FOREST COMMUNITIES OF MONTGOMERY AND STEWART COUNTIES, NORTHWESTERN MIDDLE TENNESSEE

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ABSTRACT—A 1971-1972 study of forest communities in Montgomery and Stewart counties, northwestern Middle Tennessee, provided taxonomic and distributional data on taxa of the dominant families Fagaceae and Juglandaceae (previously published) and quantitative analyses and descriptions of seven community types delimited by topographic position and, thus, aligned across a moisture gradient (presented here). The random-pairs technique was used to sample 200 trees from four relatively mature stands (all forests in the study area are secondary) in each community type (64 species; 1,400 stems sampled). For each community, an importance value was determined for each species, based on the summation of relative density, relative frequency, and relative basal area, and each community was designated according to the three dominating taxa: red cedar-white ash-chinquapin oak forests of xeric limestone bluffs; chestnut oak-white oak-post oak forests of ridges; white oak-black oak-post oak forests of slopes with southerly aspects; American beech-tulip poplar-white oak forests of slopes with northerly aspects; red elm-tulip poplar-American beech forests of ravines; box elder-silver maple-sycamore forests of streambanks; and black gum-sweet gum-red maple forests of upland flats and depressions of the Pennyroyal Plain. Ranked by importance values, major genera are *Quercus, Acer, Carya,* and *Ulmus*, while major species are *Quercus alba, Nyssa sylvatica, Ulmus rubra, Quercus velutina, Juniperus virginiana, Fagus grandifolia, Acer saccharum, Acer negundo,* and *Liquidambar styraciflua*. Results confirm the generally-considered transitional nature (mixed-mesophytic to oak-hickory) of the forest vegetation, although oak or oak-mixed hardwoods dominate most sites.

In 1971, we initiated a study of forest communities in Montgomery and Stewart counties, Tennessee, with two major objectives in mind. We sought, first, to clarify the presence, distribution, and taxonomy of members of the dominating families, Fagaceae (American beech, American chestnut, and oaks) and Juglandaceae (hickories and walnuts), and, second, to quantitatively describe the major forest communities. Fieldwork was conducted in 1971-1972, and the data compiled into theses (Jensen, 1972; Schibig, 1972). The taxonomy and description-distribution data from the theses have been published (Chester et al., 1987; Schibig et al., 1990); the quantitative data and forest community descriptions have not been published.

A recent review of area forest communities (Bryant et al., 1993) illustrates an important fact: theses, such as ours, are often unknown or unavailable and are regularly overlooked as data sources. Also, studies are underway on Tennessee forest communities (e.g., DeSelm, 1995) that could make use of our unpublished data, which are especially meaningful because most of the sampling sites now have been timbered or otherwise disturbed. Thus, the purpose of this paper is to present our quantitative characterization of the forest communities of Montgomery and Stewart counties, as these communities existed in 1971-1972. Nomenclature has been updated and additional qualitative observations over the past 25 years also are included.

STUDY AREA

Physical Setting—Montgomery and Stewart counties are adjacent to the Kentucky border in extreme northwestern Middle Tennessee (Fig. 1). These counties are within the Interior Low Plateau(s) Physiographic Province, Highland Rim Section, of Fenneman (1938). Two subsections, as mapped by Quarterman and Powell (1978), are included (Fig. 1).

The Western Highland Rim Subsection, encompassing most of the area, is a strongly dissected plateau bounded on the east by the Central (Nashville) Basin and tilted slightly westward to the Coastal Plain Province at or just west of the Tennessee River. The Southern Highland Rim Subsection is several counties southward and the Pennyroyal Plain Subsection is part of the study area to the north. The Western Highland Rim Subsection has developed primarily on St. Louis and Warsaw limestones of Mississippian age; cherty Cretaceous gravel caps some ridges, and Fort Payne Chert outcrops from and underlies many lower slopes. Drainage is by the Cumberland, Red, and Tennessee rivers and their tributaries, where alluvial deposits occur in bottomlands. Elevations are from 107 to 213 m (350 to 700 feet) above sea level (data from United States Geological Survey Topographic Quadrangle Maps). Topographic features include numerous springs, small streams, ravines, slopes of various degrees and aspects, narrow ridges, and perpendicular, often xeric bluffs.

The Pennyroyal Plain Subsection is in parts of northern Montgomery and northwestern Stewart counties (Fig. 1). This karstic landscape includes sinkhole plains, sinking streams, and extensive areas of level to slightly rolling lands with shallow basins of a few to several hectares. The Plain is underlain by Ste. Genevieve and St. Louis limestones and mostly is coincident with the historic "Big Barrens Region" of Kentucky (primarily) and Tennessee (Baskin et al., 1994).

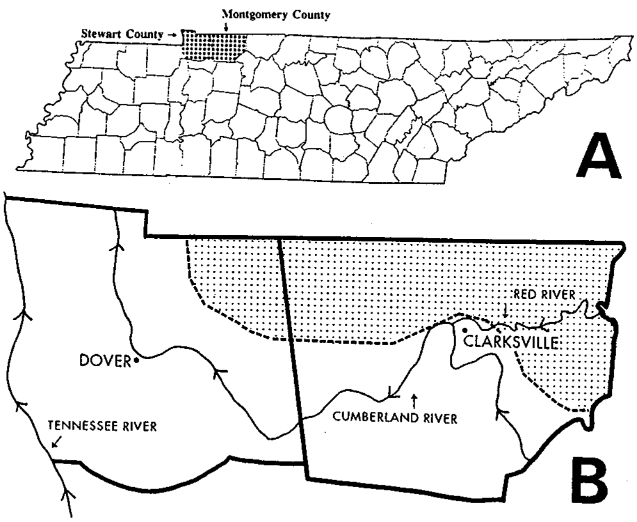

FIG. 1. A. Location of Montgomery and Stewart counties in Tennessee; B. Approximate boundary of the Pennyroyal Plain (shaded) and Western Highland Rim subsections (redrawn from Quarterman and Powell, 1977).

