

THE FALL LINE: A PHYSIOGRAPHIC–FOREST VEGETATION BOUNDARY*

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ABSTRACT. The range boundaries for many tree species in the southeastern United States correspond to the Fall Line that separates the Coastal Plain from the Appalachian Highlands. Trees in the Coastal Plain with northern range boundaries corresponding to the Fall Line occur exclusively in alluvial valleys created by lateral channel migration. These species grow mostly on lower bottomland sites characterized by a high water table, soils that are often saturated, and low annual water fluctuation. In contrast to the Coastal Plain, the southern Appalachian Highlands are occupied mostly by bedrock streams that have few sites suitable for the regeneration of these species. The Fall Line is also an approximate southern boundary for trees common in the southern Appalachians that typically occur on either dry, rocky ridgetops or in narrow stream valleys, habitats that are uncommon on the relatively flat Coastal Plain. The ranges for many trees in eastern North America are controlled by large-scale climatic patterns. Tree species with range boundaries corresponding to the Fall Line, however, are not approaching their physiological limits caused by progressively harsher climatic conditions or by competition. Instead, the Fall Line represents the approximate boundary of habitats suitable for regeneration. *Keywords:* *Appalachian Highlands, Coastal Plain, Fall Line, forest vegetation.*

Forest vegetation dominates eastern North America. Before European settlement, these forests extended nearly unbroken from the Atlantic coast westward to the Central Plains, except where Native Americans had altered them. Distinct forest regions developed in response to climatic conditions (Braun 1950; Kùchler 1964). Many of the most common species, however, occupy a large part of eastern North America. The ranges of many species extend from the Atlantic coast westward into or beyond the Ozark and Ouachita Mountains. These include some of the most common tree species in the region, such as post oak (*Quercus stellata*), southern red oak (*Q. falcata*), water oak (*Q. nigra*), persimmon (*Diospyros virginiana*), and sweet gum (*Liquidambar styraciflua*), among others. Many tree species have ranges that extend from the lower Coastal Plain northward into the Great Lakes region and New England, including American beech (*Fagus grandifolia*), black walnut (*Juglans nigra*), black tupelo (*Nyssa sylvatica*), sassafras (*Sassafras albidum*), flowering dogwood (*Cornus florida*) and several species of oak, hickory (*Carya*), and ash (*Fraxinus*).

The climate of the southeastern United States is classified as humid, subtropical. The long growing season and abundant year-round precipitation are ideal for the growth of deciduous tree species. Rainfall associated with cyclonic storms and fronts occurs throughout the year but is more common during the winter and

* Justin Hart was supported by National Science Foundation grant DGE-0538420.

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spring. Summertime convective storms occur throughout the region. These storms are more frequent nearer coastal areas. Increasing aridity and more frequent droughts limit the extension of forest vegetation to the west of the Ozark and Ouachita Mountains. Along this gradient of decreasing precipitation, the number of tree species and the density of individuals decreases as vegetation changes from forest to forest-scrub / grasslands and eventually to continuous grasslands. With distance to the north the growing season shortens, and accumulations of snow and ice become higher. Both of these are important factors influencing the northern limits of many tree species. Many deciduous species common in the southeastern United States and central Appalachians occur only on sheltered sites in New England.

Glaciers expanded to reach their maximum extent 18,000–20,000 years ago. At that time, most tree species now common throughout the eastern United States had a range restricted to the lower Coastal Plain and sites on the continental shelf that are now submerged by higher sea level (Davis 1981). The northern limits of these species were far south of the Laurentide ice sheet that extended southward into New England and the Great Lakes region. North America began to warm about 17,000 years ago, and as the ice retreated the range of many tree species expanded northward, in some cases as recently as a few thousand years ago, eventually occupying their current range (Whitehead 1981; Delcourt, Delcourt, and Spiker 1983). The progressive range expansion of these species indicates that climatic parameters related to winter conditions and length of the growing season control the northern boundaries of many tree species in eastern North America.

Climate is the dominant factor determining coarse-scale vegetation patterns in eastern North America (Delcourt and Delcourt 2000). The range boundaries of many tree species in this region, however, closely correspond to physiographic boundaries and are not controlled by large-scale climatic patterns. The Fall Line boundary separates the Coastal Plain from the Appalachian Highlands to the north. The northern range boundaries for many tree species that commonly occur in alluvial valleys within the Coastal Plain correspond to the Fall Line. The Fall Line is also a southern boundary for a smaller number of trees common in the southern Appalachian Highlands. In this article we propose that the presence or absence of suitable habitats for tree species' regeneration on either side of the Fall Line, based on geomorphic and soil characteristics, are the primary factors determining range boundaries for these species, as opposed to regional climatic conditions. To analyze the spatial distribution patterns for eastern U.S. tree species we used Elbert Little Jr.'s 1971 distribution maps and Forest Inventory and Analysis (FIA) data available from the U.S. Department of Agriculture (USDA) Forest Service (Prasad and Iverson 2003). We note the range of tree species that occur in either the Coastal Plain or Appalachian Highlands with boundaries corresponding to the Fall Line and describe hydrogeomorphic and microclimatic conditions that account for these range boundaries based on the preferred habitats of these species. Our botanical nomenclature follows that of Albert Radford, Harry Ahles, and Ritchie Bell (1968).

PHYSIOGRAPHIC REGIONS

The Coastal Plain is a region of low relief in the southeastern United States along the Atlantic and Gulf Coasts that extends southward into Mexico and includes the lower Mississippi River alluvial valley (Figure 1). The submerged portion of this plain extends under shallow water until it reaches the edge of the Continental Shelf. From sea level, the Coastal Plain rises gradually to an elevation of less than 100 meters. This region is underlain by sedimentary beds mostly of sandstone, limestone, and shale, in addition to sand and clay. The older formations gently dip seaward beneath the youngest, with several formations outcropping in progressively older parallel belts with distance from the coast. Low-gradient meandering streams that have created broad alluvial valleys with little relief occupy as much as 10 percent of the total land surface of the Coastal Plain (Shankman 1996). Late Pleistocene terraces bound the active floodplains of many alluvial streams in this region (Saucier 1987). These streams often flood during the winter and spring, during which time they submerge portions of the floodplain for a few days to several weeks, and in some years multiple inundations may occur.

To the north and west of the Coastal Plain is the Appalachian physiographic region that comprises northeast–southwest-trending highlands extending from Canada’s Maritime Provinces to central Georgia and Alabama. The southern Appalachian Highland Realm includes four physiographic provinces: the Appalachian Plateaus, Ridge and Valley, Blue Ridge, and Piedmont. The Appalachian Plateaus form the westernmost province and border the Coastal Plain in northern Alabama. The province is underlain by nearly horizontal sedimentary rocks that are in some places deeply dissected, resulting in a rugged topography. To the east of the Appalachian Plateaus is the narrow Ridge and Valley province, consisting of a belt of tightly folded and faulted sedimentary rock with alternating parallel ridges and valleys. The Blue Ridge province is the most rugged in the Appalachian Highlands and has the highest peaks. Unlike the Appalachian Plateaus and the Ridge and Valley provinces, metamorphic rock underlies this province. The highest peaks in the Blue Ridge often exceed 1,700 meters in elevation. The Piedmont province is the easternmost region of the Appalachians; from its northwestern boundary at the foothills of the Blue Ridge Mountains, it gently slopes toward the Atlantic Coastal Plain.

