TWENTY YEARS OF FOREST CHANGE AT RADNOR LAKE NATURAL AREA, DAVIDSON COUNTY, MIDDLE TENNESSEE

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ABSTRACT-A 1994 analysis of five mature forest communities at Radnor Lake Natural Area near Nashville, Tennessee, was compared with a similar 1974 study to ascertain successional trends in this protected area. The importance value, IV = (% density + % basal area + % frequency)/3, of Acer saccharum increased in all communities, and its overall IV (average of IVs for all communities) increased from 10.0 in 1974 to 15.3 in 1994. The overall IV of Celtis occidentalis rose from 3.4 to 7.6 and showed increases in four of the five communities. The IV of Acer saccharinum in the lakeshore community increased from 10.8 to 30.3, while the IV of Acer saccharum ssp. nigrum increased from 2.8 to 11.8 in the mesic-slope community and from 3.3 to 4.9 in the ravine community. Taxa that declined in IV included Carya cordiformis (10.5 to 2.7, mesic-slope community), Juglans nigra (4.0 to 2.6, mesic-slope community; 8.3 to 5.1, ravine community), Populus deltoides (12.1 to 3.1, lakeshore community), Quercus marilandica (1.2 to 0.0, ridge community), Quercus rubra (8.9 to 0.0, dry-slope community; 12.0 to 10.3, mesic-slope community; 4.0 to 1.6, ravine community), Salix nigra (14.0 to 0.9, lakeshore community), and Ulmus spp. (6.5 to 2.5, mesic-slope community; 25.1 to 0.9, ravine community; 24.7 to 15.7, lakeshore community). The other 36 sampled taxa of trees exhibited relatively minor changes in IV over the 20-year period. Total densities of stems decreased in all communities. In 1994, the dominant taxa of trees ranked by IV were Quercus montana, Fraxinus quadrangulata, and Carya ovata on the ridges; Acer saccharum, Celtis occidentalis, and Ouercus montana on the dry slopes; Acer saccharum, Fraxinus americana, and Quercus rubra on the mesic slopes; Acer saccharum, Carya cordiformis, and Celtis occidentalis in the ravines; and Acer saccharinum, Celtis laevigata, and Ulmus americana on the lakeshore.

The value of Radnor Lake Natural Area near Nashville, Tennessee. for forest-dynamics research is great because forest communities found there may be studied over long periods of time without significant human disturbances. Eickmeier (1988) noted the importance and rarity of longterm studies on forest communities and reported the results of his 10year forest-dynamics study of a north-facing-slope forest community at Radnor Lake Natural Area. The fieldwork for another published study (Carpenter et al., 1976) dealing with the forest communities of Radnor Lake Natural Area was done by two students at Volunteer State Community College, Gallatin, Tennessee, and me in 1974. We recognized five topography-based forest communities: dry ridge; dry slope; mesic slope; ravine; lakeshore. Importance values and other quantitative data were obtained by plot sampling to determine the dominant species of trees for each community type. It is the purpose of this paper to present a quantitative characterization of the forest communities of Radnor Lake Natural Area as they were in 1994 and to compare these findings with the results of the 1974 study to show successional trends over that 20-year period. Comparisons with the studies by Eickmeier (1988), Frick (1939), Chester et al. (1995), and others also are presented.

STUDY AREA

The Radnor Lake Natural Area was established in 1973 and is managed by the Tennessee Department of Environment and Conservation. The Natural Area, an outlier of the western Highland Rim, is

located in the Overton Hills of the Central Basin ca. 12 km south of the center of Nashville on Otter Creek Road. In 1974, the Natural Area consisted of 312 ha, and, by 1994, it had been enlarged to 387 ha. Radnor Lake Natural Area is within the Interior Low Plateau of Fenneman (1938).

Geologically, rocks of Mississippian age cap the hills, and, at lower elevations, Ordovician limestones occur (Miller, 1974). Radnor Lake Natural Area consists of a central lake (34 ha) with a spillway elevation of 236 m, surrounded by the hilly Otter Creek watershed (353 ha). The narrow winding ridges (as high as 335 m) are separated by steep-walled valleys with rolling land on the footslopes and narrow flood plains along drainageways. The steepness of slope for slope plots ranges from 25 to 50%, and the elevational difference between the valley floors and ridgetops generally is between 61 and 84 m. Otter Creek and its tributaries drain the area.

The ridges and upper slopes of Radnor Lake Natural Area have cherty, well-drained, acidic Bodine soils derived from the Fort Payne formation. On the slopes, immediately below the Bodine soils, Sulphura soils derived from Chattanooga shale occur. The colluvial Dellrose soils, derived from the Bodine and Sulphura soils, are found on the mid to lower slopes. Dellrose soils are deep, well-drained, cherty, brown loamy soils. Mimosa soils, often with rock outcrops, occur mostly on the lower slopes of steep hillsides, on benches, and on rolling to gently sloping footslopes. Arrington and Ocana soils occur in the ravines, and Arrington, a deep, well-drained, fertile, loamy floodplain soil, also is found at the lakeshore. Armour soils are associated with the footslopes

and stream terraces and are gently sloping to moderately steep, well-drained, and phosphorus-rich soils (United States Department of Agriculture, 1981).

Vegetatively, Radnor Lake Natural Area lies within the Western Mesophytic Forest Region of Braun (1950), who described the Region as a mosaic of forest communities transitional between the Mixed Mesophytic Forest Region to the east and the Oak-Hickory Region to the west. More recently, Bryant et al. (1993) refer to this region as Oak-Hickory Forest (Western Mesophytic/Oak-Hickory Forest) and provide descriptions of its various communities.

The climate of middle Tennessee is temperate, with long, warm summers and mild winters. The well-distributed precipitation averages ca. 125 cm, although periods of summer drought and late winter-early spring flooding do occur. Average seasonal snowfall is 28 cm. The growing season extends from early April to late October. In winter, the average temperature is 4.4°C, and the average daily minimum temperature is -1.1°C. The lowest temperature on record, which occurred at Nashville on 24 January 1963 was -26.1°C. In summer, the average temperature is 25.6°C, and the average daily maximum temperature is 31.7°C. The highest recorded temperature, which occurred at Nashville on 27 July 1952, was 41.7°C. Prevailing winds are from the south, and average wind speed is highest in March (United States Department of Agriculture, 1981). Occasional severe ice storms occur. Eickmeier (1988) reported that a serious ice storm damaged many of the trees at Radnor Lake Natural Area in 1957, and extensive damage was done to the trees of the Natural Area from the ice storm of 1994 (pers. obser.). Many large shallow-rooted trees (especially Acer saccharum, Celtis occidentalis, and Prunus serotina) were toppled by the weight of the ice, and, throughout the area, large and small limbs from all species were broken off and littered the landscape.

Eickmeier (1988) provided some historical information concerning Radnor Lake Natural Area. Several roads were constructed near the study area as early as 1836, and many small farms were located in the Overton Hills area during the Civil War period. The Louisville and Nashville Railroad Company dammed Otter Creek in 1914 to create Radnor Lake as a source of water for the nearby Radnor Railroad Yards. Two periods of selective timber harvesting occurred, one in 1918 and one in 1950. McCall (1973) indicated that the early 1900s cut was heavier, and Wiser (1956) noted the presence of many large trees in the Radnor Lake area in the 1950s. Limited fires occurred in 1948 and 1954 (Eickmeier, 1988); thus, as of 1996, no fire has disturbed the forests for 42 years, and, for 46 years, no lumbering has occurred. When I first studied the forests of Radnor Lake Natural Area in 1974, many of the trees were young, having become established after the 1950 cut. but there were some very large hackberry (Celtis), hickory (Carya), maple (Acer), oak (Quercus), tulip poplar (Populus), and white ash (Fraxinus) throughout the area. Much of the lowlands on the north side of the Lake and along the eastern section of Otter Creek Road were in early stages of old-field succession. In 1994, nearly all of the Radnor Lake Natural Area watershed was forested.

