of Williana, LA from longleaf pine ("and a variety of oaks") on the Pleistocene terraces (Bentley and Montgomery Formations in Texas) to shortleaf pine, blackgum and several species of oaks on the Vicksburg surface (=Willis or Williana of later treatments). Two additional quotes from that paper illustrate the point:

> "South of Many, Sabine Parish... the vegetation changes abruptly from a shortleaf pine-white oak-hickory type to a longleaf pine type. This change occurs between the Sabinetown and the Sparta formations."
>
> "The longleaf pine was on the terrace deposits and was absent from the Vicksburg formation; the shortleaf-hardwood vegetation, so abundant on the Vicksburg, was absent from the terrace materials. The contrast between these vegetation types is so abrupt that it is easily recognized."

These observations were made by Brown in the 1940's, but he cites data from a "Mr. P.A. Bloomer of the Louisana Longleaf Lumber Company" which confirm that the same patterns existed in "surveys made before the timber was cut" (Brown 1944, p.43).

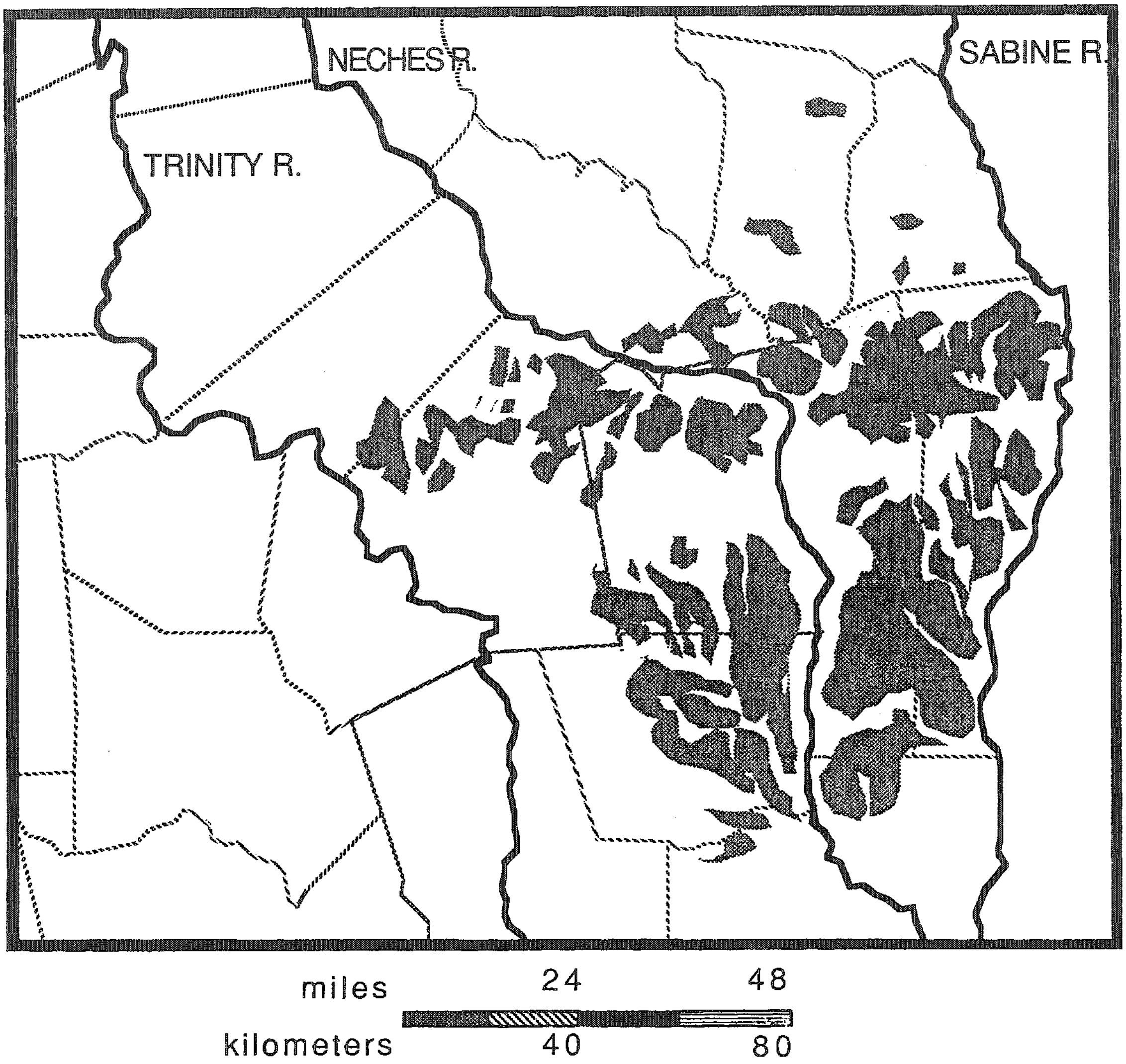

Figure 11. Landscape distribution of longleaf pine dominated forests (shaded areas) based on 1934 Forest Survey data (Cruikshank and Eldredge 1939).

