

TWENTY-FIVE YEARS OF FOREST SUCCESSION IN HAPPY VALLEY, JEFFERSON COUNTY, INDIANA

Lindsay Betz and Paul C. MacMillan: Department of Biology, Hanover College,
Hanover, Indiana 47243 USA

ABSTRACT. In April 1974 a tornado severely damaged the sugar maple/Ohio buckeye forest in Happy Valley, Jefferson County, Indiana. Virtually all canopy trees were destroyed or damaged. In the fall of 1974, the forest was sampled on three transects across the valley. The most damaged portion of the valley forest was characterized as a sugar maple/white oak spp./white ash community. Seven years later the forest was sampled on the same transects, and the most damaged part was described as a sugar maple/elm spp./Ohio buckeye/redbud community. Fifteen years after the tornado the forest was sampled on the same transects, and the most damaged part was described as a sugar maple/slippery elm community. Twenty and twenty-five years after the tornado the most damaged portion of the forest is still a sugar maple/slippery elm community, with chinkapin oak, Ohio buckeye, American basswood, white ash and hackberry of secondary importance. The less damaged portion of the valley is dominated by sugar maple, with black walnut, box-elder, white ash, slippery elm and red oak of secondary importance. Important changes in overall forest structure that occurred between 20 and 25 years after the tornado are described, and predictions of future changes are included.

Keywords: Forest composition, forest structure, Jefferson County, Indiana, oaks, Ohio buckeye, secondary succession, slippery elm, sugar maple

Temperate forests in the midwestern United States have been subjected to natural disturbances since they evolved. One dramatic cause of such disturbance is tornadic winds. On the afternoon of 3 April 1974, a series of tornadoes ripped across Indiana. One traveled through the town of Hanover, traversed the Hanover College campus, and continued northeast across the adjacent wooded Happy Valley creating extensive damage. The tornado left nine people dead in the county and damaged nearly every building on the college campus (Larking 1974; Anonymous 1974).

Bailey and MacMillan (1977) completed a census of the Happy Valley forest in the fall of 1974 and found that 90% of the canopy vegetation was removed and approximately one-third of the trees (dbh \geq 5 cm) had been destroyed. The valley floor was so littered with logs that one was forced to climb over them. Forest destruction was most severe at the northern end of the Valley. Destruction of the canopy allowed sunlight to reach the forest floor, which in turn supported abundant herbaceous plant growth. Within a few years, woody shrubs and tree saplings emerged

above the piles of fallen stems and branches; and many of the damaged standing stems branched profusely and leafed out. After seven years (1981), emergent trees began to form a canopy creating an environment that supported more shade tolerant plants (Martin & MacMillan 1982).

Data on the Happy Valley forest, gathered before the tornado of 1974, was not systematically collected; but it suggested that the forest had been a sub-climax, sugar maple/Ohio buckeye community. The summer following the tornado, Bailey & MacMillan (1977) established three west-to-east transects across the valley to census the forest. They found the remaining forest to be composed primarily of sugar maple. White ash, elm spp. and white oak spp. were of secondary importance, while Ohio buckeye was a very minor component of the forest. Prior to and since the tornado, sugar maple is the dominant species. However, many changes have taken place in the sub-dominant or secondary tree species since the tornado. Seven years later (1981), the same three transects were recensused. The dominant species in the most severely dam-

aged (northern) portion of the valley was sugar maple, with Ohio buckeye and slippery elm of secondary importance. In the less disturbed (southern) portion of the valley, sugar maple was by far the most dominant tree with white ash, white oak spp., and box-elder of secondary importance (Martin & MacMillan 1982). In 1989, 15 years after the tornado, the valley forest was described as a sugar maple/slippery elm community (MacMillan 1996). American basswood, black maple and sycamore were of secondary importance in the more damaged (northern) part of the valley, while black walnut, white ash, northern red oak, and box-elder were of secondary importance in the less damaged (southern) portion of the valley.

The objectives of this present study were to (1) describe the composition and structure of the Happy Valley forest 20 and 25 years after the tornado of 1974, (2) compare the current valley forest composition and structure with the predictions made 15 years after the tornado, and (3) predict future changes in the forest composition and structure.