METHODS

In the summer of 1994, I established 100 permanent plots in 20 forest stands which represented five forest-community types at Radnor Lake Natural Area (Fig. 1). This was a follow-up study of a 1974 forest-community study at the Natural Area. I returned to the same stands that were sampled in the 1974 study, but the plots were not made permanent in 1974, so I was not able to go to the exact areas that were sampled then. In 1994, the circular plots were made "permanent" by driving a steel rod (0.5 m long, 1.2 cm in diameter) into the ground at the center of each plot so that only ca. 10 cm of the rod projected above the soil surface; then, a white pvc pipe with a diameter of 2 cm was driven over the steel

rod to encase and protect the steel from corrosion. An aluminum tag with plot number, date, and investigator's name was affixed to the base of each stake. An altimeter was used to record the elevation of each plot center. Aspect and percent slope were recorded for each of the slope plots. In 1974 and 1994, five topography-based forest-community types were recognized at Radnor Lake Natural Area: ridge; dry slope (southerly aspect); mesic slope (northerly aspect); ravine; lakeshore. In 1974, four mature forest stands were selected to represent each community type. In each stand, eight circular plots, each with a diameter of 7.93 m and an area of 0.005 ha, were established in linear sequence. The distance between adjacent plot centers was 11 m. The 32 plots representing each community occupied an area of 0.16 ha. Lakeshore plots were placed at the eastern end of the lake, and the plot centers were established parallel to and 7 m upslope from the water's edge. The ravine sampling line followed the middle of the ravine floor. In each slope stand, the plots were set at midslope, parallel to the contour. On ridges, the sampling line ran longitudinally along each ridge. Only trees having a dbh (diameter at 1.37 m above ground) of ≥10.2 cm were recorded in the sampling. In 1994, sampling was done in the same stands and in a similar manner, but the plots were made larger and permanent. Five circular plots, each with a diameter of 16.05 m and an area of 0.02 ha, were established in each stand. The distance between adjacent plot centers was 30.5 m. The 20 plots of each community type occupied an area of 0.4 ha. In the 1994 study, small stems (dbh = 2.5-10.2 cm) as well as the larger stems (dbh \geq 10.2 cm) were recorded. In addition, a smaller circular plot (0.002 ha) was nested at the center of each 0.02-ha plot in the 1994 study to obtain data for tree seedlings (dbh < 2.5 cm), shrubs, and vines. For all plots with slope, the plot diameter was made horizontal by extending the radius rope in a horizontal plane from the pole at the plot center to the perimeter.

Upon conclusion of fieldwork in 1994, the data were entered on Quattro Pro spreadsheets for computer-assisted analysis. Density, basal area, frequency, and importance value, IV = (%density + %basal area + %frequency)/3, were determined for each species of tree with a dbh of ≥ 2.5 cm. IVs for species of trees (dbh ≥ 10.2 cm size class; larger trees) were compared with IVs for 1974 to determine successional trends. In the recent study, density, frequency, basal area, and IV also were computed for small trees (dbh = 2.5-10.2 cm); density, frequency, and IV = (%density + %frequency)/2 were determined for tree seedlings (dbh < 2.5 cm), but only frequency data were obtained for shrubs and vines. Throughout this paper, nomenclature follows Wofford and Kral (1993).

RESULTS AND DISCUSSION

Ridge Forest Community—The narrow ridges had droughty Bodine soils and were exposed to more wind and direct radiation than most of the other topographic areas. The average elevation for the ridge plots was 311 m.

Table 1 shows the IVs of the 21 taxa in the larger-tree class (dbh \geq 10.2 cm). The five most important taxa of trees of the ridge community in order of decreasing IV were Quercus montana, Fraxinus quadrangulata, Carya ovata, Ulmus spp., and Celtis occidentalis. Of the 25 sampled taxa in the small-tree class (dbh = 2.5-10.2 cm), the most important taxa ranked by IV were Ulmus spp., Q. montana, A. saccharum, C. occidentalis, and Juniperus virginiana. All subsequent lists of dominant trees of communities at Radnor Lake Natural Area also will be in order of decreasing IV.

Table 2 displays the IVs of the 23 taxa of tree seedlings that were sampled in the ridge community. The most important were Quercus montana, Ulmus spp., Fraxinus quadrangulata, Carya spp., and Celtis occidentalis. The taxa of sampled shrubs and vines for this community, in order of decreasing frequency, were Parthenocissus quinquefolia,

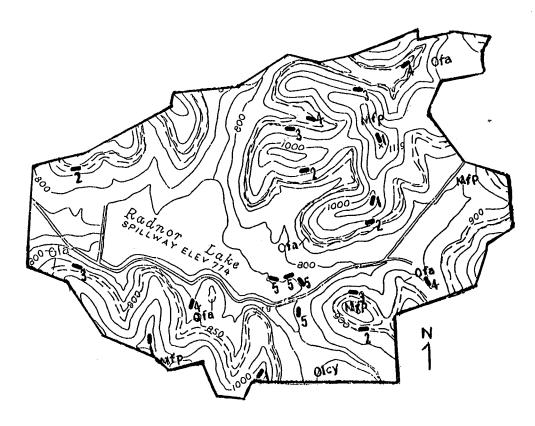


FIG. 1. Map (scale 1:1800) of Radnor Lake Natural Area, Davidson Co., Tennessee, with positions of sampled stands (1 = ridge, 2 = dry slope, 3 = mesic slope, 4 = ravine, and 5 = lakeshore). Abbreviations include Mfp (Fort Payne and Chattanooga formations), Ofa (Fernvale and Arnheim formations), and Olcy (Leipers and Catheys formations). Map modified from Wilson and Miller (1972).

Symphoricarpos orbiculatus, Vitis spp., Lonicera maackii, Bignonia capreolata, Ligustrum vulgare, Rubus argutus, Smilax spp., Vaccinium spp., and Rubus occidentalis. All subsequent lists of shrubs and vines also will be in order of decreasing frequency.

Quercus montana will probably remain the chief species in the ridge forest community indefinitely, because it was prominent in the seedling, small-tree, and large-tree classes in 1994. quadrangulata will likely remain a dominant species for the foreseeable future, because it also had a high IV in all size classes. Based on its decrease in IV from 1974 to 1994 and its low IV in the small-tree class, Carya ovata will likely become less important in this community as time goes on. Ulmus spp., especially Ulmus serotina, continued to maintain their dominance. Quercus marilandica had an IV of 1.2 in this community in 1974 but was not observed at all in 1994. The IV of Celtis occidentalis increased in the ridge community. In 1974 (20 years after the last fire in the area and 24 years after the last lumbering operation), no Acer saccharum with a dbh \geq 10.2 cm was found in the ridge plots, but, in 1994, there were 20 A. saccharum stems/ha in this size class on the ridges; thus, this species will likely become more important in this community. Data in Tables 1-3 confirm these successional trends.

The ridge community on the northwestern Highland Rim (Montgomery and Stewart counties, Tennessee) studied by Chester et al. (1995) was compared with the ridge community at Radnor Lake Natural Area in 1994. *Quercus montana* and *Carya glabra* were identified as dominants (among the top 10 taxa of trees in IV) in both areas. The ridge community of Radnor Lake Natural Area had more mesophytic species and fewer oaks. Chester et al. (1995) reported a total density of 421 trees

(dbh \geq 10.2 cm)/ha in the ridge community in 1971; at Radnor Lake Natural Area, the total density of the trees in the same size class in the ridge community was 538 trees/ha in 1974 and 497 trees/ha in 1994. In all subsequent comparisons of density, only trees with a dbh \geq 10.2 cm will be compared.

Dry-slope Forest Community—This community encompassed slopes with mostly southerly aspects (S10°E-S50°W). The average of the dry-slope plot elevations was 285 m, and the average steepness of slope was 42%. The dry-slope and mesic-slope plots were positioned at midslope and were either on or below the Chattanooga Shale. Dellrose, Sulphura, and Mimosa were the soils associated with the slope plots.

Table 4 gives the IVs of the 16 sampled taxa in the larger-tree class. The dominant trees included Acer saccharum, Celtis occidentalis, Quercus montana, Fraxinus americana, and F. quadrangulata. Of the 22 sampled taxa in the small-tree class, the most important taxa were A. saccharum, Ulmus spp., Cornus florida, Celtis occidentalis, and F. quadrangulata.

Table 2 shows the IVs of the 22 taxa of tree seedlings sampled in the dry-slope community. The most important were Celtis occidentalis, Acer saccharum, Prunus serotina, Quercus montana, and Fraxinus quadrangulata. The taxa of shrubs and vines were Lonicera maackii, Vitis spp., Bigonia capreolata, Parthenocissus quinquefolia, Lonicera japonica, Euonymus americana, Sambucus canadensis, Smilax spp., Campsis radicans, Hedera helix, and Ligustrum vulgare.