West of the Appalachian Highlands and also bordering the Coastal Plain are the Interior Low Plateaus in Central Kentucky, Tennessee, and northern Alabama and the Ozark and Ouachita Mountains in Arkansas and southern Missouri. Mountain summits in these regions are low compared with the southern Appalachians, but they can still be characterized as rugged landscapes. Incised bedrock streams have created high local relief. The narrow river valleys common to the highlands are in contrast to the broad alluvial streams of the Coastal Plain.

“Fall Line” refers to the boundary zone between the highland physiographic regions and the Coastal Plain. The term sometimes refers to the Piedmont–Coastal Plain boundary (Renner 1927), but it is often used for the entire southern Appalachian–



FIG. 1—Physiographic regions in the southeastern United States. (Map by the University of Alabama Cartographic Research Laboratory)

Coastal Plain boundary (Harper 1909, Harper 1910; Fenneman 1938). The Fall Line is a clearly distinguished boundary in some places. It is, however, a transitional zone in areas where streams have eroded through Coastal Plain sediments exposing previously underlain Appalachian formations. This transitional zone is sometimes called the Fall Line Hills. Falls and rapids occur where streams flow from erosion-resistant bedrock in the highlands onto the unconsolidated and less erosion-resistant sediments of the Coastal Plain. Stream gradients decrease below the Fall Line, and within the Coastal Plain rivers are generally deeper and wider.

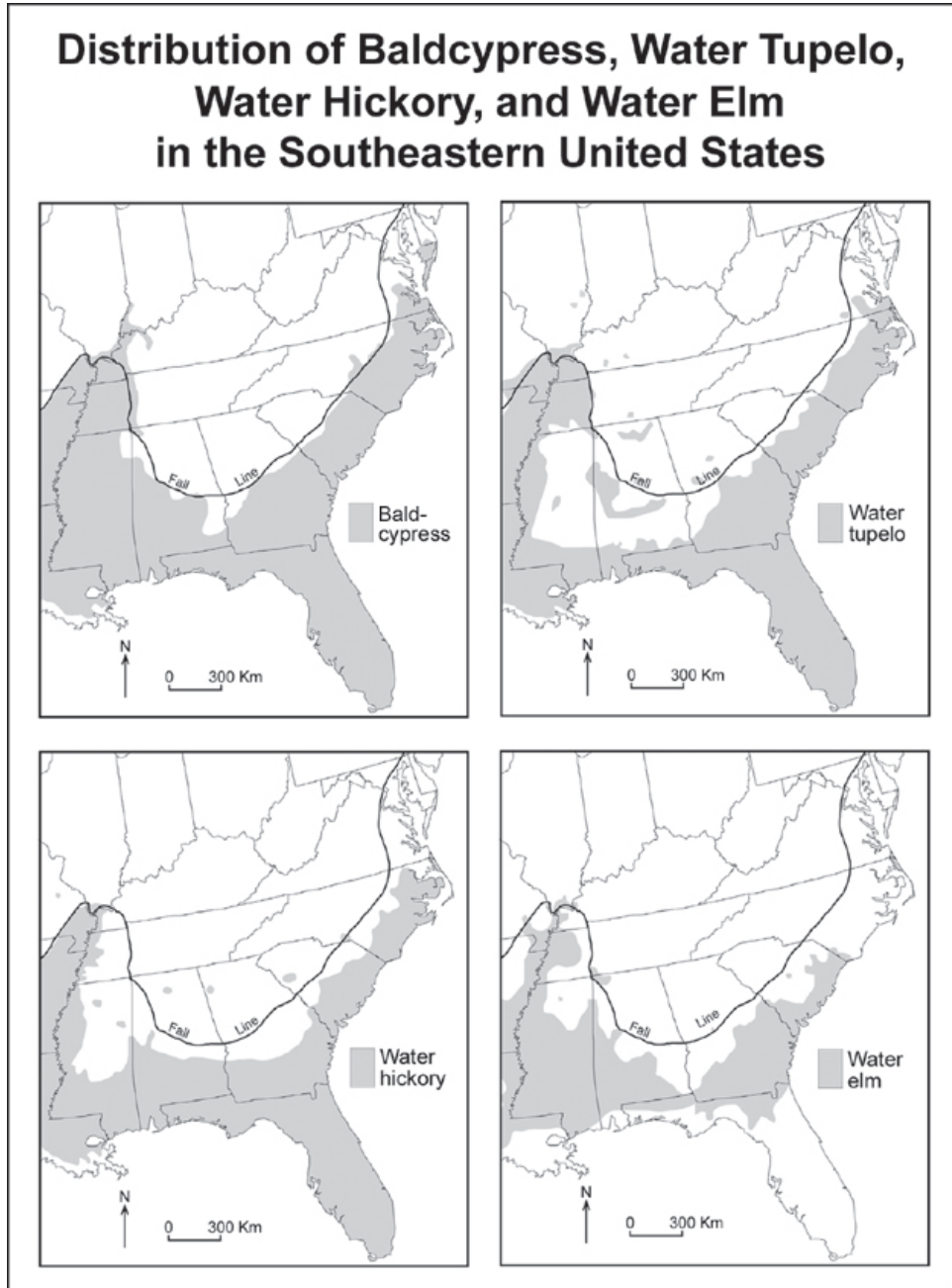


FIG. 2—Distribution maps for tree species growing on lower bottomland sites in the Coastal Plain. (Map by the University of Alabama Cartographic Research Laboratory)

COASTAL PLAIN TREE SPECIES SOUTH OF THE FALL LINE

Coastal Plain tree species with a northern boundary that corresponds closely to the Fall Line occur almost entirely within alluvial river valleys. These species are mostly absent on upland surfaces and therefore have a noncontiguous distribution within this physiographic region. These species, to varying degrees, can tolerate floods that typically occur during the winter and spring months. Those species occurring on outer floodplain surfaces that are well beyond the meander belt are subject to only occasional floods. Areas within or immediately adjacent to the meander belt will flood most years for periods ranging from a few weeks to a few months, and during a single year more than one flood event can take place. The only species in these sites are those that can survive periodic, but sometimes lengthy, inundation. Only a few species that can tolerate long-term root submersion occupy either shallow impoundments created by beaver dams and channel obstructions or abandoned channels. Periodic floods in the Coastal Plain alluvial valleys preclude most upland species.

Among the most common tree species occurring in the lower bottomlands of the Coastal Plain are baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) (Figure 2). The range for both species spreads across much of the Atlantic and Gulf Coastal Plain, but only on lower bottomland sites. The preferred habitats for each of these species are abandoned river channels, shallow swamps, and the banks of small streams. Floodwaters spread the seeds of these wetland species, so they occur almost exclusively on alluvial surfaces that regularly experience inundation (Shankman and Kortright 1994). Both species can tolerate the long periods of root submersion that preclude flood-intolerant species from regenerating on these sites. The broad floodplains of large streams in the Coastal Plain have abundant sites for their regeneration. Baldcypress and water tupelo are shade intolerant and regenerate after disturbance exposes sites to full sunlight. Regeneration ceases after development of a forest canopy, so these species occur in even-aged stands (Shankman and Drake 1990). Baldcypress and water tupelo often occur together, but on nearby sites one species may be found exclusive of the other. The exact regeneration requirements that allow them to occur together on some sites but not on others are unknown. Both species are absent in narrow stream valleys in the Appalachian, Ozark, and Ouachita Mountains; however, they occur upstream of the Coastal Plain in the alluvial valleys of the Mississippi, Ohio, and Tennessee Rivers.