STUDY SITE

Happy Valley is located at 38°43'N and 85°27'W, just east of the Hanover College campus, in Jefferson County, Indiana. The valley contains a small intermittent stream that drains from the northwest to the southeast and empties into the Ohio River. The east- and west-facing sides descend steeply (25–50% slope) *ca.* 250 ft (75 m) to a narrow valley floor. The wooded valley slopes are composed of Eden-Caneyville soils, and the valley floor is composed of Dearborn channery silt loam soils (Nickell 1985). Three west-to-east transects were laid out in 1974. These transects have been used in each subsequent survey (Fig. 1). Transects 1 and 2 are located in the more severely damaged north and central areas of the valley, Transect 3 is in the less-damaged southern portion.

METHODS

The point-center-quarter method described by Cottam & Curtis (1956) was used to sample the trees at 15 m intervals along each of three transects. Transect 1 (northern) is 345 m long and included 92 trees (23 points); Transect 2 (middle) is 405 m long and included 109 trees (27 points); Transect 3 (southern) is 390 m long and included 104 trees (26 points).

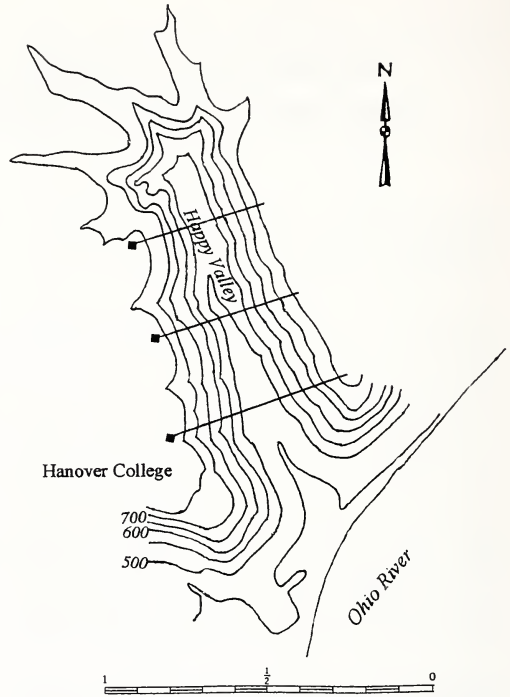


Figure 1.—Map of Happy Valley, Jefferson County, Indiana, showing the location of the three transects described in the text. Transect 1 is at the top, Transect 3 is at the bottom. Contour interval is 50 feet (~ 15 meters).

Data collected in the field included diameter at breast height (dbh) in cm, point-to-tree distance in meters, tree species, and any notes that might prove to be important such as the death of a previously measured tree along the transect line. Relative density, relative frequency, and relative dominance were calculated for each species using the methods of Cox (1990), and those values were summed to determine importance values. Finally, comparisons were made using Sorenson's quotient of similarity (Brower et al. 1990) and the Bray & Curtis (1957) similarity index. Sorenson's quotient of similarity was calculated as:

$$CC_S = 2C/(s_1 + s_2)$$

where C is the number of species common to both sites, s_1 is the number of species at site 1, and s_2 is the number of species at site 2. The Bray & Curtis similarity index was calculated as:

$$CC_B = (2W/(a + b)) 100$$

where W is the sum of the lower importance values for those species which are common to both sites, a is the sum of importance values

Table 1.—Characteristics of the Happy Valley forest on transect 1 (northern portion) twenty years after the tornado.

Species	Relative density	Relative frequency	Relative dominance	Importance value
Sugar maple <i>Acer saccharum</i> Marsh	31.25	27.02	29.17	87.44
Slippery elm <i>Ulmus rubra</i> Muhl.	29.17	28.37	18.07	75.61
American basswood <i>Tilia americana</i> L.	9.38	12.16	14.00	35.54
Redbud <i>Cercis canadensis</i> L.	10.42	8.11	4.10	22.63
Sycamore <i>Platanus occidentalis</i> L.	1.04	1.35	19.90	22.29
Chinkapin oak <i>Quercus muehlenbergii</i> Engelm.	4.16	5.40	2.72	12.28
Ohio buckeye <i>Aesculus glabra</i> Willd.	3.12	4.05	1.63	8.80
White ash <i>Fraxinus americana</i> L.	3.12	4.05	1.37	8.54
Hackberry <i>Celtis occidentalis</i> L.	3.13	2.70	0.75	6.58
Bitternut hickory <i>Carya cordiformis</i> (Wangenh.) K. Koch	1.04	1.35	3.82	6.21
Chokecherry <i>Prunus virginiana</i> L.	2.08	2.70	0.54	5.32
Royal paulownia <i>Paulownia tomentosa</i> (Thumb.) Sieb. & Zucc.	1.04	1.35	2.60	4.99
Northern red oak <i>Quercus rubra</i> L.	1.04	1.35	1.44	3.83
			Sum	300.06