From 1974 to 1994, *Acer saccharum* increased in IV from 15.2 to 20.1 in the dry-slope community. It had high IVs in all size classes in 1994; thus, it will likely remain as the chief species on the dry slopes

TABLE 1. Average dbh (diameter at 1.37 m above ground) for sampled stems ≥ 2.5 cm and density, basal area, occurrence (of 20 plots, 0.02 ha each), and importance value (IV) of small trees (dbh = 2.5-10.2 cm) and larger trees (dbh ≥ 10.2 cm) of the ridge forest community at Radnor Lake Natural Area, Davidson Co., Tennessee, in 1994.

			Small trees	trees			Larger trees	trees	
Taxon	Average dbh (cm)	Density (number/ha)	Basal area (m²/ha)	Occurrence	IV (100) ¹	Density (number/ha)	Basal area (m²/ha)	Occurrence	IV (100)
		0 7 7	3000	۰	14.0	177 8	13 244	10	32.3
Quercus montana	18.0	113.6	0.530	۰ ۰) , ,	0.771	4 320) O	14.7
Fraxinus anadrangulata	18.5	34.6	0.092	9	5.1	80.3	4.539	0 1	14.7
Come motor	3.7.8	2.5	0.011	1	9.0	32.1	3.251	S	8.4
Carya Ovala	6.9	177.8	0.421	14	20.2	42.0	0.759	7	7.0
Commer Spp.	11.4	593	0.106	10	7.6	29.6	1.846	S	6.5
Cettis Occidentalis	17.0	7.4	0.005	ю	1.3	14.8	0.778	S	4.3
Quercus veumina	7.7	71.6	0.105	12	8.7	19.8	0.628	4	4.0
Acer saccharum	11.0	20.6	0.077	ν.	4.3	12.4	0.998	4	3.9
Carya glabra	11.7	2.7.5	0.018	, er:	1.6	12.4	0.315	5	3.6
Quercus muniendergu	17.7	10.8	0.030	7	3.5	7.4	0.389	33	2.4
Fraxinus americana	V.V.	0.0	0.03	4	1.9	6.6	0.506	2	2.2
Tilia americana	14.3	7.7	0.007	. 4	1.0	12.4	0.275	2	2.1
Claarastis keniuckeu	11.7	37.1	0.067	4	4.1	12.4	0.196	1	1.5
Allanthus attissima	0.0	4.4	0.015	- 1	0.8	7.4	0.454	-	1.5
Carya ovatis	10.0	51.9	0.115	7	9.9	4.9	0.147	2	1.5
Juniperus Virginiana	15.2	0.0	0.00	0	0.0	2.5	0.045		0.7
Cents taevigata	2.5. 4.8	2.5	0.002	1	0.4	2.5	0.036	_	0.7
Cymnocidaus aioicus	17.0	0:0	0000	0	0.0	2.5	0.056	₩	0.7
Moras rabia	17.3	0.0	0000	0	0.0	2.5	0.058	-	0.7
Quercus awa Saccafras alhidum	3.8	14.8	0.00	1	1.1	2.5	0.021	-	0.7
Viburnum rufidulum	4.3	32.1	0.044	7	4.3	2.5	0.024	.	0.7
Course canadansis	3.0	39.5	0.032	33	3.2	0.0	0.000	0	0.0
Certs culturelists	8.5	14.8	0.046	က	2.5	0.0	0.000	0	0.0
Collids Johnan Volmin lotifolia	33	27.2	0.023	2	2.2	0.0	0.000	0	0.0
Natilità mitjoina Diamane caroliniana	3.0	14.8	0.011	3	1.7	0.0	0.000	0	0.0
Vaccinium arhoreum	3.0	17.3	0.012	1	1.3	0.0	0.000	0 (0.0
Assemble flow	5.6	4.9	0.013	2	1.1	0.0	0.000	0	0.0
Aralia eninoca	2.5	7.4	0.004	_	0.7	0.0	0.000	0	0.0
Total	11.93	810.2	1.612	111	100.0	496.5	28.366	70	100.0

 1 IV (100) = (% density + % basal area + % frequency)/3.

²Mostly Ulmus serotina. ³The average dbh for all 529 stems sampled in this community (area sampled = 0.4 ha) was 11.9 cm.

indefinitely. Celtis occidentalis increased in IV from 1.9 to 13.6. It too had good representation in all size classes; so, it will likely remain as the second most dominant species in the dry-slope community well into the future. Quercus montana decreased from 22.8 to 11.7. It probably will continue to diminish in importance because its density and IV were comparatively low in the small-tree class. Fraxinus americana increased in IV (gain of 5.6) while F. quadrangulata decreased (IV loss of 1.1). Carya ovata gained in IV (6.8 to 7.5). In 1994, it had a high IV in the small-tree class; so, it should maintain its position of importance. The IV (5.4) of Carya glabra remained the same over the 20-year period, but this hickory species was not prominent in the understory in 1994. The IV of Robinia pseudoacacia increased from 3.3 to 6.8, but its absence in the small-tree class and low numbers in the seedling class indicate that it will become less important in the future. The IV of *Quercus rubra* decreased from 8.9 to 0.0 on the dry slopes. Tables 2-4 support these trends.

Frick (1939) studied a south-facing-slope forest (fire disturbed) on the Highland Rim. It was located ca. 21 km northwest of Nashville close to Highway 12. He recorded Carya tomentosa, C. glabra, Quercus alba, and Q. velutina on the lower slope; Crataegus crusgalli, Fraxinus quadrangulata, Juniperus virginiana, Ulmus alata, and Viburnum rufidulum at midslope; and Castanea dentata, Oxydendrum arboreum, Sassafras albidum, Quercus marilandica, Quercus stellata, and Q. velutina on the upper slope. Most of these were observed on the dry slopes of Radnor Lake Natural Area, but the four most dominant taxa of this community type at the Natural Area (Acer saccharum, Celtis occidentalis, Quercus montana, and Fraxinum americana) were of little or no importance in the south-facing-slope forest studied by Frick (1939).

Comparing the top 10 taxa of trees in the dry-slope community of the northwestern Highland Rim in 1971 (Chester et al., 1995) with the top 10 taxa of trees in the dry-slope community at Radnor Lake Natural Area (1994) showed that *Acer saccharum*, *Carya ovata*, and *C. glabra* were common to both areas. Chester et al. (1995) reported a total density of 488 trees/ha for their dry-slope community in 1971, while, at Radnor Lake Natural Area, 526/ha in 1974 and 462/ha in 1994 were recorded.

Mesic-slope Forest Community—This community occurred on slopes with mostly northerly aspects (N20°E-N75°E). The average elevation of the mesic-slope plots was 271 m, and the average steepness of slope was 38.4%. Because they received less solar radiation than the south-facing slopes, soil moisture levels were probably greater and soil temperatures lower in this community.

Of the 22 taxa of trees in the larger-tree class, the dominant taxa on the mesic slopes included Acer saccharum, A. saccharum ssp. nigrum, Fraxinus americana, Quercus rubra, and Celtis occidentalis (Table 5). Of the 16 taxa in the small-tree class, the most important were Acer saccharum, A. saccharum ssp. nigrum, Asimina triloba, Aesculus flava, and Ulmus spp.

In the seedling class, 22 taxa were sampled, and the major taxa on the mesic slopes included Fraxinus americana, Ulmus spp., Acer spp., Celtis occidentalis, and Asimina triloba. The shrubs and vines were Vitis spp., Parthenocissus quinquefolia, Rhus radicans, Lonicera maackii, Bignonia capreolata, Lindera benzoin, Sambucus canadensis, Arundinaria gigantea, Ligustrum vulgare, Lonicera japonica, Smilax spp., and Staphylea trifolia.

Eickmeier (1988) studied a north-facing-slope forest stand (sampled area = 0.6 ha; elevational range of 300-350 m) at Radnor Lake Natural Area from 1976 to 1986. In 1986, the top 10 species (dbh ≥ 10.2 cm) were Acer saccharum (32.7), Fraxinus americana (12.8), Quercus rubra (11.0), Carya ovata (7.1), Carya glabra (5.9), Sassafras albidum (4.9), Celtis occidentalis (4.5), Ulmus spp. (3.8), Tilia americana (3.2), and Quercus muhlenbergii (3.1). A comparison with the 1994 results (Table 5) for trees in the same size class on four north-facing slopes

(sampled area = 0.4 ha) revealed much similarity. Eickmeier (1988) reported an IV for Acer saccharum (A. saccharum ssp. nigrum was probably included) of 32.7. As would be expected, this was midway between the 1974 IV of 24.4 and the 1994 IV of 39.8 for Acer saccharum (A. saccharum ssp. nigrum included) in the mesic-north-facing-slope community at Radnor Lake Natural Area. My 1994 data showed Fraxinus americana and Quercus rubra having an IV of 10.3 with the former increasing and the latter decreasing in IV from 1974 to 1994 (Table 3). These trends were corroborated by Eickmeier (1988). The 1974 and 1994 data showed an increase in dominance by Acer saccharum, accompanied by a decrease in IV for most other species. Eickmeier (1988) reported an increase in total basal area of 20.55 m²/ha (1976) to 21.39 m²/ha (1986) but a decrease in total density of 476.4 stems/ha (1976) to 412.5 stems/ha (1986). These trends also were consistent with the results of my studies of this community type at Radnor Lake Natural Area (Tables 3 and 5).