Soils of both the Western Highland Rim and Pennyroyal Plain subsections are heterogeneous and represent several associations and series (Quarterman and Powell 1978; Springer and Elder, 1980). Most are Red-Yellow Podsols derived from loess, cherty and noncherty limestones, and Coastal Plain sediments. A loess mantle often >1 m in thickness covers parts of the area. Limestone outcrops are common in the Western Highland Rim Subsection but infrequent on the Pennyroyal Plain Subsection except along streams. Fragipans often develop on soils of the Plain, but drainage is good and sometimes excessive in dissected areas where erosion has and continues to occur.

The climate of Montgomery and Stewart counties is warm-temperate with long warm summers and mild winters. This climatic type is referred to as humid-mesothermal by Thornthwaite (1948). Rainfall averages 120-125 cm (48-50 inches) a year and is well distributed, although drought years are common and heavy rains resulting in river overflow are frequent, especially in late winter to early spring. The growing season of ca. 190 days extends from mid-April to mid or late October. Soils often freeze to depths of several centimeters each winter but rarely remain frozen for more than a few days, and an average winter normally has several small (a few centimeters) snowfalls (Lampley et al., 1975). Severe ice storms occasionally damage forests.

Vegetational Setting—The counties are part of the Eastern Deciduous Forest Formation, described in the classic treatise of Braun (1950); southern portions were treated more recently by Martin et al. (1993*a*, 1993*b*). The area is part of the Western Mesophytic Forest Region of Braun (1950) or the Oak-Hickory Forest (Western Mesophytic/Oak-Hickory Forest) of Bryant et al. (1993). As described by Braun (1950), the vegetation of this Region is transitional and includes elements from the more xeric Oak-Hickory Region to the west and the more mesic Mixed Mesophytic Region to the east. Thus, there is no single climax, and the mosaic of forest types is determined by local microclimatic, edaphic, and topographic conditions.

Most forests of the Western Highland Rim and Pennyroyal Plain subsections are or were dominated by oak and oak-hickory phases (Küchler, 1964; Eyre, 1980), including a few examples of the western form of Mixed Mesophytic Forest (Carpenter and Chester, 1987, 1988); conifers dominate only in a few stands (Schibig and Chester, 1988). The Pennyroyal Plain once included extensive grass-dominated and essentially treeless areas referred to as barrens as well as unique upland wet forest-swamp complexes, but now these mostly are under tilth (Baskin et al., 1994). In addition, the Tennessee and Cumberland River systems have provided and continue to provide pathways for plant immigration. For example, the Cumberland River provides floristic input from limestone areas to the east and the extensive Tennessee system brings Appalachian elements from East Tennessee and Coastal Plain elements from the south and from West Tennessee. Thus, the vegetation is a mixture of communities and floristic elements and includes contributions from other subsections, sections, and even provinces intermixed and sorted by complex local conditions. It should be emphasized that all area forests are secondary and most of the existing remnants have been disturbed by fire, lumbering, and pasturing.

The only quantitative study of area forest communities previous to this investigation was that of Duncan and Ellis (1969), who defined the communities of Montgomery Co. based on samples taken from predetermined grid points. All data were averaged, and quantitative values presented for the entire county; community descriptions were based mainly on qualitative observations. Quantitative studies since this investigation include an analysis of a mixed hardwoods-shortleaf pine stand (Schibig and Chester, 1988) and a bottomland-hardwood remnant (Chester and Schibig, 1993). In addition, Fralish and Crooks (1989) studied forest communities and their relationships to soils at Land Between The Lakes of northwestern Stewart Co.

METHODS

Preliminary observations indicated to us that the major forest communities could be delimited by their occurrence on the various topographic forms in the area and that these topographic forms were aligned along a moisture gradient. The topographic forms and our subjectively-determined moisture gradient from xeric to mesic were xeric limestone bluffs, ridges, slopes with southerly aspects, slopes with northerly aspects, ravines, upland flats and depressions of the Pennyroyal Plain, and streambanks.

The forest vegetation of each of these seven topographic forms (communities) was sampled. For each community, four stands were selected based on three criteria, i.e., size (each stand comprised $\leq$2 ha), disturbance (no evidence of recent pasturing or timbering), and topography (representative of the topographic situation).

The random-pairs, plotless sampling technique described by Phillips (1959) was used, primarily for convenience and ease of collecting large quantities of data. This and other distance sampling methods (i.e., variable-plot or plotless methods) have been widely used, especially in forest studies, and give reasonably accurate estimations of frequency, density, and dominance (Barbour et al., 1987; Bonham, 1989). Samples were taken at 8-m intervals on one or more transects through representative sections of each stand. A total of 100 pairs (200 trees) was sampled in each community, giving a total of 1,400 trees sampled. Only trees with a diameter breast height of $\geq$10.2 cm were included in the sampling; diameter breast heights were taken to the nearest 0.25 cm. Between-tree distances were taken for all pairs except stands on bluffs.

The data were used to calculate, for each species by community type, relative (percent) density (= number of individuals of a species/number of individuals of all species x 100), relative (percent) frequency (= number of points of occurrence for a species/number of points of occurrence for all species x 100), and relative (percent) basal area (= basal area of a species in square meters/total basal area of all species x 100). An importance value was obtained by summing the relative values (maximum 300). This importance value allowed for a numerical comparison of the species within and between community types. Communities were named on the basis of the three species with highest importance values. Density (number of trees per hectare) for each community except bluffs was determined by the equation derived by Bonham (1989): trees/ha = 10,000/[(0.87)(average between-tree distance)]^2.

Qualitative observations were made of the shrub and small tree, woody vine, and herbaceous strata, and these observations were used in descriptions of communities. Nomenclature has been updated to correspond to that of Wofford and Kral (1993).

RESULTS AND DISCUSSION

Forest Communities—Jensen (1979) used density data from the original surveys in an indirect gradient analysis to reassess our subjective assumption that the communities could be differentiated based on a moisture gradient resulting from topography. His results showed that our assumption was basically correct, with two exceptions: 1) upland flats and depressions of the Pennyroyal Plain Subsection should appear immediately before ravines (instead of immediately after) in the sequence; 2) xeric limestone bluffs should appear near the middle of the gradient instead of at the most xeric position. Pending results from additional and expanded gradient analyses and community ordination studies based on our original data, we follow the originally-devised moisture-gradient sequence except that the community of the Pennyroyal Plain Subsection is separated from the six community types of the Western Highland Rim Subsection.