Two other Coastal Plain species found in lower bottomland sites are water hickory (*Carya aquatica*) and water elm (*Planera aquatica*) (see Figure 2). Both species tolerate seasonal floods, but, unlike baldcypress and water tupelo, they cannot withstand year-round root submersion. Water hickory is a major component of bottomland forests on the lower Coastal Plain and the lower Mississippi River alluvial valley (Shelford 1954; Smith 1996; Wall and Darwin 1999). It is sometimes found adjacent to baldcypress and mixed baldcypress–water tupelo stands, but it also occurs on well-drained soils on slightly higher surfaces (Smith 1996). It can grow to a large size and often occupies the forest canopy. Water elm, in contrast to water hickory, is a small tree that typically reaches a height of no more than 10 meters. It grows in

shallow swamps, tolerates seasonal floods, and sometimes occurs in the understory of baldcypress (Shankman 1991).

Additional Coastal Plain trees with northern boundaries corresponding to the Fall Line are cherrybark oak (*Quercus falcata* var. *pagodeaefolia*) and laurel oak (*Q. laurifolia*) (Figure 3). These species grow mostly within alluvial valleys, but unlike the previously mentioned trees, they cannot withstand long-term root submersion. Laurel oak often grows on sandy, well-drained soils near swamps and river channels and on hammocks in the lower Coastal Plain. Cherrybark oak also occurs on well-drained soils, but it is most common on outer, slightly higher floodplain surfaces and stream terraces (Briscoe 1961; Meier, Stanturf, and Gardiner 2006). It tolerates drier conditions better than do most other species found primarily in alluvial valleys (Gazal and Kubiske 2004). It sometimes occupies upland sites, including the loess bluffs bordering the eastern edge of the Mississippi River valley and, in very few cases, occurs in the Piedmont and Appalachian Plateaus, slightly north of the Fall Line (Krinard 1990).

The range boundaries of overcup oak (*Quercus lyrata*), swamp chestnut oak (*Q. michauxii*), and sweetbay magnolia (*Magnolia virginiana*) follow the Fall Line in some places. But they are distinguished from those mentioned above because they occur along rivers upstream of the Fall Line (Figure 4). A visual assessment of range maps and FIA data suggests a continual distribution along rivers in the southern Appalachians. But they qualify as Coastal Plain species because they have higher seedling survival rates and are more competitive on moist alluvial soils in the Coastal Plain and generally have a noncontiguous distribution along stream segments upstream of the Fall Line. Overcup oak is the most flood tolerant of these three species and inhabits lower bottomland sites (Shelford 1954; Hosner and Minckler 1963; Shankman 1991), but it cannot tolerate long-term root submersion (McCarthy and Evans 2000). In contrast, swamp chestnut oak and sweetbay magnolia regenerate on moist but well-drained soils and typically occur on slightly higher surfaces. Sweetbay magnolia is most common along small streams and only occasionally regenerates in the broad alluvial valleys of large rivers (Gemborys and Hodgkins 1971). The seeds of sweetbay magnolia are dispersed by birds and wind and may be deposited on nonalluvial surfaces where individuals sometimes establish (Vines 1960).

Other trees in the Coastal Plain have part of their northern range limits at the Fall Line but do not share the Coastal Plain species classification because in other areas they extend well beyond this boundary. The most common of these is longleaf pine (*Pinus palustris*) that occurs over large parts of the southeastern United States (Smith, Patterson, and Trendell 2000). High fire frequency that is common in large areas of the Coastal Plain facilitates longleaf pine regeneration, while limiting the success of other trees, including other pines (Gilliam and Platt 1999; Christensen 2000). In the Atlantic Coastal Plain, longleaf pine extends from the coast inland to the Fall Line. In contrast, in the Gulf Coastal Plain it extends far north of the Fall Line, occurring over large areas of the Appalachian Plateau, Ridge and Valley, and

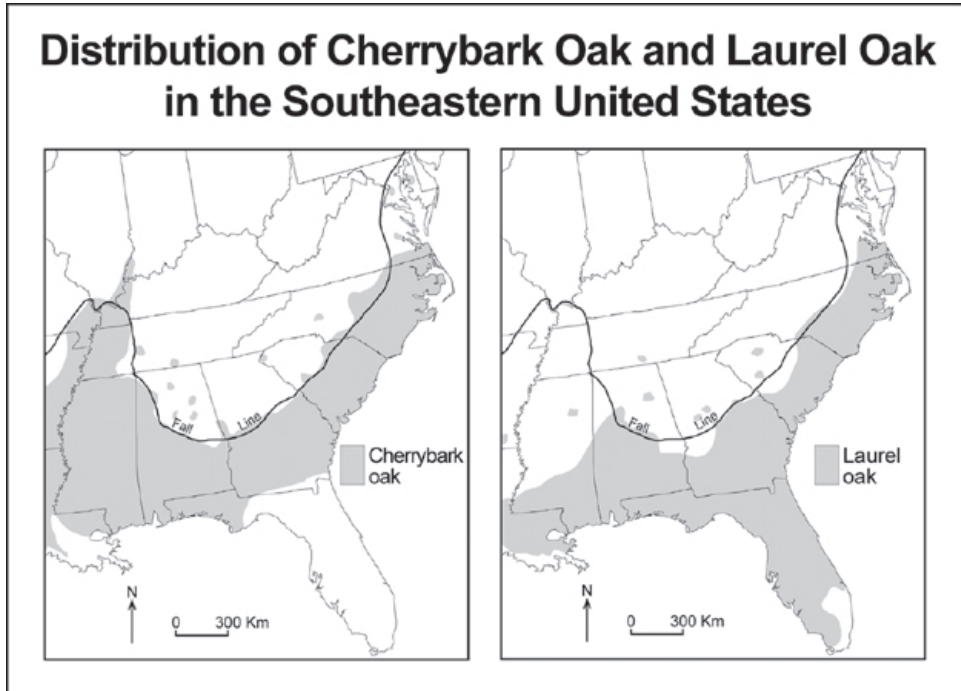


FIG. 3—Distribution maps for tree species growing on outer floodplains in the Coastal Plain. (Map by the University of Alabama Cartographic Research Laboratory)

the southern Piedmont in Alabama and Georgia. In the Appalachians it occurs mostly on dry upper slopes and ridgetops and maintains itself on these sites because of a high fire frequency and windthrow often caused by tropical cyclones that make land-fall along the Gulf Coast.

APPALACHIAN TREE SPECIES NORTH OF THE FALL LINE

Tree species common in the southern Appalachians with southern range boundaries roughly corresponding to the Fall Line include eastern hemlock (*Tsuga canadensis*), white basswood (*Tilia heterophylla*), American chestnut (*Castanea dentata*), chestnut oak (*Quercus prinus*), scarlet oak (*Q. coccinea*), and Virginia pine (*Pinus virginiana*). Each of these species, with the exception of Virginia pine, can grow to a large size, and in their preferred habitats they occupy dominant canopy positions. These species have very different regeneration requirements; however, the preferred habitats and conditions necessary for regeneration of each of these species are largely absent on the Coastal Plain.