A comparison of the 10 most important taxa of trees in the mesic-slope community on the northwestern Highland Rim in 1971 (Chester et al., 1995) with the top 10 in the mesic-slope community at Radnor Lake Natural Area (1994) revealed only two species in common, A. saccharum and Q. rubra. Chester et al. (1995) reported a total density of 323 trees/ha for their mesic-slope community in 1971, while, at Radnor Lake Natural Area, 570 stems/ha in 1974 and 385.3 trees/ha in 1994 were recorded.

Ravine Forest Community—Ravines were shaded by adjacent slopes and received runoff and nutrients from upslope topography. The average elevation of the ravine plots was 255 m. The Arrington and Ocana soils were associated with this community.

Table 6 shows the 22 sampled taxa of the larger-tree class in the ravine community. The most important were Acer saccharum, Carya cordiformis, Celtis occidentalis, Quercus shumardii, and Tilia americana. Of the 17 sampled taxa in the small-tree class, those with the highest IVs were Acer saccharum, A. saccharum ssp. nigrum, Aesculus flava, Ostrya virginiana, and Ulmus spp.

Twenty-one taxa of tree seedlings were sampled in the ravine community (Table 2), and the major ones included Acer spp., Liriodendron tulipifera, Carya spp., Fraxinus americana, and Celtis occidentalis. The taxa of shrubs and vines were Vitis spp., Lindera benzoin, Bignonia capreolata, Rhus radicans, Lonicera maackii, Sambucus canadensis, Euonymus americana, Smilax spp., Bumelia lycioides, and Ligustrum vulgare.

In the ravine community, Acer saccharum increased in IV from 13.1 in 1974 to 23.7 in 1994, and A. saccharum ssp. nigrum increased from 3.3 to 4.9 in the 20-year period. These two taxa also were well represented in the small-tree and seedling categories; so, it is likely that these maples will continue to flourish in this community well into the future. The IV of Carya cordiformis increased from 9.8 (1974) to 10.4 (1994). It was well represented in the seedling class but less so in the small-tree class; thus, it may decline in importance as time goes on. The IV of Celtis occidentalis increased from 4.2 to 9.5, and this species was well represented in the smaller-size classes; so, it will likely remain a dominant indefinitely. Quercus shumardii increased in IV from 1974 to 1994, but it did not appear at all in the small-tree and seedling classes. It will likely remain a dominant for only a limited time because of its slight reproduction. Juglans nigra remained a dominant in the largertree class but was not represented at all in the small-tree class; thus, its importance in this community is expected to diminish in the future. Of interest was the decline in importance of the larger elms (Ulmus spp.) which had an IV of 25.1 in 1974 but only 0.9 in 1994; however, in the small-tree class, the elms remained an important group in the ravine community. The data in Tables 2, 3, and 6 substantiate these changes.

Comparing the 10 most important taxa of trees in the ravine community of the northwestern Highland Rim in 1971 (Chester et al.,

TABLE 2. Density (number of stems per hectare), occurrence (of 20 plots, 0.002 ha each), and importance value (IV), defined as (relative density + relative frequency)/2, for the taxa of tree seedlings (diameter at 1.37 m above ground < 2.5 cm) in each of five topographic community types at Radnor Lake Natural Area, Davidson Co., Tennessee, in 1994.

		Ridge			Dry slope	
Taxon	Density	Occurrence	IV	Density	Occurrence	IV
Acer negundo				25	1	0.6
Acer spp.1	275	5	3.5	1,125	14	13.9
Aesculus flava				,		
Ailanthus altissima	750	4	4.7			
Aralia spinosa	50	2	1.2			
Asimina triloba						
Carya spp. ²	650	9	6.8	225	5	3.8
Celtis laevigata						
Celtis occidentalis	575	8	6.1	1,850	13	17.9
Cercis canadensis	150	4	2.5	275	6	4.6
Cladrastis kentuckea	150	3	2.0			
Cornus florida				225	2	2.4
Diospyros virginiana	150	3	2.0	50	1	0.8
Fraxinus americana ³						
Fraxinus pennsylvanica ⁴						
Fraxinus quadrangulata ⁵	800	10	7.9	575	9	8.0
Gleditsia triacanthos	50	2	1.2			
Gymnocladus dioicus	25	1	0.6			
Juglans nigra	25	1	0.6			
Juniperus virginiana	25	1	0.6	75	3	1.9
Liriodendron tulipifera				100	4	2.6
Morus rubra	25	1	0.6	25	1	0.6
Ostrya virginiana				250	2	2.5
Prunus serotina	100	3	1.9	1,325	10	13.1
Quercus muhlenbergii	125	3	1.9	50	2	1.3
Quercus prinus	6,525	8	27.3	775	9	9.2
Quercus rubra	,					
Quercus shumardii						
Quercus stellata				25	1	0.6
Quercus velutina ⁶	325	5	3.7	150	5	3.4
Rhamnus caroliniana				50	2	1.3
Robinia pseudoacacia				50	2	1.3
Sassafras albidum	1,400	8	9.0	475	4	4.9
Tilia americana	100	3	1.9	-		
Ulmus spp. ⁷	1,575	11	11.1	300	4	3.8
Vaccinium arboreum	75	2	1.3		•	
Viburnum rufidulum	75	3	1.8	50	2	1.3
Total	14,000	100	100.0	8,050	102	100.0

¹Mostly Acer saccharinum on the lakeshore; A. saccharum (including ssp. nigrum) in ravines and on moist slopes; A. saccharum on dry slopes and ridges.

²Mostly Carya cordiformis in ravines and on moist slopes; primarily C. glabra on dry slopes and ridges.

³Includes a small percentage of *Fraxinus quadrangulata* on moist slopes and in ravines.

⁴Includes a few *Fraxinus americana* on the lakeshore.

⁵Includes a small percentage of *Fraxinus americana* on dry slopes and ridges.

⁶Includes a few *Quercus rubra* on dry slopes and ridges.

⁷Mostly *Ulmus americana* on the lakeshore, on mesic slopes, and in ravines; primarily *U. serotina* on dry slopes and ridges.

TABLE 2. Continued.

	Moist slope			Ravine			Lakeshore	
Density	Occurrence	IV	Density	Occurrence	IV	Density	Occurrence	IV
50	2	1.1				225	3	4.
1,100	14	10.3	2,400	15	16.0	1,650	11	22.2
50	2	1.1	100	3	1.7	_,	**	22.2
800	9	7.0	75	3	1.6			
1,050	8	7.6	875	4	5.2	75 0	4	9.4
250	8	4.4	1,025	14	10.0		•	7
						500	6	8.7
1,025	14	10.0	1,300	9	9.0	25	1	0.9
25	1	0.5	75	3	1.6	25	1	0.9
75	2	1.2	100	4	2.1		•	0.,
75	2	1.2	225	3	2.2	575	7	10.0
100	1	0.8	125	2	1.4	25	1	0.9
5,150	17	27.4	1,125	12	9.6	23	1	0.2
			,		5.0	250	6	6.5
			75	1	0.7			
100	3	1.7	75	3	1.6			
						50	2	1.9
150	1	1.0	1,550	12	11.3			
			25	1	0.5	25	1	0.9
800	8	6.6	1,300	6	7.8	875	10	14.8
75	3	1.6	100	3	1.7	175	4	4.4
50	2	1.1						
						275	8	8.2
50	1	0.6				325	2	4.3
50	2	1.1				3 2 3	2	7.0
25	1	0.5	475	6	4.4	25	1	0.9
25	1	0.5	75	2	1.1	43	1	0.9
1,700	13	12.2	1,050	8	7.6	25	1	0.9
25	ï	0.5	200	5	2.9			
2,800	116	100.0	12,350	119	100.0	5,800	69	100.0

TABLE 3. Importance values of taxa of trees (diameter at 1.37 cm above ground ≥ 10.2 cm) within each topographic community type and averaged importance values at Radnor Lake Natural Area, Davidson Co., Tennessee, in 1974 and 1994. Total number of taxa sampled and total number of stems per hectare given in parentheses for each community type.