The absence of longleaf pine on the Willis ridge in Texas probably is related to the presence of better drainage and richer soils than on the Pleistocene terraces to the south or the Mio-Pliocene (Catahoula and Fleming) to the north. Hardwoods and less fire- resistant pines (loblolly and shortleaf) constitute the dominant vegetation. This may be the clearest example on the Coastal Plain of the limits of fire in determining vegetation structure: fire-dependent vegetation (longleaf pine forest) occurs on both sides of fire-susceptible vegetation (oak-pine forest). The most plausible explanation is that these upland sites were resistant to fire due to higher soil moisture and to the lower flammability of the hardwood-dominated fuel bed (Streng and Harcombe 1982). The existence of the strip of mesic, mixed-pine hardwood vegetation between areas of longleaf pine-dominated vegetation illustrates the importance of soils in determining vegetation composition. The non-pyric strip of vegetation would have been a barrier to northerly spread of fire. The combination of this barrier and the dissection of the landscape on the older terraces probably accounts for greater patchiness of upland pine as compared to the pine flats (Fig.11). In turn, the greater patchiness of these northern uplands probably resulted in lower fire frequencies and increasing representation of other species of trees in longleaf pine forests. Perhaps this helps explain Gow's (1904, p.43) observation of almost pure longleaf pine forests on the southern pine flats, but common post oak, "increasing northward," in the pine uplands of Newton, Tyler, Angelina and northern Jaspar counties.

CONCLUSIONS

Vegetation of the longleaf pine region of the west Gulf Coastal Plain is highly heterogeneous, and it includes a variety of forest and savanna plant communities. Differences in vegetation among these communities are related partly to fire history, but variation in soils and topography also are very important. In all likelihood, fire and edaphic factors interacted in a complicated way to determine the presettlement vegetation. Available information does not support the idea that the presettlement landscape of this area was composed entirely of continuous monospecific stands of longleaf pine. Other vegetation types occurred, mostly in the same sorts of habitats they occupy today. Even within upland longleaf pine, the arboreal vegetation was somewhat heterogenous, varying with fire frequency, patch size and dissection of the landscape. Perhaps the greatest change in the landscape has not been the replacement of pine dominated forests by hardwood dominated forests (according to Delcourt et al. 1981, between 60 and 80 percent of standing timber volume in present-day forests of the west Gulf region is still pines), but rather the replacement of longleaf pine savannas and open forests by various other types of pine communities, including loblolly and slash pine plantations. Residual longleaf stands are still common, but most now contain shortleaf and loblolly pines and hardwood-dominated understories (especially oaks, gums and shrubs; see also Quarterman and Keever 1962, Delcourt et al. 1981). Reintroducing fire to these stands is critical, in the west Gulf as elsewhere in the southeastern Coastal Plain, though prescribing an appropriate burning regime will require consideration of landscape effects on natural burning patterns.

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APPENDIX I: Species abbreviations were formed from scientific names (from Figure 2).

ACRU	*Acer rubrum* L., (red maple);
CAAQ	*Carya aquatica* (Michx.) Nutt., (water hickory);
CACA	*Carpinus caroliniana* Walt., (ironwood);
CAGL	*Carya glabra* Sweet., (pignut hickory);
CATE	*Carya texana* Buckl., (black hickory);
CATO	*Carya tomentosa* Nutt., (mockernut hickory);
CELA	*Celtis laevigata* Willd., (Texas sugarberry);
COFL	*Cornus florida* L., (flowering dogwood);
CYRA	*Cyrilla racemiflora* L., (ti ti);
DIVI	*Diospyros virginiana* L., (persimmon);
FAGR	*Fagus grandifolia* Ehrh., (American beech);
FRPE	*Fraxinus pensylvanica* Marsh, (green ash);
ILOP	*Ilex opaca* Ait., (American holly);
ILVO	*Ilex vomitoria* Ait., (yaupon);
LIST	*Liquidambar styraciflua* L., (sweetgum);
MAGR	*Magnolia grandiflora* L., (Southern magnolia);
MAVI	*Magnolia virginiana* L., (sweet bay);
NYSY	*Nyssa sylvatica* Marsh., (black gum);
OSVI	*Ostrya virginiana* (Mill.) K. Koch, (American hop-hornbeam);
PEBO	*Persea borbonia* (L.) Spreng., (red bay);
PIEC	*Pinus echinata* Mill., (shortleaf pine);
PIPA	*Pinus palustris* Mill., (longleaf pine);
PITA	*Pinus taeda* L., (loblolly pine);
QUAL	*Quercus alba* L., (white oak);
QUFA	*Quercus falcata* Michx., (Southern red oak);
QUFP	*Quercus pagoda* Raf., (Cherrybark oak);
QUIN	*Quercus incana* Bartr., (bluejack oak);
QULA	*Quercus laurifolia* Michx., (laurel oak);
QULY	*Quercus lyrata* Walt., (overcup oak);
QUMA	*Quercus marilandica* Muenchh. (blackjack oak);
QUMI	*Quercus michauxii* Nutt., (basket oak);
QUNI	*Quercus nigra* L., (water oak);
QUPH	*Quercus phellos* L., (willow oak);
QUST	*Quercus stellata* Wang., (post oak);
SAAL	*Sassafras albidum* (Nutt.) Nees., (sassafras);
SYTI	*Symplocos tinctoria* (L.) L'Her., (horse-sugar);
TADI	*Taxodium distichum* (L.) Rich, (bald cypress);
ULAL	*Ulmus alata* Michx., (winged elm);
ULAM	*Ulmus americana* L., (American elm);
ULRU	*Ulmus rubra* Muhl., (slippery elm);
VAAR	*Vaccinium arboreum* Marsh., (farkleberry);
VIRU	*Viburnum rufidulum* Raf., (rusty black-haw).

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