Eastern hemlock is a dominant species on cool, moist sites on lower slopes and stream valleys throughout large areas of the southern Appalachians. Regeneration occurs when good seed crops coincide with adequate moisture conditions (Bormann and Platt 1958; Kavanagh and Kellman 1986). Eastern hemlock seedlings are shallow

Distribution of Overcup Oak, Swamp Chestnut Oak, and Sweetbay Magnolia in the Southeastern United States

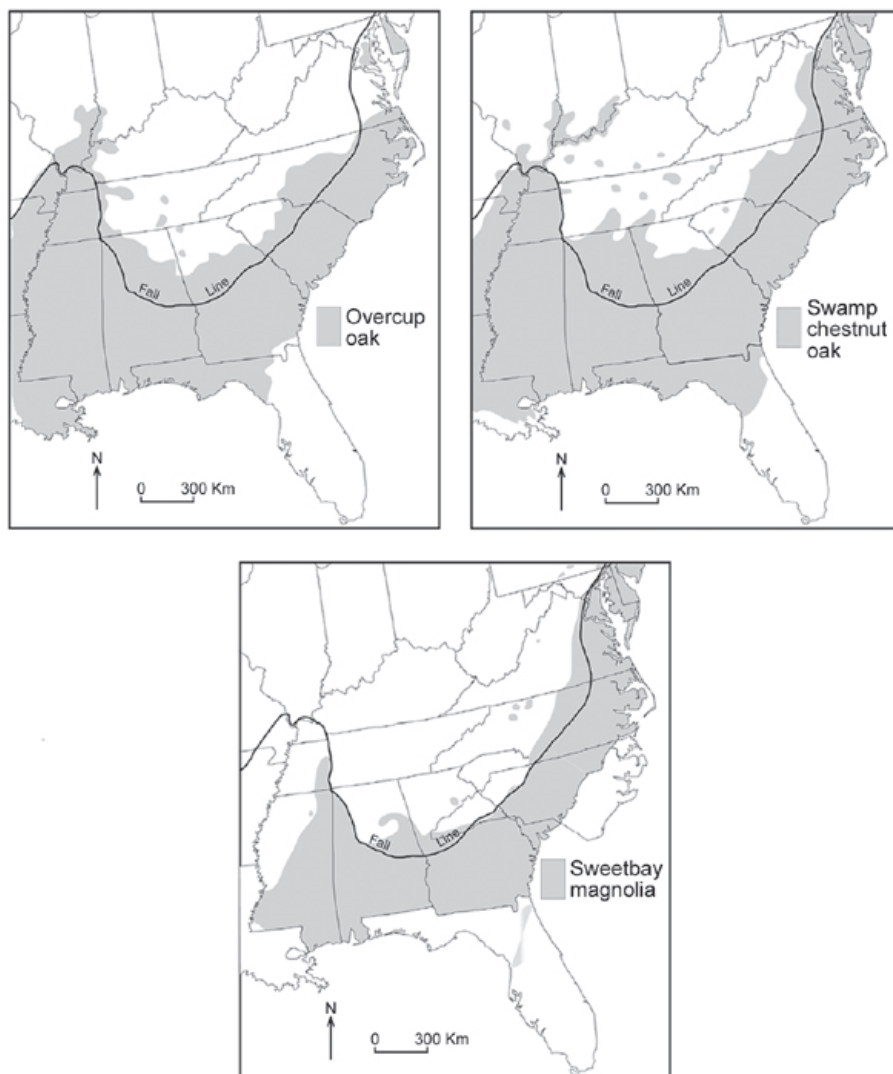


FIG. 4—Distribution maps for tree species that occur mostly in Coastal Plain floodplains but are also found upstream of the Fall Line along some streams. (Map by the University of Alabama Cartographic Research Laboratory)

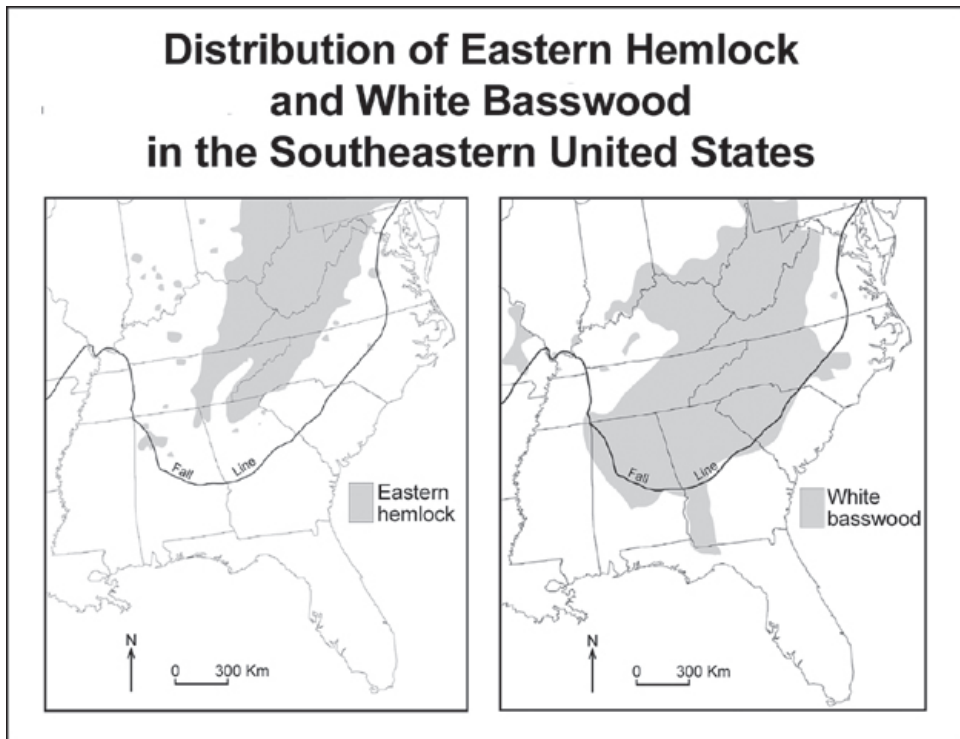


FIG. 5—Distribution maps for tree species occurring mostly north of the Fall Line. (Map by the University of Alabama Cartographic Research Laboratory)

rooted and susceptible to high temperatures and soil drying (Godman and Lancaster 1990; Mladenoff and Stearns 1993). The range of the species extends southward into central Georgia and Alabama. Hotter summers to the south restrict eastern hemlock in this part of its range to steep north-to-east-facing slopes of narrow stream valleys that maintain the microclimatic and soil moisture conditions necessary for regeneration (Oosting and Hess 1956) (Figure 5). In central Alabama, eastern hemlock occurs almost exclusively on sandstone outcrops (Hart and Shankman 2005). Surface water is available on those sites because of seepage and springs in the permeable rock, even during the dry summer and fall months. The narrow river valleys that support eastern hemlock near its southern range boundary are mostly absent on the Coastal Plain where streams have created broad valleys with little relief. An exception is in the Fall Line Hills of western Alabama, where Coastal Plain streams have eroded down into underlying Appalachian Plateau formations. Here, eastern hemlock occurs on lower slopes and in the narrow stream valleys in the Bear Creek and Buttahatchie River watersheds (Harper 1906, 1928).