	Rie	dge	Dry :	slope	Moist	slope
Taxon	1974 (15, 538)	1994 (21, 497)	1974 (18, 526)	1994 (16, 462)	1974 (19, 570)	1994 (22, 385)
Acer negundo						0.7
Acer rubrum		•				
Acer saccharinum				20.4	21.6	20.0
Acer saccharum		4.0	15.2	20.1	21.6	28.0
4. saccharum ssp. nigrum		÷	2.0		2.8	11.8
Aesculus flava			3.9		3.9	3.7
Ailanthus altissima		1.5	2.1			0.6
Carpinus caroliniana					10.5	
Carya cordiformis					10.5	2.7
Carya glabra	2.5	3.9	5.4	5.4		0.9
Carya laciniosa			, .			
Carya ovalis		1.5	1.4	7	4.0	20
Carya ovata	15.4	8.4	6.8	7.5	4.3	2.8
Celtis laevigata	1.2	0.7	1.7	10 -		1.0 6.1
Celtis occidentalis	4.3	6.5	1.9	13.6	6.6	0.1
Cercis canadensis	5.6				2.0	1.4
Cladrastis kentuckea	2.6	2.1			1.9	1.4
Cornus florida			1.1	2.0	0.9	
Diospyros virginiana						0.6
Fagus grandifolia						0.6
Fraxinus americana	10.5	2.4	3.9	9.5	5.0	10.3
Fraxinus pennsylvanica²						0.7
Fraxinus quadrangulata	16.5	14.7	8.7	7.8	•	0.7
Gleditsia triacanthos	,				2.4	
Gymnocladus dioicus		0.7				2.6
Juglans nigra					4.0	2.6
Juniperus virginiana		1.5				
Liriodendron tulipifera						
Morus rubra		0.7			1.0	
Nyssa sylvatica					1.8	
Ostrya virginiana						
Platanus occidentalis						
Populus deltoides						
Prunus serotina			2.4	4.2		
Quercus alba		0.7	2.4	1.2		
Quercus marilandica	1.2			4.0	2.0	3.5
Quercus muhlenbergii		3.6	4.8	4.0	3.8	3.5 2.6
Quercus montana	24.5	32.4	22.8	11.7	10.0	10.3
Quercus rubra			8.9	0.0	12.0	3.3
Quercus shumardii					2.4	5.5
Quercus stellata	1.4			2.2		2.4
Quercus velutina	2.8	4.3		0.9		2.4
Robinia pseudoacacia	2.1		3.3	6.8		
Salix nigra		_		2.2	2.0-	
Sassafras albidum		0.7		3.2	3.2-	1.7
Tilia americana	2.6	2.2		1.4	4.5	2.5
Ulmus spp.3	6.9	7.0	3.4	4.1	6.5	2.3
Viburnum rufidulum		0.7		0.7		

^{&#}x27;Importance value (IV) = (% density + % basal area + % frequency)/3.

²Includes a small percentage of *Fraxinus americana* in the lakeshore community.

³Consists mostly of *Ulmus serotina* on the dry ridges and dry slopes; *U. americana*, *U. rubra*, and *U. serotina* on moist slopes and in ravines; and primarily *U. americana* on the lakeshore.

TABLE 3. Continued.

Ray	vine	Lake	shore	Avera	ige IV
1974 (20, 583)	1994 (22, 356)	1974 (10, 741)	1994 (14, 726)	1974	1994
1.0	2.4	7.9	6.8	1.8	2.0
			1.0	0.0	0.2
		10.8	30.3	2.2	6.1
13.1	23.7		0.6	10.0	15.3
3.3	4.9			1.2	3.3
1.1	2.5			1.8	1.2
				0.4	0.3
_				0.0	0.1
9.8	10.4			4.1	2.6
				1.6	2.0
2.2	1.5			0.4	0.3
				0.3	0.3
				5.3	3.7
0.9		11.6	17.8	3.1	3.9
4.2	9.5		2.1	3.4	7.6
				1.5	0.0
1.1	1.9			1.1	1.1
	0.6			0.4	0.5
	1.0	4.8	4.5	1.0	1.1
• •				0.0	0.1
3.8	2.5	- ^		4.6	4.9
		7.0	9.8	1.4	2.0
2.6				5.0	4.6
2.6	0.8			1.0	0.2
0.0	. .			0.0	0.1
8.3	5.1			2.5	1.5
0.0	0.1			0.0	0.3
0.9	3.1	1.0		0.2	0.6
2.3		1.8		0.8	0.1
0.0				0.4	0.0
0.9	1.0	# A	2 7	0.2	0.0
	1.8	5.4	3.7	1.1	1.1
5.0	4.4	12.2	3.1	2.4	0.6
3.0	4.4			1.5	0.9
				0.5	0.4
3.3	2.9		1.4	0.2	0.0
3.3	۵.۶		1.4	2.4 9.5	3.1 9.3
4.0	1.6			9.3 5.0	9.3 2.4
7.3	8.0		2.1	2.0	2.4
7.0	0.0		2.1	0.3	0.0
				0.6	1.5
				1.1	1.4
		14.0	0.9	2.8	0.2
	4.4	1	0. 7	0.6	1.7
	6.1			1.4	2.3
25.1	0.9	24.7	15.7	13.3	6.0
				0.0	0.3

TABLE 4. Average dbh (diameter at 1.37 m above ground) for sampled stems ≥ 2.5 cm and density, basal area, occurrence (of 20 plots, 0.02 ha each), and importance value (TV) of small trees (dbh = 2.5-10.2 cm) and larger trees (dbh ≥ 10.2 cm) of the dry-slope forest community at Radnor Lake Natural Area, Davidson Co., Tennessee, in 1994.

	•		Small trees	trees			Larger trees	trees	
Taxon	Average dbh (cm)	Density (number/ha)	Basal area (m²/ha)	Occurrence	IV (100) ¹	Density (number/ha)	Basal area (m²/ha)	Occurrence	IV (100)
Acer saccharum	10.7	222.3	0.637	16	30.8	111.2	4.491	12	20.1
Celtis occidentalis	15.7	27.2	0.057	9	5.0	81.5	2.737	∞	13.6
Ouercus montana	26.7	12.4	0.034	m	2.6	32.1	4.176	7	11.7
Fraxinus americana	22.4	0.0	0.000	0	0.0	44.5	2.419	9	9.5
Fraxinus quadrangulata	13.5	24.7	0.09	4	4.9	51.9	1.242	5	7.8
Carya ovata	14.7	22.2	0.068	4	4.2	27.2	1.295	∞	7.5
Robinia pseudoacacia	34.8	0.0	0.000	0	0.0	19.8	2.098	S	8.9
Carya glabra	16.5	6.6	0.021	4	2.6	19.8	0.848	9	5.4
Ulmus spp. ²	6.4	133.4	0.301	∞	16.1	17.3	0.392	5	4.1
Quercus muhlenbergii	22.4	2.5	0.008	1	0.7	17.3	0.944	3	4.0
Sassafras albidum	10.7	24.7	0.046	. 7	3.0	19.8	0.609	2	3.2
Cornus florida	6.1	49.4	0.125	5	7.1	7.4	0.074	3	2.0
Tilia americana	29.7	2.5	0.010		0.7	2.5	0.531	 1	1.4
Quercus alba	24.9	0.0	0.00	0	0.0	4.9	0.269	-	1.2
Quercus velutina	30.0	0.0	0.00	0.	0.0	2.5	0.174		6.0
Viburnum rufidulum	5.1	22.2	0.030	7	2.5	2.5	0.041		0.7
Quercus rubra	2.8	7.4	0.004	3	1.7	0.0	0.000	0	0.0
Ailanthus altissima	9.9	2.5	0.008	-	0.7	0.0	0.000	0	0.0
Carya ovalis	4.3	2.5	0.004	1	9.0	0.0	0.000	0	0.0
Juniperus virginiana	5.1	34.6	0.071	4	4.8	0.0	0.000	0	0.0
Cercis canadensis	3.8	29.6	0.039	4	3.9	0.0	0.000	0	0.0
Ostrya virginiana	3.6	29.6	0.032	က	3.4	0.0	0.000	0	0.0
Rhamnus caroliniana	3.6	12.4	0.012	4	2.5	0.0	0.000	0	0.0
Nyssa sylvatica	6.1	2.5	0.007		0.7	0.0	0.000	0,	0.0
Aralia spinosa	3.8	2.5	0.003	1	9.0	0.0	0.000	0	0.0
Crataegus sp.	2.8	2.5	0.00	1	9.0	0.0	0.000	0	0.0
Total	11.93	679.3	1.618	. 62	100.0	461.9	22.340	74	100.0

 1 IV (100) = (% density + % basal area + % frequency)/3.

²Mostly Ulmus serotina. ³The average dbh for all 462 stems sampled in this community (area sampled = 0.4 ha) was 11.9 cm.

