THE DIFFERENTIATION OF THE DECIDUOUS FOREST OF THE EASTERN UNITED STATES

E. LUCY BRAUN,
University of Cincinnati

Deciduous forest originally covered a large part of the eastern United States. A certain unity is given to the formation by the dominant life form and by some of the wide-ranging genera and species. However, it is not uniform throughout, but differs in different geographic sections in its composition and dominant trees. Why? Because conditions are or have been different in different parts of the area.

Forests develop. Any change in environment causes a change in vegetation. Such vegetational changes are usually gradual and may be local or widespread depending on the magnitude of the causal factor. The reactions of occupying vegetation produce changes, gradual development. Soils undergo modifications hand in hand with vegetational change, from the time of their origin from parent materials, to the ultimate development of mature soil of a regional type. The progress of erosion cycles is accompanied by vegetational change; youthful, mature, and old age stages of the erosion cycle are vegetationally different. The environmental features of the peneplain are different from those of a mountain range or strongly dissected plateau. Continental configuration changes; here coast lines rise and continental shelves emerge; there coasts are drowned and erstwhile parts of continents submerged. Such continental change must result in vegetational change—in migration and shifts in the ranges of species and hence in the composition of communities. Climates change, becoming more humid or less humid, warmer or colder. Every change in climate is accompanied by changes in vegetation and shifts in vegetational boundaries.

The record of vegetational change or development may be preserved in fragmentary communities preserving earlier successional stages, in isolated (relic) communities apparently not in complete accord with existing conditions, in disrupted ranges of species or groups of related species, and in fossils. All of these we must use if we are to trace the changes which have taken place in extent and composition of our deciduous forest.

Differentiation of the eastern deciduous forest is a result of forest development and change in response to these (above mentioned) changing local and regional enviroments, both present and past. The great area occupied by deciduous forest is not all of the same age, nor has it all had the same history.

The Appalachian upland has been continuously available for forest development since the origin of angiosperms, now the most important constituents of deciduous forest. Its central part, especially the western slope of the unglaciated Appalachian upland, is remarkable for the diversity of aspect of its forest, which results from the large number of species and innumerable variations in groupings of species. Here is

preserved a large remnant of ancient forest, of the forest of the Tertiary age. Many of its genera and some of its species are common to this area and to the deciduous forest of Asia, two areas between which there has been no connection since late Tertiary time. Can species persist this long? The paleontological record, although very inadequate for the East, nevertheless gives evidence that they can. There are recognized instances of specific identity of Miocene and existing plants. No adequate picture can be had of deciduous forest without emphasis of its central part, no reconstruction of the history resulting in its present differentiation is possible without a knowledge of this central part, this remnant of, or lineal descendant of, the Tertiary forest.

Mixed deciduous forest occurs throughout the unglaciated Appalachian upland, and to some extent beyond it. However, only in certain parts, especially the Cumberland Mountains and southern Allegheny Mountains, and adjacent Cumberland and Alleghany Plateaus,[1] does the mixed forest that we know as *mixed mesophytic forest* prevail. Vegetationally, this is a forest made up of some twenty or twenty-five species, a forest without definite dominants, or with several important species, rather than only one or two. Slight environmental differences in the optimum area of mixed mesophytic forest result in segregation of its species into more or less well marked communities. Certain of these communities belong to drier sites—ridge tops and steep southwesterly slopes. Others reflect altitudinal influences. But even where altitudinal range is slight and extremes of moisture absent, variations in forest composition occur, and distinct association-segregates may be recognized.

Going away from the center, or region of best development of the mixed mesophytic forest, we find a tendency toward greater uniformity of type; that is, there seem to be fewer segregates in the mixed mesopytic forest. Gradually, in all except a northerly direction, the mixed mesophytic forest becomes more and more limited to favorable sites, lower ravine slopes, coves, gorges. More and more of the area is occupied by some type of forest not readily referable to the mixed mesophytic association.

Let us consider a few forest areas situated on radii diverging from the center of mixed mesophytic forest. This will illustrate the change in composition so evident in all directions.