The range of white basswood extends throughout most of the southern Appalachian Highlands (see Figure 5). It grows mostly on north-to-east-facing slopes and along mountain streams and coves and prefers moist, well-drained alluvial or colluvial soils (Quarterman, Turner, and Hemmerly 1972; Muller 1982). It occupies lo-

Distribution of Chestnut Oak, Scarlet Oak, Virginia Pine, and American Chestnut in the Southeastern United States

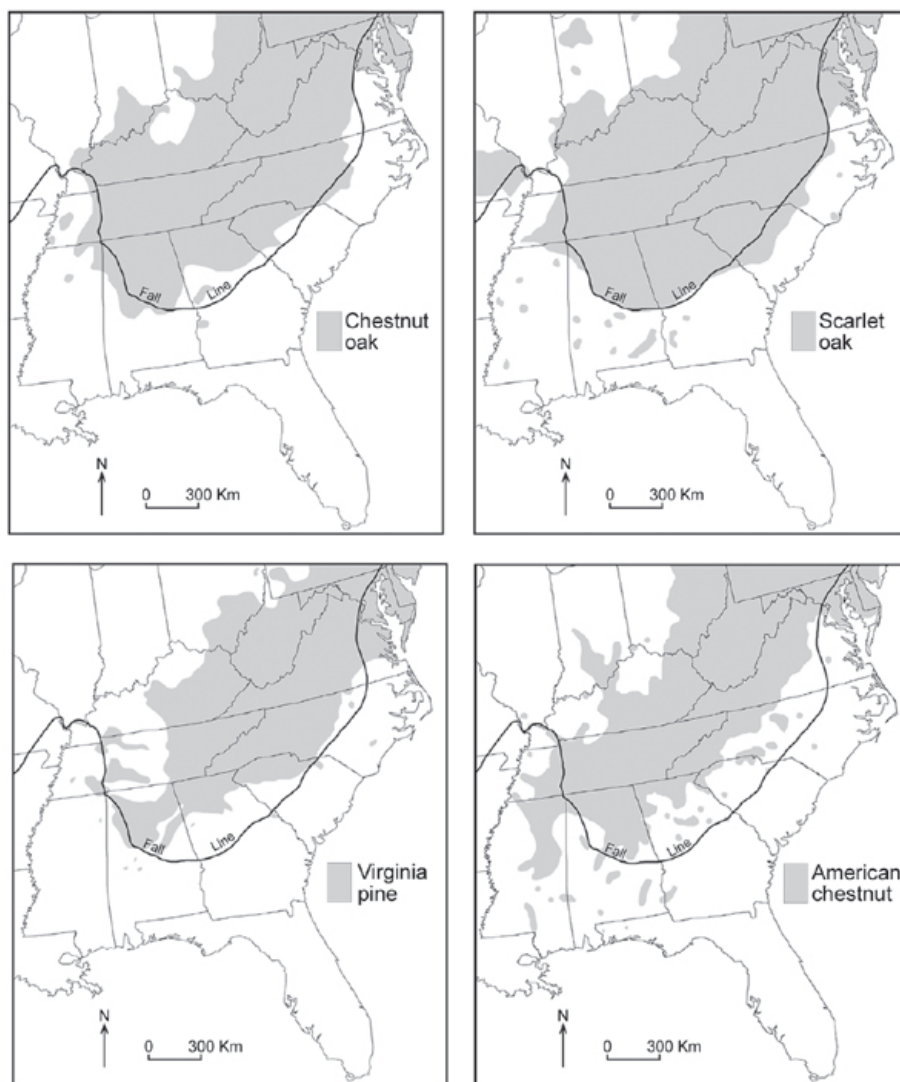


FIG. 6—Distribution maps for tree species occurring mostly north of the Fall Line. (Map by the University of Alabama Cartographic Research Laboratory)

cations mostly above 900 meters, and on favorable sites it is among the dominant canopy species. At lower elevations it becomes progressively less common, but it is occasionally found in the Coastal Plain in Alabama and Georgia. Dissected river bluffs and ravines along the Appalachian River and its tributaries constitute its restricted range. The absence of deeply incised streams on the Coastal Plain and the sandy, infertile soils with lower moisture-holding capacity are likely the major factors limiting its distribution in this region.

Chestnut oak, scarlet oak, and Virginia pine are found throughout much of the central and southern Appalachians. The southern range boundary for each species corresponds closely to the Fall Line, but they do occur in the northernmost sections of the Atlantic Coastal Plain and in a few scattered locations in the Gulf Coastal Plain (Figure 6). In contrast to eastern hemlock and white basswood that grow on lower slopes and narrow stream valleys, these species prefer the dry, south-to-west-facing upper slopes and rocky ridgetops with shallow soils that preclude many species, otherwise common to the region, from these sites (Racine 1971; Quarterman, Turner, and Hemmerly 1972). Both chestnut oak and scarlet oak grow to a large size and typically share canopy dominance (McCormick and Platt 1980; Muller 1982; Mikan, Orwig, and Abrams 1994). Virginia pine is much smaller and typically does not exceed about 20 meters in height.

In the southern Appalachians these three species dominate on west- and south-facing slopes and on ridgetop positions where conditions are xeric. On slopes of the southern Appalachians, dry conditions limit the upper boundary of scarlet oak and chestnut oak, and competition with more mesophytic species controls the lower limits (Mowbray and Oosting 1968). Scarlet and chestnut oak can outcompete other hardwoods on xeric sites because they grow rapidly and are drought tolerant. In contrast to the southern Appalachians, the Coastal Plain has low local relief and lacks the rocky ridgetops where these species commonly occur. Because relief is low on the Coastal Plain, more mesic species can dominate at low-, mid-, and high-slope positions.

American chestnut was one of the most common and largest trees in the southern Appalachians until the introduction of the chestnut blight (*Cryphonectria parasitica*) at the beginning of the twentieth century (Keever 1953; Woods and Shanks 1959). It was most common on midslope positions in the central and southern Appalachians, and on some sites constituted more than 50 percent of the trees present (see Figure 6). American chestnut cannot tolerate the dry sandy soils common on the lower Coastal Plain. It was present, however, in relatively small numbers in the northernmost sections of the Atlantic Coastal Plain and in Tennessee and Mississippi and a few other scattered locations in the Gulf Coastal Plain. Throughout its range, chestnut blight killed most mature individuals before the 1960s, and large individuals are now rare (McCormick and Platt 1980). The root systems of many chestnuts survive the blight, and root sprouting is common. But blight kills most young stems before they reach a reproductive age, so American chestnut continues mostly as an understory species (Paillet 1984; Ellison and others 2005).