TABLE 5. Average dbh (diameter at 1.37 m above ground) for sampled stems ≥ 2.5 cm and density, basal area, occurrence (of 20 plots, 0.02 ha each), and importance value (IV) of small trees (dbh = 2.5-10.2 cm) and larger trees (dbh ≥ 10.2 cm) of the mesic-slope forest community at Radnor Lake Natural Area, Davidson Co., Tennessee, in 1994.

			Small trees	trees	-		Larger trees	trees	
Taxon	Average dbh (cm)	Density (number/ha)	Basal area (m²/ha)	Occurrence	IV (100) ¹	Density (number/ha)	Basal area (m²/ha)	Occurrence	IV (100)
Acer saccharum	10.2	242.1	0.681	18	51.1	168.0	7 656	6	0
A. saccharum ssp. niorum	13.6	37 1	0 122	2 5	77.7	100.0	4.020	8	78.0
Fraxing americana	37.4	1.70	0.124	01	12.3	51.9	1.843	13	11.8
Querous when	t: /6	0.0	0.00	0 (0.0	29.6	3.375	6	10.3
Guercus rubra	4.00	0.0	0.000	0	0.0	22.2	4.749	9	10.3
Celtis occidentalis	22.4	4.9	0.003	7	1.5	22.2	1.516	9	6.1
Aesculus Hava	12.9	27.2	0.047	∞	8.0	7.4	1.470	m	3.7
Quercus muhlenbergii	26.4	0.0	0.000	0	0.0	12.4	0.701	4	3. 6
Quercus shumardii	8.49	0.0	0.000	0	0.0	4.9	1.628	. 2	, c
Carya ovata	35.1	0.0	0.000	0	0.0	7.4	0.790	۱ (۳) C
Carya cordiformis	34.8	0.0	0.000	0	0.0	7.4	0.722	· «) (
Juglans nigra	33.3	0.0	0.000	0	0.0	7.4	0.678) (r	
Quercus montana	42.3	2.5	0.015	1	1.2	4.9	1.422	· —	5; C
Ulmus spp. ²	8.8	19.8	0.012	4	4.0	6.6	0.375	1 (7)	0.4 V
Quercus velutina	48.6	0.0	0.000	0	0.0	4.9	0.940	2	. 4 . 4
Illia americana	15.0	7.4	0.00	3	2.5	4.9	0.430	5 2	1.7
Cladrastis kentuckea	15.3	2.5	0.004	-	6.0	4.9	0.176	7	. 4
Celtrs laaevigata	38.4	0.0	0.000	0	0.0	2.5	0.285	-	1.0
carya glabra	36.3	0.0	0.000	0	0.0	2.5	0.256	-	60
Acer negundo	8.6 8.5	2.5	0.007	_	8.0	2.5	0.051		0.7
Fraxinus quadrangulata	16.5	0.0	0.000	0	0.0	2.5	0.053	· 🕶	0.7
Carpinus caroliniana	5.5	12.4	0.024		2.3	2.5	0.020	-	0.6
ragus grandifolia	10.2	0.0	0.000	0	0.0	2.5	0.020	-	90
Asimina triloba	3.5	59.3	0.052	'n	9.0	0.0	0.000	· C	0:0
Cornus florida	4.2	6.6	0.004	33	2.5	0.0	0000). C	0 0
Cercis canadensis	3.2	4.9	0.004	7	1.6	0.0	0.00	· C	200
Euonymus atropurpureus	2.5	2.5	0.001		0.8	0.0	0.00	o C	9 0
Liriodendron tulipifera	3.8	2.5	0.003		0.8	0.0	0000	o	9.0
Viburnum rufidulum	2.5	2.5	0.001	-	0.8	0.0	0.00	o c	9.0
Total	14.4³	439.7	0.984	62	100.0	385.3	26.157	, &	100.0
								1))

 1 IV (100) = (% density + % basal area + % frequency)/3.

²Ulmus alata, U. americana, U. rubra, and U. serotina. ³The average dbh for all 334 stems sampled in this community (area sampled = 0.4 ha) was 14.4 cm.

TABLE 6. Average dbh (diameter at 1.37 m above ground) for sampled stems ≥ 2.5 cm and density, basal area, occurrence (of 20 plots, 0.02 ha each), and importance value (IV) of small trees (dbh = 2.5-10.2 cm) and larger trees (dbh ≥ 10.2 cm) of the ravine forest community at Radnor Lake Natural Area, Davidson Co., Tennessee, in 1994.

			Small trees	trees	,		Larger trees	trees	
Taxon	Average dbh (cm)	Density (number/ha)	Basal area (m²/ha)	Occurrence	IV (100) ¹	Density (number/ha)	Basal area (m²/ha)	Occurrence	IV (100)
Acor cacharum	9.1	298.9	0.694	20	46.8	121.0	4.192	19	23.7
Carva cordiformis	25.0	4.9	0.00	 	1.0	42.0	2.762	∞	10.4
Coltis occidentalis	20.8	4.9	0.023	-	1.4	34.6	1.987	10	9.5
Ouercus shumardii	70.7	0.0	0.000	0	0.0	12.4	4.942	7	8.0
Tilia americana	31.8	2.5	0.003	1	0.7	17.3	2.125	5	6.1
Juglans nigra	34.7	0.0	0.000	0	0.0	14.8	1.436	'n	5.1
Acer saccharum ssp. nigrum	7.7	61.8	0.180	10	13.6	19.8	0.342	7	4.9
Prunus serotina	42.8	0.0	0.000	0	0.0	6.6	1.584	4	4.4
Sassafras albidum	34.5	0.0	0.000	0	0.0	14.8	1.489	ĸ	4.4
Liriodendron tulipifera	33.7	0.0	0.000	0	0.0	6.6	1.118	7	3.1
Ouercus muhlenbergii	16.0	2.5	0.002	1	0.7	6.6	0.346	4	2.9
Fraxinus americana	23.2	2.5	9000	-	0.8	7.4	0.566	æ	2.5
Aesculus flava	8.9	61.8	0.122	6	11.5	7.4	0.507	æ	2.5
Acer negundo	17.8	4.9	0.014	7	1.7	7.4	0.416	m	2.4
Cladrastis kentuckea	26.2	2.5	0.002	1	0.7	4.9	0.568	7	1.9
Platanus occidentalis	71.1	0.0	0.000	0	0.0	2.5	0.981		1.8
Ouercus rubra	62.7	0.0	0.000	0	0.0	2.5	0.764		1.6
Carva laciniosa	24.4	0.0	0.000	0	0.0	4.9	0.258	2	1.5
Diospyros virginiana	40.1	0.0	0.000	0	0.0	2.5	0.312	-	1.0
$Ulmus spp.^2$	0.9	17.3	0.030	7	5.3	4.9	0.054	-	6.0
Gleditsia triacanthos	29.2	0.0	0.000	0	0.0	2.5	0.166		8.0
Cornus florida	6.2	19.8	0.047	4	4.5	2.5	0.025	-	9.0
Ostrva virginiana	4.2	49.4	0.077	4	7.1	0.0	0.000	0	0.0
Asimina triloba	5.1	4.9	0.013	7	1.6	0.0	0.000	9	0.0
Carpinus caroliniana	7.6	2.5	0.011		1.0	0.0	0.000	0	0.0
Fagus grandifolia	6.4	2.5	0.008		6.0	0.0	0.000	0	0.0
Viburnum rufidulum	2.5	2.5	0.001	-	0.7	0.0	0.000	0	0.0
Total	13.5³	545.9	1.242	<i>L</i> 9	100.0	355.7	26.939	&	100.0

¹IV (100) = (% density + % basal area + % frequency)/3. ²Ulmus alata, U. americana, U. rubra, and U. serotina.

³The average dbh for all 365 stems sampled in this community (area sampled = 0.4 ha) was 13.5 cm.