Southward, in the region of the higher southern Appalachians, the significance of the forester's term, "cove hardwoods," becomes apparent. "Cove hardwoods" and mixed mesophytic forest are one and the same, but here in the mountains of eastern Tennessee and western North Carolina, the mixed mesophytic forest is largely limited to coves. The Joyce Kilmer Forest in North Carolina contains a much higher percentage of chestnut than is found in the typical mixed mesophytic forest. In the Great Smoky Mountains, mixed mesophytic forest occupies the coves and deeper valleys, chestnut is (or rather was) important over a much larger part of the mountain slopes than in the Cumberland Mountains.

[1]Physiographic regions are used as defined by Fenneman, N. M., Physiography of eastern United States, McGraw-Hill Co., 1938.

Eastward, in the George Washington National Forest in Virginia, on one of the ranges of the Ridge and Valley Province, we find an apparently mesophytic forest tract which is quite evidently the oak-chestnut-tulip tree type distinguished on some vegetation maps. Farther east, on the Blue Ridge of Virginia, we find (in White Oak Canyon) a mixed forest which is about half oaks and chestnut. Both of these forest tracts are in situations in which any one familiar with the mixed mesophytic forest would expect to find that association. Yet both of these, though mixed forests, might be considered as belonging to the oak-chestnut association. In the narrow gorge of Ceder Creek near Natural Bridge, Va., is forest which is definitely of the mixed mesophytic type. Farther east, on the Piedmont, the prominence of oaks is well known.

Southwestward, toward the southern end of the Cumberland Plateau, the slope forest has a lower percentage of the typical trees of the mixed mesophytic, especially basswood and buckeye, and a higher percentage of oaks, although the forest still retains the aspect of the mixed mesophytic forest, and typical stands of that forest occupy the most mesophytic slopes.

Westward, too, we find this limitation of mixed mesophytic to the most favorable sites. For instance, in the gorge of Clifty Creek in Todd County in western Kentucky, there is good mixed mesophytic forest with a high percentage of beech. Forests of ravine slopes in the Mammoth Cave region contain many of the trees of the mixed mesophytic forest, yet there is a pronounced increase in oaks and hickories. In the Ozark region of Missouri and Arkansas, there is no question but that oak-hickory forest is the prevailing association. Nevertheless there are small areas of forest in this region—in canyons and deep valleys—which closely resemble the mixed mesophytic forest to the east.

What is the situation northward? Mixed mesophytic forest extends through the mountains of West Virginia and into Pennsylvania, gradually changing because of the increased importance of maple and beech, and because of an admixture of more northern species, to the northern beech-maple forest or to the hemlock-white pine-northern hardwoods type, or northeastward, to the "mixed transition forest" distinguished by foresters.

Where the boundary of Wisconsin glaciation is reached, whether it be in western New York State or in Ohio, anywhere west of the longitudinal ranges of the Alleghanies, there is an abrupt change in forest composition. Beech and sugar maple at once assume greater importance than in the mixed mesophytic association. The area of the beech-maple climax has been reached. Farther west, in Indiana, there appears to be a division of dominance between beech-maple and oak-hickory, beech-maple generally occupying the more mesophytic sites.

Let us try to reconstruct the events which lead to the present forest pattern. Fossil records show that a broad-leaf forest, with many existing genera, and hence a mixed forest, extended across the now prairie and plains states in late Cretaceous and early Tertiary time. These early forests contained also representatives of many genera not now found in the forests of north temperate regions today, for the climate for at least part of that time was probably milder than now.

Zonal shifts in vegetation, readjustments of species distribution, doubtless accompanied the cooling of the late Tertiary. The Rocky Mountains began to rise (in post-Cretaceous time), and the land to the east of them was deprived of rain-bearing westerly winds. The drying continental interior was no longer suitable to deciduous forest and its boundary receded eastward contemporaneously with the development of the great interior grassland. Increasing aridity in the interior meant the withdrawal of the most mesophytic tree species, while those of lesser moisture requirements found the somewhat diversified topographic conditions of the Ozark Upland favorable. This then became the stronghold for what is now known as the oak-hickory forest. (Other east-west shifts in forest and forest species have of course taken place, at least some of which are Pleistocene or later.)