PHYSIOGRAPHIC CONTROLS ON RANGE BOUNDARIES

The preferred habitats for most tree species with range boundaries corresponding to the Fall Line have been noted many times in the geographical and botanical literature. Much is known about their life-history characteristics, particularly long-lived, canopy-dominant species and those that are economically important, such as eastern hemlock and American chestnut in the Appalachians and baldcypress in the Coastal Plain alluvial valleys. The exact regeneration requirements for many of these trees are not well understood. Certainly, however, these species have a narrow range of conditions necessary for regeneration that restrict them to specific habitats and therefore preclude them from being common within both the Appalachians and the Coastal Plain because of differences in topography that affect microclimatic and hydrogeomorphic conditions. The range boundaries for both Coastal Plain and Appalachian species do not correspond precisely to the Fall Line. Suitable habitats for species with Fall Line boundaries occur beyond their contiguous range. These, however, can generally be viewed as outliers limited to such an extent that the Appalachian–Coastal Plain physiographic boundary is a fairly accurate, and in some cases a precise, range boundary for these species.

All Coastal Plain tree species with northern range boundaries corresponding to the Fall Line occur almost exclusively in alluvial valleys created by lateral channel migration. The flood tolerance of these species is highly variable, but all can tolerate the at least occasional root submersion that precludes most other tree species common to the region from these habitats. Most river valleys in the southern Appalachians, Interior Plateaus, and Ozark and Ouachita Mountains have topographic, hydrologic, and soil characteristics that inhibit the regeneration of Coastal Plain species. Streams in the highland provinces typically have narrow, steep-sided valleys with little floodplain surface area, compared with those in the Coastal Plain. The Tennessee, Ohio, and Mississippi Rivers upstream of the Coastal Plain have alluvial valleys and therefore are exceptions in regions characterized by bedrock streams. In highland provinces, little lateral movement exists to create new floodplain surfaces, and in many cases the stream channel occupies much of the valley bottom. The narrow valley bottoms of these streams typically comprise coarse material, as opposed to the richer alluvial soils with a high organic content that are more suitable for the regeneration of Coastal Plain species. Also, the annual water-level fluctuation in upland stream valleys is usually much greater than that in Coastal Plain streams, where rising floodwater spreads out across the broad floodplains. In contrast, floodwater moves up the valley sides along upland streams with little floodplain surface. Increased flood depth will submerge small individual trees. Many of the Coastal Plain species can survive short-term root submersion, but most will not survive total submersion. The exception is water tupelo. Seed dispersal is another factor that may limit the distribution of Coastal Plain species whose seeds rely on floodwaters for dispersal. Water-dispersed seeds rarely move upstream. Steeper water-surface gradients and higher water velocity with distance upstream possibly affect their distribution or the availability of suitable germination sites (Schneider

and Sharitz 1988), but it is not clear to what extent limited seed dispersal affects species boundaries.

Appalachian species with southern range boundaries corresponding to the Fall Line include eastern hemlock and white basswood, which require cool, moist conditions and therefore occur mostly in incised river valleys near their southern extents. A second group of Appalachian tree species—chestnut oak, scarlet oak, and Virginia pine—occur on dry, upper slopes and rocky ridgetops. These species have different regeneration requirements and grow in entirely different habitats. Both groups, however, depend on high local relief that creates microclimatic and soil moisture conditions suitable for regeneration. Tectonic uplift of the Appalachians and stream incision resulted in this rugged topography. In contrast, the Coastal Plain is underlain by successive marine formations that were not uplifted. The development of drainage patterns after the sea level receded following the Tertiary Period and the resistance of underlying strata to erosion determined local relief in this region. Most areas of the Coastal Plain have low relief compared with the Appalachians and do not contain steep river bluffs or high ridges. Although the preferred habitats for Appalachian tree species are mostly absent in the Coastal Plain, they are found downstream of the Fall Line in some cases. As previously mentioned, white basswood grows in the Coastal Plain in southern Alabama and Georgia, and eastern hemlock grows in western Alabama. In both cases, stream incision created steep river bluffs and microclimatic and soil conditions suitable for regeneration. The Appalachian species found on upper slopes and ridgetops also occur in the Coastal Plain, mostly in the Fall Line Hills and a few other sites with erosion-resistant outcrops in the upper Coastal Plain that has created a rugged topography.

The Fall Line does not correspond to any regional climatic boundary. It extends over a wide latitudinal range, from 39° N along the Atlantic coast and 37° N in the lower Mississippi River valley to 32° N in southern Alabama. Climatic parameters control the northern range boundaries for many wide-ranging tree species in eastern North America, whereas competition determines southern boundaries (Woodward 1987; Schenk 1996; Loehle 1998). In contrast, tree species with ranges corresponding to this physiographic boundary, in most cases, are not approaching their physiological limits caused by progressively harsher climatic conditions, nor is competition controlling their limit. Increasing physiological stress when approaching range boundaries would be shown by species occupying fewer sites and by decreasing abundance. This is not true for Fall Line trees. The “abundant-center distribution” is an assumption among biogeographers that species occur in greater numbers toward the center of their range, where optimal conditions exist, and decrease when approaching their range boundaries (Brown 1984; Brown and others 1995; Sagarin and Gaines 2002). Helen Murphy, Jeremy VanDerWal, and Jon Lovett-Doust analyzed abundance throughout the geographical ranges of 135 tree species in the eastern United States (2006), using FIA data from the USDA Forest Service (Prasad and Iversen 2003). They found that peaks of abundance could occur at any position in the range but noted that suitable sites are found with less frequency toward the range

edges. In most cases, suitable habitats for Fall Line species are still common when approaching this boundary, and within these sites the abundance of species does not vary significantly compared with more distant locations.

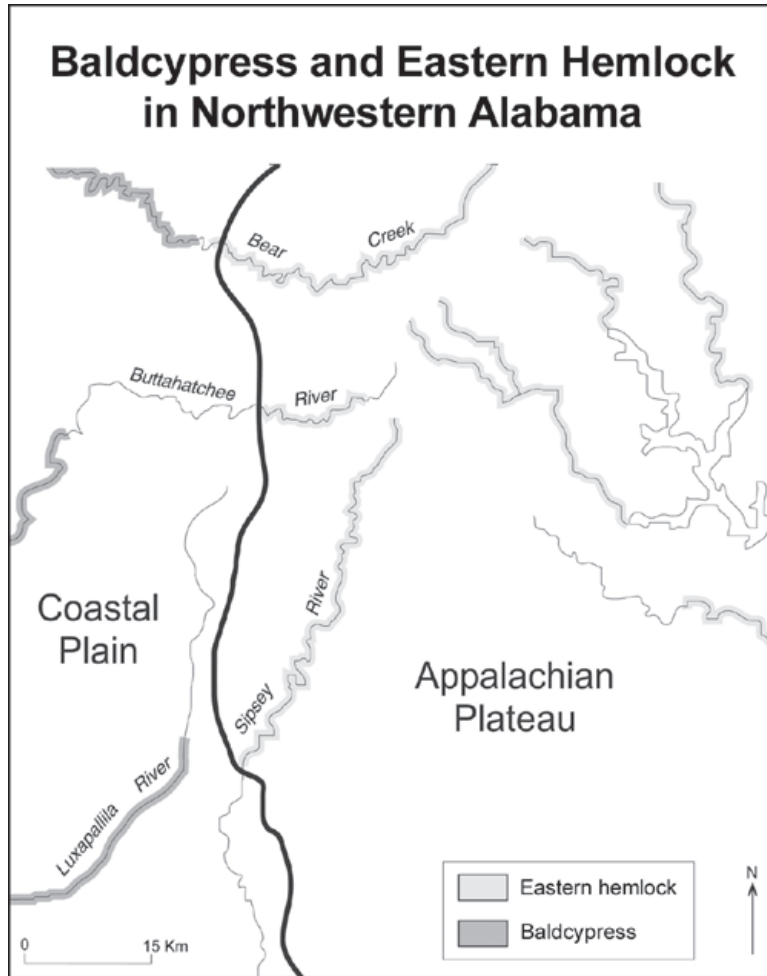


FIG. 7.—The distribution of baldcypress and eastern hemlock at their range boundaries in northwestern Alabama. (Map by the University of Alabama Cartographic Research Laboratory)