1995) with the top 10 taxa of trees in the ravine community at Radnor Lake Natural Area (1994) revealed that *Acer saccharum*, *Carya cordiformis*, and *Liriodendron tulipifera* were common to both areas. Chester et al. (1995) reported a total density of 303 trees/ha for ravine forests of the northwestern Highland Rim in 1971, while, at Radnor Lake Natural Area, 583 trees/ha (1974) and 355.7 trees/ha (1994) were recorded.

Lakeshore Forest Community—This community consisted primarily of flood-tolerant trees that germinated after 1914 (the date of stream impoundment). The lakeshore plots varied in elevation from 236 (spillway elevation) to 237 m. Arrington was the soil associated with this community.

Table 7 shows only 14 taxa in the larger-tree category were sampled on the lakeshore. The dominants included Acer saccharinum, Celtis laevigata, Ulmus spp. (mostly U. americana), Fraxinus spp. (mostly F. pennsylvanica), and Acer negundo. Of the 21 sampled taxa in the small-tree class, the most significant were Acer saccharinum, Celtis laevigata, Ulmus spp., Acer negundo, Fraxinus spp., and Quercus shumardii.

Of the 17 sampled taxa of tree seedlings in the lakeshore community, the most important were Acer saccharinum, Prunus serotina, Cornus florida, Asimina triloba, and Celtis laevigata (Table 2). The taxa of shrubs and vines were Rhus radicans, Lonicera maackii, Lonicera japonica, Lindera benzoin, Ligustrum vulgare, Campsis radicans, Euonymus americana, Rubus argutus, Bignonia capreolata, Rosa spp., Symphoricarpos orbiculatus, Parthenocissus quenquefolia, Smilax spp., Arundinaria gigantea, and Euonymus atropurpureus.

From 1974 to 1994, drastic changes in forest composition occurred in the lakeshore community at Radnor Lake Natural Area. IV increased from 10.8 to 30.3 for *Acer saccharinum* and from 11.6 to 17.8 for *Celtis laevigata*. The IV for *Fraxinus* spp. (mostly *F. pennsylvanica*) increased from 7.0 to 9.8. These taxa will probably retain their dominance in this community for the foreseeable future, because they also were well represented in the small-tree and seedling classes in 1994. Certain taxa decreased greatly in IV. *Salix nigra* decreased from 14.0 to 0.9, *Populus deltoides* decreased from 12.2 to 3.1, and *Ulmus* spp. (mostly *U. americana*) decreased from 24.7 to 15.7. These trends are supported by the data in Tables 2, 3, and 7.

The 1971 streambank community of the northwestern Highland Rim (Chester et al., 1995) was similar in composition to the 1994 lakeshore community at Radnor Lake Natural Area. Six taxa were dominants in both areas: Acer saccharinum; Acer negundo; Celtis occidentalis; Platanus occidentalis; Populus deltoides; Ulmus spp. A total density of 470 trees/ha was reported for the streambank community of the northwestern Highland Rim (1971), while 741 (1974) and 726 stems/ha (1994) were recorded for the lakeshore community at Radnor Lake Natural Area.

CONCLUSIONS

Radnor Lake Natural Area is home to a rich flora, including some species that are generally rare in Middle Tennessee, such as *Kalmia latifolia*, *Aesculus flava*, *Cladrastis kentuckea*, and *Gymnocladus dioicus*. There is a mosaic of forest communities at Radnor Lake Natural Area, and it appears that they are arrayed along a moisture gradient that is affected strongly by topography. Other major influences have been climate, soils, diseases, and human disturbances prior to 1973, such as clearing of the lowlands for agriculture, logging, fires, and the dam construction in 1914.

In the summer of 1994, 100 plots, each with an area of 0.02 ha, were established in five different forest-community types at Radnor Lake Natural Area, and a total of 2,293 stems (dbh \geq 2.5 cm) was sampled. In addition, 2,120 tree seedlings were sampled in 100 nested plots (each with an area of 0.002 ha). The results of this study were compared with

an earlier study (1974) to ascertain successional trends in the forest communities. In 20 years, significant changes in IV for some species of trees occurred in all community types.

Comparing the composition of communities at Radnor Lake Natural Area with topographically similar communities on the northwestern Highland Rim revealed that, generally, there was a greater representation by such mixed-mesophytic species as Acer saccharum, Aesculus flava, and Tilia americana in the forests at the Natural Area, while there was better representation of the more xerophytic Quercus and Carya species in the forests of the northwestern Highland Rim. Another difference was that Celtis occidentalis, a species common in the Central Basin, was much more important at the Natural Area.

My results were in agreement with those of Eickmeier (1988). He concluded that, in a 10-year period (1976-1986), only Acer saccharum and Fraxinus americana showed significant increases in IV (for trees with a dbh \geq 10.2 cm) on a north-facing hillside at Radnor Lake Natural Area and that most other species declined in IV in that community. Data from my 20-year study (1974-1994) of four stands representing the north-facing (mesic) slope community at Radnor Lake Natural Area showed a similar trend. Eickmeier (1988) reported a decrease in total density in the north-facing slope community of 13.4%. My study from 1974 to 1994 showed a 32.5% decrease of density in this community type. I found that Acer saccharum had attained greater importance on the ridges and south-facing slopes as well as on the north-facing slopes and in ravines, but it had not yet invaded the Acer saccharinumdominated lakeshore community as an overstory species by 1994. Fig. 2 shows how much the overall IV of the maples increased from 1974 to 1994 relative to the other major genera. I concur with the opinion of Eickmeier (1988) and Kettler et al. (1990) that A. saccharum increases in importance when protected from periodic disturbances such as fire and logging.

A review of other long-term studies on forest dynamics in protected mature forests (Boggess and Bailey, 1964; Weaver and Ashby, 1971; Abrell and Jackson, 1977; Parker and Leopold, 1983) shows only two changes common to all, an increase in the total basal area and a rise in the importance value of *Acer saccharum*. Change in total density varied; it increased in the Illinois forest (10-year study) analyzed by Weaver and Ashby (1971) and in the Indiana forest (50-year study) studied by Parker and Leopold (1983), but density decreased in the Illinois forest (35-year study) examined by Boggess and Bailey (1964) and in the Indiana forest (10-year study) analyzed by Abrell and Jackson (1977).

At Radnor Lake Natural Area, from 1974 to 1994, total density of stems diminished in all five community types with the greatest decrease in the ravine community (38.9%) and the least in the lakeshore community (2.0%). One contributing factor to the large decrease in total density in the ravine and mesic-slope communities was the death of many of the larger elms. In 1971 on the northwestern Highland Rim, Chester et al. (1995) found a higher total density in the xeric-ridge and dry-slope communities than in the mesic-north-facing-slope and ravine communities.

At Radnor Lake Natural Area in 1994, total basal area was highest in the ridge community, was intermediate in the slope and ravine communities, and was least in the relatively young lakeshore community. On the northwestern Highland Rim in 1971, Chester et al. (1995) found that total basal area was higher in the mesic-slope and ravine communities than in the dry-slope and ridge communities.

At Radnor Lake Natural Area in 1974, species richness was greatest in the ravine and mesic-slope communities, intermediate in the dry-slope and ridge communities, and least in the lakeshore community. This also was the pattern in 1994. The presence of sampled and unsampled taxa of trees in the various communities of the Natural Area in 1974 was documented by Carpenter et al. (1976). The only observed changes in presence were the complete disappearance of *Quercus*

TABLE 7. Average dbh (diameter at 1.37 m above ground) for sampled stems ≥ 2.5 cm and density, basal area, occurrence (of 20 plots, 0.02 ha each), and importance value (IV) of small trees (dbh = 2.5-10.2 cm) and larger trees (dbh ≥ 10.2 cm) of the lakeshore forest community at Radnor Lake Natural Area, Davidson Co., Tennessee, in 1994.