The mixed forest for the most part retreated to the east of the Mississippi River, although, as has been mentioned, remnants of that forest are seen in isolated situations in the Ozarks, and curiously enough, on Crowley's Ridge, a low ridge of Tertiary age rising above the wide alluvial flood-plain of the Mississippi River.

Cycles of erosion, resulting in peneplains more or less extensive, were affecting the eastern forest area, for slopes change and soils change with the progress of the erosion cycle. Unreduced areas, on an otherwise peneplained surface, afford habitats not general on the peneplain. Hence these sloping areas could have been, and probably were, the most favorable sites for mixed forests similar to those which now occupy slopes. Uplift brings about renewed erosion and renewed soil development. Much of the land surface will again be sloping. Remnants of old peneplains will remain, and parts of newer ones be forming.

The physiographic features of the East are in large measure due to the work of two erosion cycles, resulting respectively in the Schooley and Harrisburg peneplains. Today, over the great area where the upland levels represent the reduced Schooley peneplain, and where no later peneplain was extensively developed, the mixed mesophytic forest prevails.[2] This is an area, for the most part, of mature topography.

The development of a later peneplain—the Harrisburg and its more or less contemporaneous representatives in the interior—again curtailed the area occupied by mixed forests of slopes. Subsequent erosion has considerably dissected the interior representatives of this peneplain, but has little affected the broad valleys of the Ridge and Valley Province.

Cycles in soil development must have more or less paralleled these cycles of erosion. Young soils, showing the characteristics of their parent materials, will cover newly eroding slopes. As time goes on, the soils will become mature, will reach "a stage of development marked by the practical absence of geological features."[3] Such soils, and only such,

---

[2]Some may wish to include additional peneplains, and assign to the Allegheny or even to the Harrisburg peneplain, the upland levels of the Appalachian Plateau in eastern Ohio. Whatever peneplain interpretation may be followed, the correlation between the area of mixed mesophytic forest and the oldest peneplain of the Plateau remains.

[3]See Wolfanger, Louis A., The major soil divisions of the United States. John Wiley & Sons. 1930.

can support the regional climax vegetation. Soils may become old, and lose some of the essential characteristics of normal soils of their climatic region. Such old soils generally "occupy old flat surfaces of earlier topographic cycles where they have been undisturbed for long periods of time."[4] As most of the former Schooley peneplain has been reduced to slopes, few if any such old soils occur; most of the soils are mature. Many parts of the Harrisburg peneplain, however, are still flat. The forest of these areas in places seems out of accord with the regional type. White oak is the dominant tree.

Glaciation was a major event affecting the forests of eastern United States. Only 30,000 years, more or less, have been available for the revegetation of the glacially denuded land; only a fractional part of this time has been available for deciduous forest development. This is in contrast to the millions of years of undisturbed occupancy of the unglaciated land to the south, occupancy of course affected by cycles of erosion and of soil development. After long developmental stages, climax forests have in places become established in the glaciated territory, although in much of the area development is still in progress, species ranges are shifting. Due to the limitations of climate, of soils, of migration capacities, all of the species involved have not moved equal amounts or at equal rates. The post-Wisconsin xerothermic period favored an eastward movement of the constituents of the oak-hickory forest migrating northward from the Ozark upland. It thus became established in the western part of the now forested glaciated territory. The maximum movement of the more mesophytic species was to the east of the prairie lobe. Thus arose the beech-maple forest, so well represented in parts of Michigan, Indiana, Ohio, and western New York.

Ecologists generally recognize four major subdivisions or climax associations of the deciduous forest: mixed mesophytic, oak-hickory, oak-chestnut, and beech-maple. The areal distribution of each of these is related to climatic and physiographic features, past and present, and the inter-related process of soil development.