An examination of baldcypress and eastern hemlock in northwestern Alabama provides further evidence that Fall Line range boundaries represent differences in landscape characteristics in adjoining physiographic regions, as opposed to limits of physiological stress. Here, baldcypress stands occur in alluvial valleys immediately downstream of river sections in the Appalachian Plateau that support eastern hemlock (Figure 7). Though occurring at only slight differences in elevation and in close proximity, these species never occur along the same river segments because

they have a different set of regeneration requirements and because suitable habitats exist along stream segments in either the Coastal Plain or the Appalachian Plateau, but not in both. No evidence of increasing physiological stress exists among these species when approaching their range boundaries. The northernmost range of baldcypress extends up the Ohio River valley into southern Indiana. This location is more than 5° latitude north of its southern range boundary. Compared with the Fall Line boundary in Alabama and Georgia, it has a much shorter growing season, lower average temperature for the entire year, and much heavier snow and ice accumulation. Yet, in the Ohio River valley baldcypress occurs in dense stands that predictably occur on favorable sites within alluvial valleys. Baldcypress has been planted innumerable times in the central and southern Appalachians, which is well outside its natural range. Individuals in this region often live for decades and grow to a large size. They do not, however, regenerate on these sites. Furthermore, David Shankman and Rosa Maria Kortright compared growth rates of baldcypress at its upstream limits and well within its range and found no significant difference (1994). Both baldcypress and eastern hemlock are abundant in their favored sites and, when approaching the Fall Line, have characteristics similar to stands well within their range (Shankman and Kortright 1994; Hart and Shankman 2005).

Like baldcypress, the other Coastal Plain species growing in river valleys with Fall Line boundaries are found in abundance on their favored sites. Similarly, Appalachian species that occur on upper slopes and ridgetops, such as chestnut oak and scarlet oak, show no evidence of increasing physiological stress with distance south. The steep-sided ridges with shallow soils and bedrock outcrops that favor these species are uncommon on the Coastal Plain. Therefore, these species rarely occur in this region. In contrast to a gradient of progressively harsher climatic conditions and a corresponding decline as a species approaches its physiological limits, the Fall Line marks abrupt changes in topography, hydrology, and soils and is thus a boundary for many tree species common in either the Coastal Plain or the Appalachian Highlands.

REFERENCES

- Bormann, F. H., and R. B. Platt. 1958. A Disjunct Stand of Hemlock in the Georgia Piedmont. *Ecology* 39 (1): 16–23.
- Braun, E. L. 1950. *Deciduous Forests of Eastern North America*. Philadelphia: Blakiston.
- Briscoe, C. B. 1961. Germination of Cherrybark and Nuttall Oak Acorns following Flooding. *Ecology* 42 (2): 430–431.
- Brown, J. H. 1984. On the Relationship between Abundance and Distribution of Species. *American Naturalist* 124: 255–279.
- Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial Variation in Abundance. *Ecology* 76 (7): 2028–2043.
- Christenson, N. L. 2000. Vegetation of the Southeastern Coastal Plain. In *North American Terrestrial Vegetation*, edited by M. G. Barbour and W. D. Billings, 397–448. 2nd ed. Cambridge, England: Cambridge University Press.
- Davis, M. D. 1981. Quaternary History and the Stability of Forest Communities. In *Forest Succession: Concepts and Application*, edited by D. C. West, H. H. Shugart, and D. B. Botkin, 132–153. New York: Springer-Verlag.

- Delcourt, H. R., and P. A. Delcourt. 2000. Eastern Deciduous Forests. In *North American Terrestrial Vegetation*, edited by M. G. Barbour and W. D. Billings, 357–395. 2nd ed. Cambridge, England: Cambridge University Press.
- Delcourt, H. R., P. A. Delcourt, and E. C. Spiker. 1983. A 12,000-Year Record of Forest History from Cahaba Pond, St. Clair County, Alabama. *Ecology* 64 (4): 874–887.
- Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, and others. 2005. Loss of Foundation Species: Consequences for the Structure and Dynamics of Forested Ecosystems. *Frontiers in Ecology and the Environment* 3 (9): 479–486.
- Fenneman, N. M. 1938. *Physiography of Eastern United States*. New York: McGraw-Hill.
- Gazal, R. M., and M. E. Kubiske. 2004. Influence of Initial Root Length on Physiological Responses of Cherrybark Oak and Shumard Oak Seedlings to Field Drought Conditions. *Forest Ecology and Management* 189 (1–3): 295–305.
- Gemborys, S. R., and E. J. Hodgkins. 1971. Forests of Small Stream Bottoms in the Coastal Plain of Southwestern Alabama. *Ecology* 52 (1): 70–84.
- Gilliam, F. S., and W. J. Platt. 1999. Effects of Long-Term Fire Exclusion on Tree Species Composition and Stand Structure in an Old-Growth *Pinus palustris* (Longleaf Pine) Forest. *Plant Ecology* 140 (1): 15–26.
- Godman, R. M., and K. Lancaster. 1990. Eastern hemlock (*Tsuga canadensis*). In *Silvics of North America*, vol. 1, *Conifers*, edited by R. M. Burns and B. H. Honkala, 604–612. Washington, D.C.: U.S. Department of Agriculture, Forest Service.
- Harper, R. M. 1906. Notes on the Distribution of Some Alabama Plants. *Bulletin of the Torrey Botanical Club* 33 (10): 523–536.
- . 1909. Some Coastal Plain Plants in the Piedmont Region of Georgia. *Bulletin of the Torrey Botanical Club* 36 (10): 583–593.
- . 1910. A Botanical and Geological Trip on the Warrior and Tombigbee Rivers in the Coastal Plain of Alabama. *Bulletin of the Torrey Botanical Club* 37 (3): 107–126.
- . 1928. *Catalogue of the Trees, Shrubs and Vines of Alabama, with Their Economic Properties and Local Distribution*. Geological Survey of Alabama Monograph 9. Tuscaloosa: University of Alabama; Birmingham Print Co.
- Hart, J. L., and D. Shankman. 2005. Disjunct Eastern Hemlock (*Tsuga canadensis*) Stands at Its Southern Range Boundary. *Journal of the Torrey Botanical Society* 132 (4): 602–612.
- Hosner, J. E., and L. S. Minckler. 1963. Bottomland Hardwood Forests of Southern Illinois—Regeneration and Succession. *Ecology* 44 (1): 29–41.
- Kavanagh, K., and M. Kellman. 1986. Performance of *Tsuga canadensis* (L.) Carr. at the Centre and Northern Edge of Its Range: A Comparison. *Journal of Biogeography* 13 (2): 145–157.
- Keever, C. 1953. Present Composition of Some Stands of the Former Oak-Chestnut Forest in the Southern Blue Ridge Mountains. *Ecology* 34 (1): 44–54.
- Krinard, R. M. 1990. Cherrybark oak (*Q. falcata* var. *pagodifolia*). In *Silvics of North America*, vol. 1, *Conifers*, edited by R. M. Burns and B. H. Honkala, 644–649. Washington, D.C.: U.S. Department of Agriculture, Forest Service.
- Küchler, A. W. 1964. *Potential Natural Vegetation of the Conterminous United States*. Special Publication No. 36. New York: American Geographical Society.
- Little, E. L., Jr. 1971. *Atlas of United States Trees*. Vol. 1. Miscellaneous Publication 1146. Washington, D.C.: U.S. Department of Agriculture, Forest Service.
- Loehle, C. 1998. Height Growth Rate Tradeoffs Determine Northern and Southern Range Limits for Trees. *Journal of Biogeography* 25 (4): 735–742.
- McCarthy, S. E., and J. P. Evans. 2000. Population Dynamics of Overcup Oak (*Quercus lyrata*) in a Seasonally Flooded Karst Depression. *Journal of the Torrey Botanical Society* 127 (1): 9–18.
- McCormick, J. F., and R. B. Platt. 1980. Recovery of an Appalachian Forest following the Chestnut Blight, or Catherine Keever—You Were Right! *American Midland Naturalist* 104 (2): 264–273.
- Meier, C. E., J. A. Stanturf, and E. S. Gardiner. 2006. Litterfall in the Hardwood Forest of a Minor Alluvial-Floodplain. *Forest Ecology and Management* 234 (1–3): 60–77.
- Mikan, C. J., D. A. Orwig, and M. D. Abrams. 1994. Age Structure and Successional Dynamics of a Presettlement-Origin Chestnut Oak Forest in the Pennsylvania Piedmont. *Bulletin of the Torrey Botanical Club* 121 (1): 13–23.
- Mladenoff, D. J., and F. Stearns. 1993. Eastern Hemlock Regeneration and Deer Browsing in the Northern Great Lakes Region: A Re-Examination and Model Simulation. *Conservation Biology* 7 (4): 889–900.