for all the species at site 1, and b is the sum of importance values for all the species at site 2.

RESULTS

These results are from the censuses in 1994 and 1999 (20 and 25 years after the tornado, respectively). Complete transect data by diameter classes for the 1994 and 1999 censuses were reported by Betz (unpubl. report). This report is a summary of the transect data collected in 1994 and 1999. Data by diameter classes can be found in Betz's report available in the Hanover College Library.

Composition of the forest after 20 years (1994).—On Transect 1, across the northern portion of the valley, sugar maple and slippery elm were the dominant trees (importance values 87 and 76, respectively) based on their large relative density, frequency, and dominance (i.e., dbh) (Table 1). American basswood, redbud and sycamore were of secondary importance (importance values 36, 23 and

22, respectively). The frequency and diameter of basswood contributed to its importance value. The importance value of redbud was due to its density and frequency. There was one large sycamore, with a badly damaged top, accounting for its importance. Eight other species, including chinkapin oak, Ohio buckeye, white ash, and hackberry, had lower importance values (Table 1).

On Transect 2, across the middle portion of the valley, sugar maple was the dominant tree (importance value 101) and slippery elm ranked second (importance value 64), again due to their large relative density, frequency, and dominance (Table 3). Trees of secondary importance included chinkapin oak, Ohio buckeye, white ash, box-elder, and hackberry (importance values 33, 26, 18, 14, and 11, respectively). The large diameter of a few chinkapin oaks contributed to its importance value. The importance value of Ohio buckeye was due to many small-diameter stems. Nine

Table 2.—Characteristics of the Happy Valley forest on transect 1 (northern portion) twenty-five years after the tornado.

Species	Relative density	Relative frequency	Relative dominance	Importance value
Sugar maple <i>Acer saccharum</i> Marsh	34.05	35.00	41.58	110.63
Slippery elm <i>Ulmus rubra</i> Muhl.	25.54	23.75	18.86	68.15
American basswood <i>Tilia americana</i> L.	10.63	10.00	14.42	35.05
Chinkapin oak <i>Quercus muehlenbergii</i> Engelm.	5.32	6.25	7.94	19.51
Redbud <i>Cercis canadensis</i> L.	8.51	7.50	2.85	18.86
Ohio buckeye <i>Aesculus glabra</i> Willd.	5.32	5.00	3.04	13.36
Hackberry <i>Celtis occidentalis</i> L.	3.19	3.75	1.58	8.52
White ash <i>Fraxinus americana</i> L.	2.12	2.50	1.17	5.79
Bitternut hickory <i>Carya cordiformis</i> (Wangenh.) K. Koch	1.06	1.25	3.35	5.66
Royal paulownia <i>Paulownia tomentosa</i> (Thumb.) Sieb. & Zucc.	1.06	1.25	2.66	4.97
Tulip tree, Yellow poplar <i>Liriodendron tulipifera</i> L.	1.06	1.25	1.20	3.51
Northern red oak <i>Quercus rubra</i> L.	1.06	1.25	1.15	3.46
Chokecherry <i>Prunus virginiana</i> L.	1.06	1.25	0.21	2.52
			Sum	299.99

other species, including red oak, black walnut, and American basswood, had lower importance values (Table 3).