Red Cedar-White Ash-Chinquapin Oak Forests of Xeric Limestone Bluffs—The most xeric bluffs are adjacent to the major rivers (Cumberland and Tennessee) or border river bottomlands. They are characterized by thin and dry alkaline soils, severe (mostly westwardly-southerly) exposure, and steepness (many almost perpendicular). Areas with enough soil to support vegetation are inhabited by numerous apparent calciphiles. Nineteen species were sampled (Table 1) with an average diameter breast height of 17.6 cm. Community density data are not available since between-tree distances were not taken. Greater than 87% of importance values (given in order of highest to lowest in Table 1 and in the discussion of other community types) is made up of *Juniperus virginiana*, *Fraxinus americana* (including *Fraxinus quadrangulata* as a minor but definite component), *Quercus muehlenbergii*, *Ulmus alata*, *Quercus rubra*, *Maclura pomifera*, *Carya ovata*, and *Acer saccharum*.

Common shrubs and small trees are *Bumelia lycioides, Cercis canadensis*, *Hypericum frondosum*, *Hypericum prolificum*, *Physocarpus opulifolius*, *Symphoricarpos orbiculatus*, *Vaccinium arboreum*, and *Viburnum rufidulum*. *Bignonia capreolata*, *Parthenocissus quinquefolia*, *Toxicodendron radicans*, and *Vitis* spp. are woody vines on bluffs and in all other area forests. As might be expected, the herbaceous flora is usually scant but includes *Aster* (several species), *Aureolaria flava*, *Hepatica acutiloba*, *Heuchera villosa*, *Manfreda virginica*, *Opuntia humifusa*, *Saxifraga virginiensis*, *Sedum ternatum*, *Silene virginica*, *Sporobolus asper*, and several species of *Solidago*. Rarities include *Lesquerella globosa* on some Cumberland River bluffs and *Dioclea multiflora* on many Tennessee River bluffs.

A few bluffs along the Tennessee River (the western boundary of the study area) are west-facing and even more xeric and barren than those along the Cumberland. Samples were not taken from them due to steepness, but observations indicate the presence of *Pinus virginiana* in a few cases and an apparent increase in numbers for such xerophytic oaks as *Quercus prinus*.

Chestnut Oak-White Oak-Post Oak Forests of Ridges—Dry ridges, many capped with extensive chert deposits, become prevalent in southwestern Montgomery Co. and occur throughout the Western Highland Rim Subsection of Stewart Co. A few "chert pits" resulting from surface mining of this upland gravel, mostly for roadway construction, show the porous profile with only a thin soil layer.

The vegetation of these oak forests includes a relatively small number of mostly xeric species (Table 2; 15 species sampled, average diameter breast height = 20.6 cm, density = 421 trees/ha). More than 94% of importance values (Table 2) is made up of *Quercus prinus*, *Quercus alba*, *Quercus stellata*, *Carya glabra*, *Quercus marilandica*, *Quercus coccinea*, *Quercus velutina*, *Oxydendrum arboreum*, *Carya tomentosa*, and *Nyssa sylvatica*. Specimens which appear to be *Quercus* x *fontana* (*Q. coccinea* x *Q. velutina*) as described by Laughlin (1967) are sometimes seen. *Carya pallida* was not sampled but is found on some ridges in Stewart Co., as is *Pinus echinata* (Schibig and Chester, 1988).

Constant shrubs and small trees include *Ascyrum stragalum*, *Vaccinium arboreum* (and often *Vaccinium stamineum* and *Vaccinium vacillans*, especially in western Stewart Co.), and *Ceanothus americanus*. The spring herbaceous flora is limited, but *Cynoglossum virginianum*, *Dentaria laciniata*, and *Podophyllum peltatum* are usually present. Conspicuous in summer and fall are various species of *Aster*, *Desmodium*, *Galium*, *Lespedeza*, *Liatris*, and *Solidago* as well as *Cunila origanoides* and *Gillenia stipulata*.

White Oak-Black Oak-Post Oak Forests of Slopes with Southerly Aspects—Aspects of these slopes range from south to west, and most are relatively xeric, especially toward the crests. Degree of slope frequently exceeds 45%, and limestone outcrops are not uncommon. These oak forests are the major forest type seen in the area, but a number of other genera are usually represented and dominants may vary in any given stand (Table 3; 25 species sampled, average diameter breast height = 23.4 cm, density = 488 trees/ha). Making up nearly 90% of importance values are *Quercus alba*, *Q. velutina*, *Q. stellata*, *Acer saccharum*, *Carya tomentosa*, *Carya ovalis*, *C. glabra*, *Quercus falcata*, *Nyssa*

TABLE 1. Statistical data for red cedar-white ash-chinquapin oak forest of xeric limestone bluffs.

Species	No. of stems	No. of Points	Basal area (m^2)	Importance value
Juniperus virginiana	90	60	2.517	125.70
Fraxinus americana[1]	26	22	0.645	37.82
Quercus muehlenbergii	18	16	0.591	29.14
Ulmus alata	16	15	0.663	28.76
Quercus rubra	6	6	0.394	13.51
Maclura pomifera	6	5	0.175	9.13
Carya ovata	5	5	0.200	90.6
Acer saccharum	6	6	0.129	8.96
Prunus serotina	6	5	0.101	7.86
Ostrya virginiana	6	6	0.062	7.81
Cornus florida	4	4	0.048	5.32
Ulmus rubra[2]	3	3	0.039	4.05
Quercus shumardii	1	1	0.120	3.19
Liquidambar styraciflua	2	1	0.023	2.02
Quercus alba	1	1	0.035	1.73
Celtis occidentalis	1	1	0.033	1.70
Gleditsia triacanthos	1	1	0.029	1.63
Quercus falcata	1	1	0.013	1.35
Cercis canadensis	1	1	0.009	1.28
Total	200	160	5.826	300.00

[1]Including *Fraxinus quadrangulata*.
[2]Including *Ulmus serotina*.

TABLE 2. Statistical data for chestnut oak-white oak-post oak forest of ridges.