- Mowbray, T. B., and H. J. Oosting. 1968. Vegetation Gradients in Relation to Environment and Phenology in a Southern Blue Ridge Gorge. *Ecological Monographs* 38 (4): 309–344.
- Muller, R. N. 1982. Vegetation Patterns in the Mixed Mesophytic Forest of Eastern Kentucky. *Ecology* 63 (6): 1901–1917.
- Murphy, H. T., J. VanDerWal, and J. Lovett-Doust. 2006. Distribution of Abundance across the Range in Eastern North American Trees. *Global Ecology and Biogeography* 15 (1): 63–71.
- Oosting, H. J., and D. W. Hess. 1956. Microclimate and a Relic Stand of *Tsuga canadensis* in the Lower Piedmont of North Carolina. *Ecology* 37 (1): 28–39.
- Paillet, F. L. 1984. Growth-Form and Ecology of American Chestnut Sprout Clones in Northeastern Massachusetts. *Bulletin of the Torrey Botanical Club* 111 (3): 316–328.
- Prasad, A. M., and L. R. Iverson. 2003. *Little's Range and FIA Importance Value Distribution Maps: Spatial Database for 135 Eastern US Tree Species*. RWU NE-4153. Delaware, Ohio: U.S. Department of Agriculture, Northeastern Research Station, Research Laboratory. [www.fs.fed.us/ne/delaware/4153/global/littlefia/index.html].
- Quarterman, E., B. H. Turner, and T. E. Hemmerly. 1972. Analysis of Virgin Mixed Mesophytic Forests in Savage Gulf, Tennessee. *Bulletin of the Torrey Botanical Club* 99 (5): 228–232.
- Racine, C. H. 1971. Reproduction of Three Species of Oak in Relation to Vegetational and Environmental Gradients in the Southern Blue Ridge. *Bulletin of the Torrey Botanical Club* 98 (6): 297–310.
- Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. *Manual of the Vascular Flora of the Carolinas*. Chapel Hill: University of North Carolina Press.
- Renner, G. T. 1927. The Physiographic Interpretation of the Fall Line. *Geographical Review* 17 (2): 278–286.
- Sagarin, R. D., and S. D. Gaines. 2002. The “Abundant Centre” Distribution: To What Extent Is It a Biogeographical Rule? *Ecology Letters* 5 (1): 137–147.
- Saucier, R. T. 1987. *Geomorphological Interpretations of Late Quaternary Terraces in Western Tennessee and Their Regional Tectonic Implications*. U.S. Geological Survey Professional Paper 1336-A. Washington, D.C.: U.S. Government Printing Office.
- Schenk, H. J. 1996. Modeling the Effects of Temperature on Growth and Persistence of Tree Species: A Critical Review of Tree Population Models. *Ecological Modeling* 92 (1): 1–32.
- Schneider, R. L., and R. R. Sharitz. 1988. Hydrochory and Regeneration in a Bald Cypress–Water Tupelo Swamp Forest. *Ecology* 69 (4): 1055–1063.
- Shankman, D. 1991. Forest Regeneration on Abandoned Meanders of a Coastal Plain River in Western Tennessee. *Castanea* 56 (3): 157–167.
- . 1996. Stream Channelization and Changing Vegetation Patterns in the U.S. Coastal Plain. *Geographical Review* 86 (2): 216–232.
- Shankman, D., and L. G. Drake. 1990. Channel Migration and Regeneration of Bald Cypress in Western Tennessee. *Physical Geography* 11 (4): 343–352.
- Shankman, D., and R. M. Kortright. 1994. Hydrogeomorphic Conditions Limiting the Distribution of Baldcypress in the Southeastern United States. *Physical Geography* 15 (3): 282–295.
- Shelford, V. E. 1954. Some Lower Mississippi Valley Flood Plain Biotic Communities: Their Age and Elevation. *Ecology* 35 (2): 126–142.
- Smith, G. C., M. W. Patterson, and H. R. Trendell. 2000. The Demise of the Longleaf Pine Ecosystem. *Southeastern Geographer* 40 (1): 75–92.
- Smith, R. D. 1996. Composition, Structure, and Distribution of Woody Vegetation on the Cache River Floodplain, Arkansas. *Wetlands* 16 (3): 264–278.
- Vines, R. A. 1960. *Trees, Shrubs, and Woody Vines of the Southwest*. Austin: University of Texas Press.
- Wall, D. P., and S. P. Darwin. 1999. Vegetation and Elevational Gradients within a Bottomland Hardwood Forest of Southeastern Louisiana. *American Midland Naturalist* 142 (1): 17–30.
- Whitehead, D. R. 1981. Late-Pleistocene Vegetational Changes in Northeastern North Carolina. *Ecological Monographs* 51 (4): 451–471.
- Woods, F. W., and R. E. Shanks. 1959. Natural Replacement of Chestnut by Other Species in the Great Smoky Mountains National Park. *Ecology* 40 (3): 349–361.
- Woodward, F. I. 1987. *Climate and Plant Distribution*. Cambridge, England: Cambridge University Press.