On Transect 3, across the southern end of the valley, sugar maple was the dominant tree (importance 105) with large relative density, frequency, and dominance values (Table 5). Of secondary importance were box-elder, black walnut, white ash, and slippery elm (importance values 31, 31, 30, and 28, respectively). The importance of box-elder and white ash was due to their many small-diameter stems. The importance of black walnut and slippery elm was due to a few large-diameter stems. Ten other species, including chinkapin oak, red oak, Ohio buckeye, and pawpaw, had lower importance values (Table 5).

In 1994, twenty years after the tornado, Transects 1 & 2 (the more damaged part of the valley) remained a sugar maple/slippy elm community with chinkapin oak, Ohio

buckeye, basswood, and white ash of secondary importance (Table 7).

Composition of the forest after 25 years (1999).—On Transect 1, sugar maple was the dominant species (importance 111) due to large relative density, frequency, and dominance values (Table 2). Slippery elm was second in importance (68) due to fewer large-diameter trees. American basswood, chinkapin oak, redbud, and Ohio buckeye were of secondary importance (importance values 35, 20, 19, and 13, respectively). The importance of basswood was due to rapid growth of many stems. Chinkapin oak importance was due to its relative dominance. The importance of redbud and Ohio buckeye was due to their many small-diameter stems. Seven other species, including hackberry, white ash, and bitternut hickory, had lower importance values (Table 2).

On Transect 2, the importance value of sugar maple (124) was twice that of slippery elm (62) (Table 4). Large relative density, frequen-

Table 3.—Characteristics of the Happy Valley forest on transect 2 (middle portion) twenty years after the tornado.

Species	Relative density	Relative frequency	Relative dominance	Importance value
Sugar maple <i>Acer saccharum</i> Marsh	36.69	30.68	33.82	101.19
Slippery elm <i>Ulmus rubra</i> Muhl.	23.85	22.74	17.28	63.87
Chinkapin oak <i>Quercus muehlenbergii</i> Engelm.	5.51	6.83	20.23	32.57
Ohio buckeye <i>Aesculus glabra</i> Willd.	10.09	11.37	4.84	26.30
White ash <i>Fraxinus americana</i> L.	5.50	6.82	5.26	17.58
Box-elder <i>Acer negundo</i> L.	4.58	5.68	3.71	13.97
Hackberry <i>Celtis occidentalis</i> L.	3.67	3.42	4.03	11.12
Northern red oak <i>Quercus rubra</i> L.	0.92	1.14	5.52	7.58
Black walnut <i>Juglans nigra</i> L.	0.92	1.14	3.75	5.81
American basswood <i>Tilia americana</i> L.	1.83	2.27	0.15	4.25
Pawpaw <i>Asimina triloba</i> (L.) Dunal	1.83	2.27	0.11	4.21
Eastern hop hornbeam <i>Ostrya virginiana</i> (Mill.) K. Koch	0.92	1.14	0.59	2.65
Sycamore <i>Platanus occidentalis</i>	0.92	1.14	0.42	2.48
Osage orange <i>Maclura pomifera</i> (Raf.) Schneid.	0.92	1.14	0.16	2.22
Black cherry <i>Prunus serotina</i> Ehrh.	0.92	1.14	0.09	2.15
White mulberry <i>Morus alba</i> L.	0.92	1.14	0.05	2.11
			Sum	300.06

cy, and dominance values provide the high importance value of sugar maple. Slippery elm values were smaller, and there were fewer large-diameter trees. Of secondary importance were Ohio buckeye, chinkapin oak, white ash, and box-elder (importance values 24, 22, 16, and 15, respectively). The importance of Ohio buckeye was due to many small-diameter stems. A few larger-diameter stems of chinkapin oak contributed to its importance. Eight other species, including hackberry, red oak, black walnut, and American basswood, had lower importance values (Table 4).

On Transect 3, the importance value of sugar maple was 98 (Table 6). Of secondary importance were black walnut, box-elder, white

ash, slippery elm, and red oak (importance values 34, 28, 26, 24, and 24, respectively). The importance of box-elder and ash was due to the rapid growth of many small stems. The importance of walnut, slippery elm, and red oak was due to a few larger-diameter stems. Ohio buckeye and chinkapin oak had lower importance values on this transect. Seven other species, including black maple, hackberry, and Osage orange, had lower importance values (Table 6).