Species	No. of stems	No. of points	Basal area (m^2)	Importance value
Quercus prinus	44	35	2.750	77.34
Quercus alba	32	28	1.390	50.07
Quercus stellata	29	23	0.970	40.33
Carya glabra	24	20	0.396	28.82
Quercus marilandica	15	12	0.476	20.59
Quercus coccinea	12	10	0.585	19.29
Quercus velutina	6	6	0.529	13.21
Oxydendrum arboreum	11	10	0.132	13.08
Carya tomentosa	8	7	0.164	10.21
Nyssa sylvatica	8	7	0.152	10.05
Quercus x *fontana*	5	5	0.198	7.95
Acer saccharum	3	3	0.069	4.15
Carya ovata	1	1	0.067	1.93
Quercus rubra	1	1	0.053	1.76
Cornus florida	1	1	0.010	1.22
Total	200	169	7.941	300.00

TABLE 3. Statistical data for white oak-black oak-post oak forest of slopes with southerly aspects.

Species	No. of stems	No. of points	Basal area (m^2)	Importance value
Quercus alba	43	35	4.315	81.31
Quercus velutina	38	33	2.316	59.37
Quercus stellata	21	18	1.014	30.25
Acer saccharum	20	17	0.699	26.27
Carya tomentosa	16	13	0.499	20.12
Carya ovalis	11	9	0.220	12.74
Carya glabra	9	7	0.266	11.00
Quercus falcata	6	6	0.439	10.50
Nyssa sylvatica	8	7	0.111	9.09
Carya ovata	6	6	0.118	7.57
Quercus muehlenbergii	4	3	0.126	4.89
Quercus rubra	2	2	0.176	3.77
Ostrya virginiana	2	2	0.034	2.47
Sassafras albidum	2	2	0.032	2.45
Cornus florida	2	2	0.024	2.38
Fraxinus americana	1	1	0.111	2.10
Ulmus americana	1	1	0.108	2.07
Fagus grandifolia	1	1	0.101	1.96
Quercus x *fontana*	1	1	0.057	1.60
Quercus coccinea	1	1	0.056	1.59
Quercus shumardii	1	1	0.049	1.53
Carya laciniosa	1	1	0.021	1.27
Quercus marilandica	1	1	0.021	1.27
Juglans nigra	1	1	0.018	1.25
Oxydendrum arboreum	1	1	0.011	1.18
Total	200	172	10.935	300.00

sylvatica, and *C. ovata*. Upper slopes are similar to and intergrade with ridge vegetation while lower slopes often include more mesophytic species.

Common woody understory species are *Cercis canadensis*, *Cornus florida*, *Ostrya virginiana*, *Vaccinium arboreum*, and *Viburnum rufidulum*. *Kalmia latifolia* sometimes is found on upper slopes of the Tennessee River drainage in western Stewart Co. The herbaceous flora is often diverse on lower slopes and similar to that of more mesic sites. In general, species more typical of dry habitats are prevalent, including various taxa of *Aster*, *Desmodium*, *Eupatorium*, *Geum*, and *Solidago*.

American Beech-Tulip Poplar-White Oak Forests of Slopes with Northerly Aspects—These slopes usually are quite mesic and are dominated by *Fagus grandifolia*, *Liriodendron tulipifera*, *Quercus alba*, *Q. velutina*, *Acer saccharum*, *Nyssa sylvatica*, *Carya ovalis*, and *Q. rubra*, although a number of other taxa regularly occur (Table 4; 32 species sampled, average diameter breast height = 26.5 cm, density = 323 trees/ha). The predominance of American beech is probably an artifact of historical selective cutting where oaks were removed and beech avoided.

The common shrubs and small trees on these mesic slopes include *Carpinus caroliniana*, *Cercis canadensis*, *Cornus florida*, *Euonymus americanus*, *Euonymus atropurpureus*, *Lindera benzoin*, *Ostrya virginiana*, and *Staphylea trifolia*. *Hydrangea arborescens* often occurs in abundance on limestone outcrops. A luxuriant herbaceous flora is found on these mesic slopes, including some or all of the following species: *Arisaema triphyllum*; *Asarum canadense*; *Claytonia virginica*; *Dentaria laciniata*; *Dodecatheon meadia*; *Epifagus virginiana*; *Erigenia bulbosa*; *Erythronium americanum*; *Geranium maculatum*; *Iris cristata*; *Phlox divaricata*; *Polemonium reptans*; *Polygonatum biflorum*; *Podophyllum peltatum*; *Saxifraga virginiensis*; *Sedum ternatum*; *Sanguinaria canadensis*; *Smilacina racemosa*; *Stellaria pubera*; *Trillium cuneatum*; *Trillium flexipes*; several species of *Viola*.

Red Elm-Tulip Poplar-American Beech Forests of Ravines—Most ravines are narrow, some only a few meters wide, and often are drained by gullies several meters deep. The vegetation is strongly influenced by that of the surrounding slopes but includes species presumably with greater moisture requirements as well (Table 5; 36 species sampled, average diameter breast height = 26.2 cm, density = 303 trees/ha). *Ulmus rubra* is always a significant constituent in the canopy and understory, but co-dominants vary and include *Liriodendron tulipifera*, *Fagus grandifolia*, *Platanus occidentalis*, *Juglans nigra*, *Quercus alba*, *Acer negundo*, *A. saccharum*, *Carya cordiformis*, and *Celtis laevigata*.

The shrub and small-tree layer also is diverse and includes *Asimina triloba* (often dense stands), *Carpinus caroliniana*, *Hydrangea arborescens*, *Lindera benzoin*, and *Staphylea trifolia*. The herbaceous flora is quite like that of mesic slopes but also regularly includes *Boehmeria cylindrica*, *Corydalis flavula*, species of *Eupatorium* and *Hydrophyllum*, *Iodanthus pinnatifidus*, *Laportea canadensis*, *Parietaria pensylvanica*, *Pilea pumila*, *Ruellia strepens*, and *Senecio glabellus*.

Box Elder-Silver Maple-Sycamore Forests of Streambanks—Most of the formerly extensive bottomlands of the mainstream Cumberland and Tennessee rivers and their tributaries were either inundated by Kentucky Lake on the Tennessee River (dam closed in 1944) or Lake Barkley on the Cumberland River (dam closed in 1966) or in tilth. One bottomland-hardwood remnant in the Cross Creeks National Wildlife Refuge in Stewart Co. has been studied (Chester and Schibig, 1993). Existing streambank remnants are dominated by expected mesic-hydric species (Table 6; 24 species sampled, average diameter breast height = 22.9 cm, density = 470 trees/ha), such as *Acer negundo*, *A. saccharinum*, *Platanus occidentalis*, *Ulmus rubra*, *Populus deltoides*, *Celtis*

TABLE 4. Statistical data for American beech-tulip poplar-white oak forest of slopes with northerly aspects.