			Small trees	trees			Larger trees	trees	
Taxon	Average dbh (cm)	Density (number/ha)	Basal area (m²/ha)	Occurrence	IV (100) ¹	Density (number/ha)	Basal area (m²/ha)	Occurrence	IV (100)
A con a cool of contrast	13.0	3,992	0.583	18	29.2	274.2	2.235	. 71	30.3
Acer succina numi	12.2	128.4	0.316	11	15.5	153.1	1.045	15	17.8
Ceuts they guid	15.2	64.2	0.195	: 21	10.6	111.2	0.879	17	15.7
Cumus spp. Frazinus sm 3	19.6	37.1	0.076	,∞	5.7	59.3	0.674	10	8.6
Acer neoundo	11.9	69.2	0.149	12	6.6	42.0	0.381	∞	6.8
Diosnoros viroiniana	27.4	2.5	0.007		9.0	22.2	0.262	9	4.5
Platanus occidentalis	17.5	14.8	0.032	5	2.9	14.8	0.175	9	3.7
Ponulus deltoides	61.2	0.0	0.000	0	0.0	6.6	0.241	4	3.1
Coltis occidentalis	12.7	0.0	0.000	0	0.0	6.6	0.050	4	2.1
Ouercus shumardii	11.7	37.1	0.046	∞	5.1	7.4	0.209	7	2.1
Ouercus muhlenheroii	6.7	22.2	0.040	5	3.4	7.4	0.073	7	1.4
Keer ruhrum	18.0	0.0	0.000	0	0.0	7.4	0.053	-	1.0
Salix niora	32.0	0.0	0.000	0	0.0	4.9	0.063		0.9
Acer saccharum	5.3	39.5	0.072	4	4.5	2.5	0.017	-1	9.0
Acimina triloha	80,	24.7	0.038	4	3.1	0.0	0.000	0	0.0
Cormus florida	4.1	19.8	0.032	4	2.8	0.0	0.000	0	0.0
Sassafras albidum	4.1	12.4	0.020	e	1.9	0.0	0.000	0	0.0
Ostrva virginiana	6.1	4.9	0.012		8.0	0.0	0.000	0	0.0
Prums seroting	5.3	4.9	0.011	-	0.8	0.0	0.000	0	0.0
Carva cordiformis	2.5	2.5	0.003	_	0.5	0.0	0.000	0	0.0
Carva ovata	2.8	2.5	0.003		0.5	0.0	0.000	0	0.0
Hex onaca	5.3	2.5	0.005	-	0.5	0.0	0.000	0	0.0
Iminerus viroiniana	5.3	2.5	0.005	-	0.5	0.0	0.000	0	0.0
I iriodendron tulinifera	5.1	2.5	0.005	-	0.5	0.0	0.000	0	0.0
Morus rubra	5.8	2.5	9000	-	0.5	0.0	0.000	0	0.0
Total	13.54	763.2	1.655	103	100.0	726.2	6.356	\$	100.0

 1 IV (100) = (% density + % basal area + % frequency)/3.

²Mostly Ulmus americana.

³Mostly Fraxinus pennsylvanica.

The average dbh for all 603 stems sampled in this community (area sampled = 0.4 ha) was 13.5 cm.

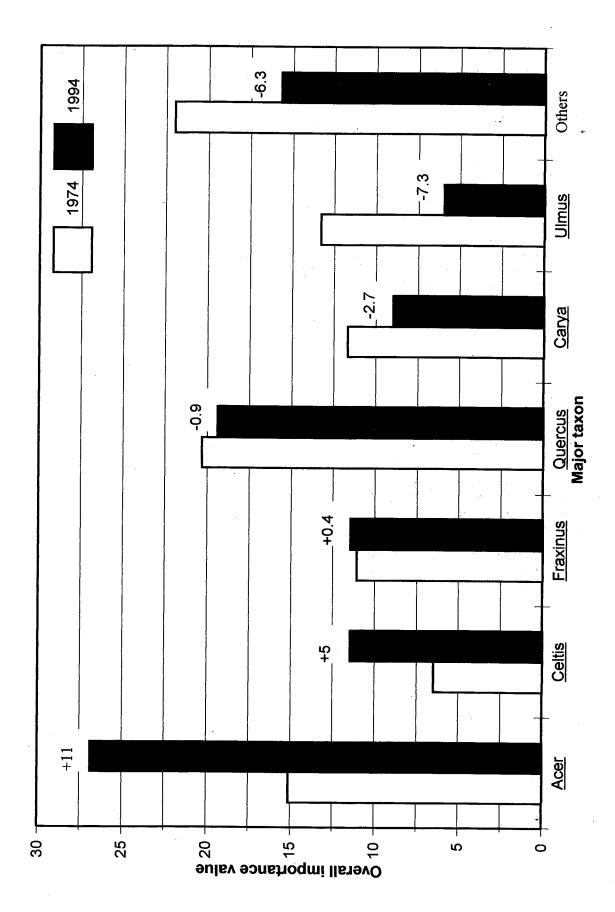


FIG. 2. Overall importance value (average for all community types) of each major taxon at Radnor Lake Natural Area, Davidson Co., Tennessee, and change in importance value over time for each taxon.

marilandica from the Natural Area by 1994 and the presence in 1994 of four species that were not observed in 1974: one 25-year-old specimen of *Pinus virginiana* in a cedar-hardwood community; two *Ilex opaca* seedlings in the lakeshore and young cedar-hardwood communities; three *Acer rubrum* saplings in the lakeshore community; several specimens of *Cornus drummondii* in a cedar-hardwood community. In my 1974 and 1994 studies combined, I sampled or observed a total of 64 species of trees and 24 taxa of shrubs and woody vines at Radnor Lake Natural Area.

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LITERATURE CITED

- ABRELL, D. B., AND M. T. JACKSON. 1977. A decade of change in an old-growth beech-maple forest in Indiana. Amer. Midland Nat., 98:22-32.
- BOGGESS, W. R., AND L. W. BAILEY. 1964. Brownfield Woods, Illinois: woody vegetation and changes since 1925. Amer. Midland Nat., 71:392-401.
- BRAUN, E. L. 1950. Deciduous forests of eastern North America. Hafner Publishing Company, New York.
- BRYANT, W. S., W. C. MCCOMB, AND J. S. FRALISH. 1993. Oakhickory forests (western mesophytic/oak-hickory forests). Pp. 143-201 in Biodiversity of the southeastern United States, upland terrestrial communities (W. H. Martin, S. G. Boyce, and A. C. Echternacht, eds.). John Wiley & Sons, New York.
- CARPENTER, L., J. TURNER, AND J. SCHIBIG. 1976. Forest communities of the Radnor Lake Natural Area, Davidson County, Tennessee. J. Tennessee Acad. Sci., 51:68-72.

- CHESTER, E.W., R. J. JENSEN, AND J. SCHIBIG. 1995. Forest communities of Montgomery and Stewart counties, northwestern Middle Tennessee. J. Tennessee Acad. Sci., 70:82-89.
- EICKMEIER, W. G. 1988. Ten years of forest dynamics at Radnor 1. Lake, Tennessee. Bull. Torrey Bot. Club, 115:100-107.
- FENNEMAN, N. M. 1938. Physiography of eastern United States. McGraw-Hill Book Company, Inc., New York.
- FRICK, T. A. 1939. Slope vegetation near Nashville, Tennessee. J. Tennessee Acad. Sci., 14:342-420.
- KETTLER, S., J. FRALISH, AND F. CROOKS. 1990. Forest succession patterns at Land Between The Lakes, Kentucky and Tennessee. Proceedings of the third annual symposium on the natural history of lower Tennessee and Cumberland river valleys. Center for Field Biology, Austin Peay State Univ., Clarksville, Tennessee.
- MCCALL, T. 1975. Master plan for Radnor Lake Natural Area, Davidson County, Tennessee. Tennessee Dept. Conserv., Nashville, Tennessee.
- MILLER, R. A. 1974. The geologic history of Tennessee. Tennessee Div. Geol., Bull., 74:1-63.
- PARKER, G. W., AND D. J. LEOPOLD. 1983. Replacement of *Ulmus americana* L. in a mature east-central Indiana woods. Bull. Torrey Bot. Club, 110:482-488.
- UNITED STATES DEPARTMENT OF AGRICULTURE. 1981. Soil survey of Davidson County, Tennessee. US Government Printing Office, Washington.
- WEAVER, G. T., AND W. C. ASHBY. 1971. Composition and structure of an old-growth forest remnant in unglaciated southwestern Illinois. Amer. Midland Nat., 86:46-56.
- WILSON, C. W., AND R. A. MILLER. 1972. Geologic map of the Oak Hill Quadrangle, Tennessee. Tennessee Div. Geol., Tennessee Dept. Conserv., Nashville, Tennessee.
- WISER, C. W. 1956. A comparative limnological study of Marrowbone and Radnor lakes in Central Tennessee. PhD dissert., Vanderbilt Univ., Nashville, Tennessee.
- WOFFORD, B. E., AND R. KRAL. 1993. Checklist of the vascular plants of Tennessee. Sida, Bot. Miscellany, 10:1-66.