Tables 7 and 8 contain data combined from the more heavily damaged northern and middle portions of the valley (Transects 1 and 2) collected 20 and 25 years after the tornado, respectively. These data show changes that

Table 4.—Characteristics of the Happy Valley forest on transect 2 (middle portion) twenty-five years after the tornado.

Species	Relative density	Relative frequency	Relative dominance	Importance value
Sugar maple <i>Acer saccharum</i> Marsh	43.11	37.78	43.09	123.98
Slippery elm <i>Ulmus rubra</i> Muhl.	21.09	22.22	18.51	61.82
Ohio buckeye <i>Aesculus glabra</i> Willd.	9.17	10.00	4.40	23.57
Chinkapin oak <i>Quercus muehlenbergii</i> Engelm.	4.59	5.55	12.10	22.24
White ash <i>Fraxinus americana</i> L.	6.42	6.66	2.52	15.60
Box-elder <i>Acer negundo</i> L.	4.59	5.55	4.46	14.60
Hackberry <i>Celtis occidentalis</i> L.	2.75	2.22	4.07	9.04
Northern red oak <i>Quercus rubra</i> L.	0.92	1.11	5.25	7.28
Black walnut <i>Juglans nigra</i> L.	0.92	1.11	3.49	5.52
American basswood <i>Tilia americana</i> L.	1.83	2.22	0.25	4.30
Pawpaw <i>Asimina triloba</i> (L.) Dunal	1.83	2.22	0.14	4.19
Black cherry <i>Prunus serotina</i> Ehrh.	0.92	1.11	1.04	3.07
Sycamore <i>Platanus occidentalis</i> L.	0.92	1.11	0.51	2.54
Osage orange <i>Machura pomifera</i> (Raf.) Schneid.	0.92	1.11	0.20	2.23
			Sum	299.98

occurred in the tornado-damaged area, and allow comparison with the less-damaged southern portion (Transect 3). Over the 5 years of this study sugar maple, slippery elm, chinkapin oak, Ohio buckeye, American basswood, and white ash keep the same descending order of importance although the importance value of sugar maple increased about 15%. In 1999, twenty-five years after the tornado, the more damaged (northern and middle) part of the valley remained a sugar maple/slippery elm community with chinkapin oak, Ohio buckeye, basswood, and white ash of secondary importance (Table 8). In the less disturbed southern part of the valley, sugar maple was clearly the dominant tree, with black walnut, box-elder, white ash, slippery elm, and red oak of secondary importance (Table 6).

Similarity indices.—Sorenson's quotient of similarity showed a general increase in simi-

larity within transects from 1989–1994 and into 1999 (Table 9). Transects 1 and 2 (across the northern and middle portions of the valley) had relatively low similarities. Transects 1 and 3 (northern and southern) also had low similarities. Transects 2 and 3 (middle and southern) had the highest similarity indices in each of the three survey years. The comparison of Transects 1 + 2 and 3 showed increasing similarity through time.

The Bray & Curtis similarity index also showed a trend of increasing similarity between transects from 1989–1999 (Table 9), except for the comparison of Transects 1 and 3, which decreased. The similarity between Transects 1 and 2 increased over the 10 years. Likewise, the similarity between Transects 2 and 3 increased somewhat. And the comparison between Transects 1 + 2 and 3 showed an increasing trend of similarity.

Table 5.—Characteristics of the Happy Valley forest on transect 3 (southern portion) twenty years after the tornado.

Species	Relative density	Relative frequency	Relative dominance	Importance value
Sugar maple <i>Acer saccharum</i> Marsh	34.83	37.23	33.10	105.16
Box-elder <i>Acer negundo</i> L.	14.28	9.57	7.35	31.20
Black walnut <i>Juglans nigra</i> L.	6.25	7.44	17.02	30.71
White ash <i>Fraxinus americana</i> L.	11.61	11.71	6.47	29.79
Slippery elm <i>Ulmus rubra</i> Muhl.	8.04	7.44	12.98	28.46
Northern red oak <i>Quercus rubra</i> L.	1.79	1.06	8.43	11.28
Chinkapin oak <i>Quercus muehlenbergii</i> Engelm.	3.57	4.25	2.49	10.31
Ohio buckeye <i>Aesculus glabra</i> Willd.	4.46	5.32	0.44	10.22
Pawpaw <i>Asimina triloba</i> (L.) Dunal	5.36	4.26	0.45	10.07
Osage orange <i>Maclura pomifera</i> (Raf.) Schneid.	1.78	2.12	5.20	9.10
Hackberry <i>Celtis occidentalis</i> L.	2.68	3.19	0.90	6.77
Black maple <i>Acer nigrum</i> Michx.	1.79	2.13	2.25	6.17
Redbud <i>Cercis canadensis</i> L.	1.79	2.13	0.27	4.19
Sycamore <i>Platanus occidentalis</i> L.	0.89	1.06	2.59	4.54
Black cherry <i>Prunus serotina</i> Ehrh.	0.89	1.06	0.06	2.01
			Sum	299.98