Species	No. of stems	No. of points	Basal area (m^2)	Importance value
Fagus grandifolia	29	23	4.029	56.04
Liriodendron tulipifera	19	18	1.129	27.60
Quercus alba	17	15	1.113	24.80
Quercus velutina	12	11	1.548	23.17
Acer saccharum	16	14	0.890	22.16
Nyssa sylvatica	13	13	0.780	19.31
Carya ovalis	16	12	0.363	17.28
Quercus rubra	8	8	0.517	12.15
Sassafras albidum	7	6	0.436	9.95
Quercus pagoda	6	5	0.489	9.27
Prunus serotina	8	7	0.107	8.67
Cornus florida	6	6	0.138	7.33
Carya cordiformis	4	4	0.422	7.23
Carya glabra	4	4	0.399	7.07
Carya tomentosa	4	4	0.343	6.67
Ostrya virginiana	6	5	0.091	6.44
Ulmus rubra	5	4	0.184	6.04
Fraxinus pennsylvanica	2	2	0.247	3.88
Quercus falcata	2	2	0.147	3.17
Carya ovata	2	2	0.121	2.98
Juglans nigra	2	2	0.110	2.90
Liquidambar styraciflua	2	2	0.030	2.33
Quercus muehlenbergii	1	1	0.117	1.89
Acer nigrum	1	1	0.103	1.79
Quercus michauxii	1	1	0.059	1.48
Ulmus alata	1	1	0.035	1.31
Quercus imbricaria	1	1	0.032	1.29
Quercus stellata	1	1	0.022	1.22
Carpinus caroliniana	1	1	0.013	1.15
Acer rubrum	1	1	0.013	1.15
Cercis canadensis	1	1	0.009	1.12
Fraxinus americana	1	1	0.009	1.12
Total	200	179	14.045	300.00

TABLE 5. Statistical data for red elm-tulip poplar-American beech forest of ravines.

Species	No. of stems	No. of points	Basal area (m^2)	Importance value
Ulmus rubra	33	22	3.796	55.46
Liriodendron tulipifera	22	17	1.211	29.30
Fagus grandifolia	15	11	1.425	23.74
Platanus occidentalis	14	12	0.987	20.83
Juglans nigra	9	8	0.689	13.93
Quercus alba	11	9	0.432	13.75
Acer negundo	9	7	0.330	10.88
Acer saccharum	8	7	0.286	10.08
Carya cordiformis	7	7	0.316	9.79
Celtis laevigata	6	5	0.535	9.61
Carya ovalis	7	7	0.272	9.48
Carpinus caroliniana	8	8	0.102	9.41
Populus deltoides	3	3	0.869	9.22
Carya laciniosa	3	3	0.757	8.45
Prunus serotina	7	6	0.164	8.15
Ailanthus altissima	5	5	0.177	6.65
Carya ovata	4	4	0.313	6.50
Quercus rubra	4	4	0.279	6.26
Quercus shumardii	1	1	0.593	5.15
Acer rubrum	3	3	0.163	4.38
Nyssa sylvatica	3	3	0.052	3.62
Ulmus alata	2	2	0.137	3.12
Liquidambar styraciflua	2	2	0.112	2.95
Quercus muehlenbergii	2	2	0.066	2.63
Quercus pagoda	1	1	0.141	2.06
Juglans cinerea	1	1	0.122	1.93
Carya tomentosa	1	1	0.072	1.58
Gleditsia triacanthos	1	1	0.037	1.34
Quercus imbricaria	1	1	0.033	1.32
Cercis canadensis	1	1	0.029	1.29
Celtis occidentalis	1	1	0.025	1.26
Fraxinus americana	1	1	0.021	1.23
Morus rubra	1	1	0.014	1.19
Cornus florida	1	1	0.011	1.17
Sassafras albidum	1	1	0.011	1.17
Asimina triloba	1	1	0.009	1.15
Total	200	170	14.588	300.00

occidentalis, *Carya cordiformis*, *Gleditsia triacanthos*, *Juglans nigra*, and *Salix nigra*.

The shrub and small-tree layer is similar to that of ravines but also includes *Aesculus glabra*, *Alnus serrulata*, *Cephalanthus occidentalis*, *Ilex decidua*, *Sambucus canadensis*, and *Salix caroliniana*. Extensive stands of *Arundinaria tecta* are regular occurrences, especially along the Cumberland River, and a few old meander channels (e.g., Long Pond Slough in Montgomery Co.) are of floristic interest.

Woody vines often found in streambank forests, in addition to those mentioned for other communities, are *Ampelopsis cordata*, *Aristolochia tomentosa*, *Brunnichia cirrhosa*, *Cocculus carolinus*, *Calicocarpum lyoni*, *Menispermum canadense*, *Wisteria frutescens*, and *Vitis* spp. Common herbs are those noted for ravines with the addition of *Impatiens capensis*, *Impatiens pallida*, and *Mertensia virginica* among many others.

Black Gum-Sweet Gum-Red Maple Forests of Upland Flats and Depressions on the Pennyroyal Plain—Quarterman and Powell (1978) noted that forests of dissected portions of the Pennyroyal Plain are quite similar to those of the Highland Rim. Most forests of the upland flats and depressions have been removed, and the fertile soils now are in rowcrops (Baskin et al., 1994). To our knowledge, no undisturbed remnant of the Plain forests occurs in Tennessee. Our sampling results from the least-disturbed remnants we could locate in the study area are given in Table 7 (26 species sampled, average diameter breast height = 26.2 cm, density = 470 trees/ha). These remnants are dominated by *Nyssa sylvatica*, *Liquidambar styraciflua*, and *Acer rubrum*, with *Ulmus rubra*, *Quercus velutina*, *Q. phellos*, *Carya glabra*, *Platanus occidentalis*, and several other taxa. A few specimens were tentatively identified as *Ulmus thomasii* (which is known from but is rare in the area) and that identification is maintained in this account. In a few cases, large upland swamps such as the Cedar Hill Swamp in adjacent Robertson Co. include *Populus heterophylla* and *Quercus bicolor* (Ellis and Chester, 1989).