The mixed mesophytic association occupies a central position in the deciduous forest. This is a region of moderate to high rainfall, of cold, though not extreme winters. The area of its best development, the Cumberland Mountains and Cumberland Plateau and southern Allegheny Mountains, is an area of mature topography, for the most part the area of the reduced and dissected Schooley peneplain. Within this area the complex mixed forest displays many segregates demonstrating the sensitiveness of its constituents to minor variations in environment—microclimates and soils, both of which are affected by physiographic history. The extent of mixed forest (of which our mixed mesophytic association is a lineal descendant) has been curtailed in the past by climatic changes—increasing aridity in the west, and later, glaciation in the north. Its limits have been modified by the progress of erosion cycles, by the progress of soil development and the establishment of zonal soil types. None of these influences has brought about sharp

[4]Wolfanger, loc cit., p. 13.

areal limits of the mixed mesophytic association. Yet certain correlations may be pointed out. The Allegheny Front, and southward, the Cumberland Front, form the eastern boundary of the area where mixed mesophytic forest prevails. East of this, except in the southern Blue Ridge, the land was profoundly affected by the Harrisburg cycle of erosion. The boundary of the Wisconsin ice sheet forms the northern boundary of mixed mesophytic forest, except that, in the higher longitudinal ranges of the Allegheny Mountains, transitional forest occurs. Roughly, the southern limit of the gray-brownerth, or the northern limit of the red-and-yellowerths, forms the southern boundary of the mixed mesophytic association. This soil boundary reflects a climatic boundary, for the red-and-yellowerths are the result of the open winters of the climate in which they have developed. The red-and-yellowerths are poorer soils than the gray-brownerths and do not support the mixed mesophytic forest. On those poorer soils, oak-hickory forest, or in places oak-chestnut forest prevails. Along the western edge of mixed mesophytic forest is a broad transition belt. There is no zonal soil line, no line related to a past erosion cycle. The climatic limit, in the absence of other factors affecting or affected by climate, is indefinite. Within the area of the mixed mesophytic association, both oak-hickory and oak-chestnut forest occur. That neither is climax in this area is at once evident from the fact that both occupy either immature soil areas, ridge tops or dry slopes on which the soil does not have the normal soil profile, or old soils of a former topographic cycle. Which type is present on a ridge or slope depends upon the nature of the underlying rock—certain evidence that neither is climax in the area of the mixed mesophytic association. In the climatic areas in which these prevail, this relation to underlying rock does not exist. The mull type of humus layer prevails in mixed mesophytic forest.

The oak-hickory association is to the west, northwest, and to some extent to the south of the mixed mesophytic association. The higher rainfall of its southeastward extension is compensated by the poorer zonal soil.

The oak-chestnut forest is, for the most part, to the east and southeast of the mixed mesophytic, although areas of typical oak-chestnut or oak-chestnut-tulip tree forest occur farther west. Throughout the extent of the oak-chestnut association (except perhaps far to the northeast) areas of mixed mesophytic forest are of frequent occurrence on mature soils of valleys dissecting the Harrisburg peneplain, and in coves on the long slopes between the Schooley and Harrisburg levels. This suggests, of course, that the boundary is not climatic, and that the oak-chestnut might be replaced by an extending mixed mesophytic forest. Such extensions have reached the outer edge of the coastal plain.

The beech-maple forest is the northern mesophytic expression of deciduous forest. The transition toward beech-maple demonstrated above 3000 feet in the Allegheny Mountains, shows the climatic relation between mixed mesophytic and beech-maple. The sharp southern boundary farther west, at the boundary of Wisconsin glaciation, is in part historic. This boundary may shift by invasion of additional mesophytic species. Northward, beech-maple gives way to the hem-

lock-white pine-northern hardwoods or lake forest. Westward, the boundary of beech-maple and oak-hickory is approximately the boundary of the prairie peninsula. Past and present climates have affected this boundary.

To summarize: All of the associations of the deciduous forest are genetically related. Within the area of the mixed mesophytic forest, association-segregates suggest the mode of origin of a variety of types from the mixed forest, and demonstrate the relationship of oak-hickory, oak-chestnut, and beech-maple forest to the mixed mesophytic forest. The differentiation which we see today is the result not alone of existing conditions, but also of past history, climatic and physiographic. The more or less gradual change in forest composition, from the area of mixed mesophytic forest outward in all directions, reflects the influence of past and present differences of environment. Transitions between associations are generally gradual, hence boundaries are indistinct. Yet these boundaries may in part be correlated with soil development and the establishment of zonal soil groups; with cycles of erosion; with changes in climate, increasing aridity in the interior and later, glaciation.