Changes in forest structure.—On all three transects the mean point-to-tree distance decreased from 1974–1989 and 1994 (15–20 years) then increased in 1999 (Table 10). Likewise, the mean area per tree decreased from 1974–1989 and 1994; then increased in 1999 on all three transects. In the most damaged portion of the valley (Transects 1 & 2), mean area per tree decreased from 23.7 in 1974, to 11.0 in 1981, to 8.5 in 1989, then increased to 10.3 in 1994 and 11.2 in 1999. On all three transects, the density of trees (stems/ha) increased from 1974–1989 and 1994, then decreased in 1999 (Table 10). The more damaged portion of the valley (Transects 1 & 2) increased in density from 425 in 1974 to 1186 in 1989. These three sets of data illustrate the rapid growth of new trees in Hap-

py Valley following the tornado of 1974, even on the less damaged southern portion (Transect 3).

DISCUSSION

Changes in forest composition.—Over the past 25 years, sugar maple has remained the most important tree in the northern and middle portions (Transects 1 & 2) of Happy Valley. It reproduces and grows successfully in shade and in clearings (Elias 1980). It grows rapidly and resists wind damage. Following the census in 1989, MacMillan (1996) suggested that if the relative density and relative frequency of sugar maple continued to decrease, as they had over the first 15 years, then the fast-growing slippery elm would become the most important tree in this area of the valley. Now

Table 6.—Characteristics of the Happy Valley forest on transect 3 (southern portion) twenty-five years after the tornado.

Species	Relative density	Relative frequency	Relative dominance	Importance value
Sugar maple <i>Acer saccharum</i> Marsh	35.08	36.08	27.26	98.42
Black walnut <i>Juglans nigra</i> L.	7.90	9.28	17.28	34.46
Box-elder <i>Acer negundo</i> L.	11.40	9.27	7.34	28.01
White ash <i>Fraxinus americana</i> L.	10.52	10.30	4.68	25.50
Slippery elm <i>Ulmus rubra</i> L.	7.01	6.18	10.76	23.95
Northern red oak <i>Quercus rubra</i> L.	3.51	3.09	17.08	23.68
Ohio buckeye <i>Aesculus glabra</i> Willd.	5.26	6.19	0.47	11.92
Chinkapin oak <i>Quercus muehlenbergii</i> Engelm.	4.38	5.15	2.18	11.71
Black maple <i>Acer nigrum</i> Michx.	2.63	3.09	4.03	9.75
Hackberry <i>Celtis occidentalis</i> L.	4.38	4.12	1.05	9.55
Osage orange <i>Maclura pomifera</i> (Raf.) Schneid.	1.76	2.06	5.33	9.15
Pawpaw <i>Asimina triloba</i> (L.) Dunal	3.51	2.06	0.34	5.91
Sycamore <i>Platanus occidentalis</i> L.	0.88	1.03	2.01	3.92
Redbud <i>Cercis canadensis</i> L.	0.88	1.03	0.15	2.06
Black cherry <i>Prunus serotina</i> L.	0.88	1.03	0.08	1.99
			Sum	299.98

after an additional 10 years, the importance of sugar maple is increasing: 80 in 1989 (Mac-Millan 1996), 100 in 1994 (Table 7), and 118 in 1999 (Table 8). Although sugar maple has increased in all three components of the importance value, most of the increase has been in their relative dominance (i.e., basal area). We predict that sugar maple will continue to increase in importance over the next 10 years in this most damaged portion of the valley, then it will decrease as other canopy species increase in density and basal area.