TABLE 6. Statistical data for box elder-silver maple-sycamore forest of streambanks.

Species	No. of stems	No. of points	Basal area (m^2)	Importance value
Acer negundo	48	38	2.076	65.11
Acer saccharinum	27	22	2.956	53.15
Platanus occidentalis	24	20	1.653	38.69
Ulmus rubra	25	22	0.928	33.82
Populus deltoides	8	6	1.257	18.89
Celtis occidentalis	13	11	0.427	16.83
Carya cordiformis	10	9	0.371	13.64
Gleditsia triacanthos	7	7	0.289	10.23
Juglans nigra	6	6	0.270	8.97
Salix nigra	5	5	0.159	6.88
Celtis laevigata	5	4	0.061	5.40
Quercus shumardii	3	3	0.162	4.72
Fraxinus pennsylvanica	4	3	0.068	4.37
Morus rubra	3	3	0.066	3.86
Carya laciniosa	2	2	0.025	2.41
Quercus rubra	2	1	0.083	2.34
Maclura pomifera	1	1	0.052	1.56
Quercus michauxii	1	1	0.039	1.44
Quercus imbricaria	1	1	0.035	1.41
Juglans cinerea	1	1	0.031	1.37
Prunus serotina	1	1	0.025	1.32
Morus alba	1	1	0.016	1.23
Betula nigra	1	1	0.011	1.19
Quercus macrocarpa	1	1	0.009	1.17
Total	200	170	11.069	300.00

TABLE 7. Statistical data for black gum-sweet gum-red maple forest of upland flats and depressions on the Pennyroyal Plain.

Species	No. of stems	No. of points	Basal area (m^2)	Importance value
Nyssa sylvatica	64	49	3.734	87.80
Liquidambar styraciflua	37	37	3.042	62.29
Acer rubrum	27	22	2.208	42.51
Ulmus rubra	11	10	0.518	15.07
Quercus velutina	6	5	0.994	13.26
Quercus phellos	3	3	0.620	7.83
Carya glabra	6	5	0.201	7.36
Ulmus thomasii	4	4	0.277	6.35
Carpinus caroliniana	5	5	0.095	6.07
Platanus occidentalis	3	3	0.273	5.24
Fraxinus pennsylvanica	4	4	0.113	5.13
Ulmus alata	4	3	0.122	4.62
Celtis occidentalis	3	3	0.114	4.06
Acer saccharum	3	3	0.098	3.94
Cornus florida	3	3	0.055	3.62
Quercus alba	2	2	0.196	3.60
Quercus palustris	2	2	0.154	3.29
Diospyros virginiana	3	2	0.069	3.15
Carya ovata	2	2	0.053	2.53
Fagus grandifolia	1	1	0.179	2.40
Liriodendron tulipifera	2	2	0.030	2.36
Quercus falcata	1	1	0.095	1.78
Quercus lyrata	1	1	0.088	1.73
Ulmus americana	1	1	0.079	1.66
Morus rubra	1	1	0.014	1.17
Quercus pagoda	1	1	0.012	1.16
Total	200	175	13.433	300.00

Interesting shrubs of Pennyroyal wet woods are *Itea virginica*, *Salix humilis*, *Salix tristis*, and *Spiraea tomentosa*. The spring herbaceous flora is limited because of flooded or saturated soils, while the fall flora is dominated by numerous and often showy composites such as *Bidens*, *Eupatorium*, and *Vernonia*.

Species Distributions Across the Community Types—Importance values for each sampled species in each community type are given in Table 8. Some species are apparently tolerant to conditions across the topographic-moisture gradients. For example, species with a community occurrence >70% (i.e., sampled in at least five of the seven communities) are *Acer saccharum*, *Carya ovata*, *Cornus florida*, *Nyssa sylvatica*, *Quercus alba*, *Q. rubra*, and *Ulmus rubra*. In addition, species sampled in at least four of the seven communities are *Carya glabra*, *Carya tomentosa*, *Celtis occidentalis*, *Fagus grandifolia*, *Fraxinus americana*, *Juglans nigra*, *Liquidambar styraciflua*, *Prunus serotina*, *Quercus falcata*, *Q. muehlenbergii*, *Q. shumardii*, *Q. velutina*, and *Ulmus alata*.

Several distributional patterns are exhibited by widely-occurring taxa. Some (e.g., *Fagus grandifolia* and *Acer saccharum*) reach a peak importance value in one of the more mesic but upland communities and decrease in significance toward the extremes of the moisture gradient. Others peak in one of the extremes (e.g., *Quercus muehlenbergii* = xeric, *Liquidambar styraciflua* = most mesic) and taper in importance in other communities. Still others (e.g., *Carya ovata*) are found across a range of communities but with a small importnce value in all.

Some species exhibit restricted distributions, e.g., *Acer saccharinum* and *Salix nigra* to streambanks, *Acer rubrum* and *Liriodendron tulipifera* to mesic sites, *Quercus prinus* and *Q. stellata* to xeric sites, and *Juniperus virginiana* to limestone sites. The last species is a common member of old-field succession and in younger forests of slopes and ridges but is rarely found in mature stands except on bluffs.

Major Species—To further indicate the relative importance of species, the raw data were pooled and a composite importance value was determined for the 1,400 sampled stems. This composite importance value is based solely on sampled stems without adjustment for relative areal coverage per importance of the seven topographic forms. Based on data in Table 9, *Quercus alba*, *Nyssa sylvatica*, *Ulmus rubra*, *Quercus velutina*, *Juniperus virginiana*, *Fagus grandifolia*, *Acer saccharum*, *Acer negundo*, and *Liquidambar styraciflua* are the major species in the study area. These nine species (14.1% of all species) comprise almost 45.2% of total stems sampled (633 of 1,400) and 46.3% of total importance value (138.9 of 300).

Major Genera—The four major genera were *Quercus* (18 species, 27.3% of stems sampled, importance value = 86.79/300), *Acer* (5 species, 12.3% of stems, importance value = 37.20/300), *Carya* (6 species, 10.9% of stems, importance value = 29.88/300), and *Ulmus* (5 species, 7.6% of stems, importance value = 23.78/300). These four genera provided 34 of 64 species (53.1%), 813 of 1,400 stems (58.1%), and 177.65 of total importance value (59.2%). Table 10 shows the importance value of each of these genera in the seven community types. *Quercus* was best represented on xeric sites, especially southerly-facing

TABLE 8. Importance values of all taxa within seven topographic-community types.

Species	Xeric limestone bluffs	Ridges	Southerly-facing slopes	Northerly-facing slopes	Ravines	Streambanks	Upland flats
Acer negundo				P[1]	10.88	65.11	P
Acer nigrum				1.79	P	P	
Acer rubrum				1.15	4.38	P	42.51
Acer saccharinum					P	53.15	P
Acer saccharum	8.96	4.15	26.27	22.16	10.08	P	3.94
Ailanthus altissima			P	P	6.65		
Asimina triloba			P	P	1.15	P	P
Betula nigra						1.19	P
Carpinus caroliniana			P	1.15	9.41	P	6.07
Carya cordiformis			P	7.23	9.79	13.64	P
Carya glabra	P	28.82	11.00	7.07	P		7.36
Carya laciniosa			1.27	P	8.45	2.41	
Carya ovalis	P	P	12.74	17.28	9.48		
Carya ovata	9.06	1.93	7.57	2.98	6.50	P	2.53
Carya tomentosa	P	10.21	20.12	6.67	1.58		
Celtis laevigata	P	P	P	P	9.61	5.40	P
Celtis occidentalis	1.70		P	P	1.26	16.83	4.06
Cercis canadensis	1.28	P	P	1.12	1.29	P	P
Cornus florida	5.32	1.22	2.38	7.33	1.17	P	3.62
Diospyros virginiana	P	P	P	P	P	P	3.15
Fagus grandifolia		P	1.96	56.04	23.74	P	2.40
Fraxinus americana	37.82[2]	P	2.10	1.12	1.23	P	P
Fraxinus pennsylvanica				3.88	P	4.37	5.13
Gleditsia triacanthos	1.63	P	P	P	1.34	10.23	
Juglans cinerea				P	1.93	1.37	
Juglans nigra			1.25	2.90	13.93	8.97	P
Juniperus virginiana	125.70	P	P				
Liquidambar styraciflua	2.02			2.33	2.95	P	62.29
Liriodendron tulipifera			P	27.60	29.30	P	2.36
Maclura pomifera	9.13				P	1.56	P
Morus alba					P	1.23	
Morus rubra	P	P	P	P	1.19	3.86	1.17
Nyssa sylvatica	P	10.05	9.09	19.31	3.62	P	87.80
Ostrya virginiana	7.81	P	2.47	6.44	P	P	P
Oxydendrum arboreum		13.08	1.18				
Platanus occidentalis				P	20.83	38.69	5.24
Populus deltoides					9.22	18.89	P
Prunus serotina	7.86	P	P	8.67	8.15	1.32	P
Quercus alba	1.73	50.07	81.31	24.80	13.75	P	3.60
Quercus coccinea	P	19.29	1.59	P	P		
Quercus falcata	1.35	P	10.50	3.17			1.78
Quercus x *fontana*		7.95	1.60				
Quercus imbricaria			P	1.29	1.32	1.41	P
Quercus lyrata						P	1.73
Quercus macrocarpa						1.17	
Quercus marilandica	P	20.59	1.27				
Quercus michauxii				1.48	P	1.44	P
Quercus muehlenbergii	29.14	P	4.89	1.89	2.63	P	
Quercus pagoda			P	9.27	2.06	P	1.16
Quercus palustris					P	P	3.29
Quercus phellos						P	7.83
Quercus prinus	P	77.34	P	P			
Quercus rubra	13.51	1.76	3.77	12.15	6.26	2.34	P
Quercus shumardii	3.19		1.53	P	5.15	4.72	P
Quercus stellata	P	40.33	30.25	1.22			P

TABLE 8. Continued.

Speices	Xeric limestone bluffs	Ridges	Southerly-facing slopes	Northerly-facing slopes	Ravines	Streambanks	Upland flats
Quercus velutina	P	13.21	59.37	23.17	P	P	13.26
Salix nigra						6.88	
Sassafras albidum	P	P	2.45	9.95	1.17	P	P
Ulmus alata	28.76	P	P	1.31	3.12	P	4.62
Ulmus americana	P	P	2.07	P	P	P	1.66
Ulmus rubra	4.05[3]	P	P	6.04	55.46	33.82	15.07
Ulmus thomasii							6.35

[1]P = known to be present in this community type but not in sampling plots.
[2]Includes *Fraxinus quadrangulata* in this community.
[3]Includes *Ulmus serotina* in this community.

slopes, but was present in all communities. *Carya* occurred in all communities but was most important on southerly-facing slopes. *Acer* was widely distributed but reached greatest importance value on streambanks. *Ulmus* occurred in all communities (not sampled on ridges) but was most important in ravines.

Other Taxa—While this work did not attempt to elucidate all taxa of trees in the study area, several species not mentioned previously should be noted (all quite rare and not encountered in the sampling). These include *Carya illinoensis*, *Carya carolinae-septentrionalis*, *Castanea dentata* (remnants only), *Celtis tenuifolia*, *Chionanthus virginicus*, *Cladrastis lutea*, *Gymnocladus dioica*, *Halesia carolina*, *Ilex opaca*, *Nyssa aquatica*, *Populus grandidentata*, *Quercus nigra*, *Salix exigua* (*interior*), and the *Tilia americana-heterophylla* complex. Species of trees often found in old-field succession and in young forest stands include *Crataegus* spp., *Prunus americana*, and *Robinia pseudoacacia*. In addition, large plantations of *Pinus taeda*, and to a lesser extent *P. strobus*, are commonplace. Numerous exotics (e.g., *Ailanthus altissima*, *Albizzia julibrissin*, *Populus alba*, and *Ulmus pumila*) regularly persist and sometimes appear in forests.