Slippery elm and American elm were both found in this most damaged portion of Happy Valley in 1974 and 1981, although only slippery elm was found in 1986, 1994, and 1999. The American elm apparently died off due to Dutch elm disease, as it had on the adjacent

Hanover College campus. Slippery elm grows in many habitats in eastern North America, including dry slopes and well-drained bottomlands. It grows moderately fast and is often found growing with sugar maples (Elias 1980). The rank of slippery elm importance increased from fifth in 1974, to third in 1981, to second in 1989. It has been second to sugar maple since 1989 (Tables 7 & 8). Over the past 25 years the importance value of slippery elm has rested on its relative density and relative frequency, indicative of many smaller stems. It has not become the most important tree in the valley, as was suggested by Mac-Millan (1996). It now appears that few slippery elm saplings become 5 cm diameter trees (Betz unpubl. data). If this pattern persists, the importance of slippery elm will increase as

Table 7.—Characteristics of the most damaged (northern and middle) portions of the Happy Valley forest twenty years after the tornado.

Species	Relative density	Relative frequency	Relative dominance	Importance value
Sugar maple <i>Acer saccharum</i> Marsh	34.64	31.14	33.87	99.65
Slippery elm <i>Ulmus rubra</i> Muhl.	26.35	24.55	18.05	68.95
Chinkapin oak <i>Quercus muehlenbergii</i> Engelm.	4.87	5.40	11.67	21.94
Ohio buckeye <i>Aesculus glabra</i> Willd.	6.83	7.78	3.89	18.50
American basswood <i>Tilia americana</i> L.	5.37	6.58	4.91	16.86
White ash <i>Fraxinus americana</i> L.	4.39	6.00	4.08	14.47
Redbud <i>Cercis canadensis</i> L.	4.88	3.59	1.40	9.87
Hackberry <i>Celtis occidentalis</i> L.	3.42	3.00	3.03	9.45
Sycamore <i>Platanus occidentalis</i> L.	0.98	1.20	7.12	9.30
Box-elder <i>Acer negundo</i> L.	1.96	3.00	1.94	6.90
Northern red oak <i>Quercus rubra</i> L.	0.98	1.20	4.29	6.47
Black walnut <i>Juglans nigra</i> L.	0.49	0.60	2.59	3.68
Bitternut hickory <i>Carya cordiformis</i> (Wangenh.) K. Koch	0.49	0.60	1.31	2.40
Chokecherry <i>Prunus virginiana</i> L.	0.98	1.20	0.19	2.37
Pawpaw <i>Asimina triloba</i> (L.) Dunal	0.98	1.20	0.08	2.26
Royal paulownia <i>Paulownia tomentosa</i> (Thumb.) Seib. & Zucc.	0.49	0.60	0.88	1.97
Eastern hop hornbeam <i>Ostrya virginiana</i> (Mill.) K. Koch	0.49	0.60	0.41	1.50
Osage orange <i>Maclura pomifera</i> (Raf.) Schneid.	0.49	0.60	0.11	1.20
Black cherry <i>Prunus serotina</i> Ehrh.	0.49	0.60	0.07	1.16
White mulberry <i>Morus alba</i> L.	0.49	0.60	0.04	1.13
			Sum	300.03

the present stems increase in diameter but over the longer term it will decrease due to lack of recruitment.

The importance of sycamore has changed dramatically over the past 25 years. Sycamore only grows where it has a continual water supply, in this case, only in the valley bottom. Following the tornado of 1974, Bailey (unpubl. data) recorded only three sycamores on

Transects 1 & 2, although all were large trees. What did not show in that tree census was the number of large-diameter sycamore logs on the valley floor, making it impossible to walk through the valley. As MacMillan (1996) described, many of the sycamore logs remained rooted and their branches became trees. This is the history of sycamore importance over the past 25 years. In 1974 there were 3 sycamore

Table 8.—Characteristics of the most damaged (northern and middle) portions of the Happy Valley forest twenty-five years after the tornado.