CONCLUSIONS

The data indicate distinct community types based on topography. Ravines (dominated by a red elm-tulip poplar-American beech community) and north-facing slopes (American beech-tulip poplar-white oak) were most diverse floristically with 36 and 32 species sampled, respectively. Ridges (chestnut oak-white oak-post oak) with 15 species and xeric limestone bluffs (red cedar-white ash-chinquapin oak) with 19 species were least diverse floristically. Streambanks and bottomlands (box elder-silver maple-sycamore) with 24 species, southerly-facing slopes (white oak-black oak-post oak) with 25 species, and Pennyroyal Plain upland flats and depressions (black gum-sweet gum-red maple) with 26 species were intermediate. Calculated densities, based on between-tree distances, ranged from 303 trees/ha in ravines to 488 trees/ha on south-facing slopes. Average diameter breast heights ranged from 17.6 cm on xeric limestone bluffs to 26.5 cm on north-facing slopes. High densities and relatively low diameters probably reflect the secondary nature of the forests in 1971-1972; further and greater disturbances have occurred since then. Future studies will evaluate our subjectively-determined moisture gradient.

The major genera of the study area were *Quercus*, *Acer*, *Carya*, and *Ulmus*, providing 34 of 64 species, 58.1% of stems sampled, and 59.2% of total importance value. Major species, determined by pooling all data, were *Quercus alba*, *Nyssa sylvatica*, *Ulmus rubra*, *Quercus velutina*, *Juniperus virginiana*, *Fagus grandifolia*, *Acer saccharum*, *Acer negundo*, and *Liquidambar styraciflua*.

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TABLE 9. Statistical data for all sampling points (1,400 stems).

Species	No. of stems	No. of points	Basal area (m^2)	Importance value
Quercus alba	106	90	7.481	24.71
Nyssa sylvatica	96	79	4.829	19.67
Ulmus rubra[1]	77	61	5.465	17.62
Quercus velutina	62	55	5.387	15.95
Juniperus virginiana	90	60	2.517	14.68
Fagus grandifolia	46	36	5.727	13.66
Acer saccharum	56	50	2.171	10.97
Acer negundo	57	45	2.406	10.93
Liquidambar styraciflua	43	42	3.207	10.70
Quercus stellata	51	42	2.006	9.73
Platanus occidentalis	41	35	2.913	9.60
Quercus prinus	44	35	2.750	9.60
Liriodendron tulipifera	43	37	2.370	9.21
Carya glabra	43	36	1.262	7.70
Acer saccharinum	27	22	2.956	7.57
Acer rubrum	31	26	2.384	7.45
Carya ovalis	34	28	0.855	5.87
Carya tomentosa	29	25	1.078	5.54
Quercus rubra	23	22	1.502	5.41
Fraxinus americana[2]	29	25	0.786	5.17
Quercus muehlenbergii	25	22	0.900	4.79
Ulmus alata	23	21	0.957	4.63
Carya cordiformis	21	20	1.109	4.59
Populus deltoides	11	9	2.126	4.27
Carya ovata	20	20	0.872	4.22
Juglans nigra	18	17	1.087	4.11
Prunus serotina	22	19	0.397	3.67
Celtis occidentalis	18	16	0.599	3.40
Cornus florida	17	17	0.286	3.00
Quercus marilandica	16	13	0.497	2.87
Quercus coccinea	13	11	0.641	2.67
Carpinus caroliniana	14	14	0.210	2.44
Quercus falcata	10	10	0.694	2.44
Ostrya virginiana	14	13	0.187	2.33
Celtis laevigata	11	9	0.596	2.31
Quercus shumardii	6	6	0.924	2.12
Sassafras albidum	10	9	0.479	2.08
Fraxinus pennsylvanica	10	9	0.428	2.01
Quercus pagoda	8	7	0.642	1.98
Carya laciniosa	6	6	0.803	1.96
Oxydendrum arboreum	12	11	0.143	1.96
Gleditsia triacanthos	9	9	0.355	1.85
Maclura pomifera	7	6	0.227	1.29
Quercus x fontana	6	6	0.255	1.26
Quercus phellos	3	3	0.620	1.26
Ailanthus altissima	5	5	0.177	1.03
Salix nigra	5	5	0.159	0.98
Ulmus thomasii	4	4	0.277	0.98
Morus rubra	5	5	0.094	0.90
Quercus imbricaria	3	3	0.100	0.59
Ulmus americana	2	2	0.187	0.55
Cercis canadensis	3	3	0.047	0.52
Juglans cinerea	2	2	0.153	0.51
Quercus palustris	2	2	0.154	0.51
Quercus michauxii	2	2	0.098	0.48
Diospyros virginiana	3	2	0.069	0.47
Acer nigrum	1	1	0.103	0.28
Quercus lyrata	1	1	0.088	0.26
Morus alba	1	1	0.016	0.17
Asimina triloba	1	1	0.009	0.16
Betula nigra	1	1	0.011	0.16
Quercus macrocarpa	1	1	0.009	0.16
Total	1,400	1,195	77.837	300.00

TABLE 9. Continued.

[1]Includes *Ulmus serotina* in xeric limestone bluffs.
[2]Includes *Fraxinus quadrangulata* in xeric limestone bluffs.

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TABLE 10. Importance values for major genera (number of species given in parentheses) in seven community types.

Genus	Xeric limestone bluffs	Ridges	Southerly-facing slopes	Northerly-facing slopes	Ravines	Streambanks	Upland flats
Quercus (18)	48.92 (5)	230.54 (8)	196.08 (10)	78.44 (9)	31.17 (6)	11.08 (5)	32.65 (7)
Carya (6)	9.06 (1)	40.96 (3)	52.70 (5)	41.23 (5)	35.80 (5)	16.05 (2)	9.89 (2)
Acer (5)	8.96 (1)	4.15 (1)	26.27 (1)	25.10 (3)	25.34 (3)	118.26 (2)	46.45 (2)
Ulmus (5)	32.81 (3)	P[1]	2.07 (1)	7.35 (2)	58.58 (2)	33.82 (1)	27.70 (4)
Total for four genera (34)	99.75 (10)	275.65 (12)	277.12 (17)	152.12 (19)	150.89 (16)	179.21 (10)	116.69 (15)
All others (30)	200.25 (11)	24.35 (3)	22.88 (8)	147.88 (13)	149.11 (20)	120.79 (14)	183.31 (11)
Total (64)	300.00 (21)	300.00 (15)	300.00 (25)	300.00 (32)	300.00 (36)	300.00 (24)	300.00 (26)

[1]Known from this community type but not sampled.

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