Species	Relative density	Relative frequency	Relative dominance	Importance value
Sugar maple <i>Acer saccharum</i> Marsh	38.92	36.47	42.45	117.84
Slippery elm <i>Ulmus rubra</i> Muhl.	23.15	22.94	18.62	64.71
Chinkapin oak <i>Quercus muehlenbergii</i> Engelm.	4.93	5.88	10.51	21.32
Ohio buckeye <i>Aesculus glabra</i> Willd.	7.39	7.65	3.98	19.02
American basswood <i>Tilia americana</i> L.	5.91	5.88	5.63	17.42
White ash <i>Fraxinus americana</i> L.	4.43	4.70	2.00	11.13
Hackberry <i>Celtis occidentalis</i>	2.97	2.95	3.11	9.03
Redbud <i>Cercis canadensis</i> L.	3.95	3.53	1.08	8.56
Box-elder <i>Acer negundo</i> L.	2.46	2.95	2.76	8.17
Northern red oak <i>Quercus rubra</i> L.	0.98	1.18	3.69	5.85
Black walnut <i>Juglans nigra</i> L.	0.49	0.59	2.16	3.24
Bitternut hickory <i>Carya cordiformis</i> (Wangenh.) K. Koch	0.49	0.59	1.27	2.35
Pawpaw <i>Asimina triloba</i> (L.) Dunal	0.99	1.18	0.08	2.25
Royal paulownia <i>Paulownia tomentosa</i> (Thumb.) Seib. & Zucc.	0.49	0.59	1.01	2.09
Black cherry <i>Prunus serotina</i> Ehrh.	0.49	0.59	0.65	1.73
Tulip tree, Yellow poplar <i>Liriodendron tulipifera</i> L.	0.49	0.59	0.46	1.54
Sycamore <i>Platanus occidentalis</i> L.	0.49	0.59	0.31	1.39
Osage orange <i>Maclura pomifera</i> (Raf.) Schneid.	0.49	0.59	0.12	1.20
Chokecherry <i>Prunus virginiana</i> L.	0.49	0.59	0.08	1.16
			Sum	300

stems in the most damaged area, and it ranked second to sugar maple in relative dominance. In 1981 there were 2 stems, and it ranked second to sugar maple. In 1989 there were 4 stems, and it ranked second to sugar maple. In 1994 there were 2 stems, and it ranked fourth to sugar maple. In 1999 there was 1 stem, and it ranked fifteenth in relative dominance. Clearly, the large-diameter stems that remained after the tornado started dropping out after 1989. We suggest that sycamore will

remain a very minor component of this damaged portion of the valley for many years to come, until new saplings along the creek are recruited into tree diameter classes. Chinkapin oak is found throughout the American Midwest (Elias 1980). It grows in well-drained soils on upland sites, limestone outcrops, and slopes. Because leaf and bark characters are often not distinct in young oak trees, earlier studies only distinguished "red oak spp." and "white oak spp." In 1989 chinka-

Table 9.—Comparison of Sorenson's quotient of similarity (Brower et al. 1990) and the Bray & Curtis (1957) similarity index between transects from 1989 to 1999.

	1989	1994	1999
Transects 1 & 2			
Sorenson	0.563	0.621	0.593
Bray & Curtis	58.64	66.73	75.79
Transects 1 & 3			
Sorenson	0.600	0.643	0.571
Bray & Curtis	57.30	55.61	55.29
Transects 2 & 3			
Sorenson	0.600	0.839	0.897
Bray & Curtis	61.91	72.20	69.67
Transects 1 + 2 & 3			
Sorenson	0.556	0.800	0.824
Bray & Curtis	60.63	68.04	64.03

pin oak ranked fourth, in 1994 and 1999 it ranked third; each time the importance value was influenced by its large relative dominance value. However, these importance values are 20–30% smaller than those of sugar maple, suggesting that several larger-diameter trees survived the tornado of 1974 because young oak trees would not grow to that diameter in 25 years (Elias 1980). We predict that chin-kapin oak will remain an important secondary

species in this most damaged portion of the valley and that it will maintain its current rank.

Ohio buckeye is found throughout the Mid-western states in well-drained soils (Elias 1980). It is commonly found as a minor component although the trees are usually large. Its seedlings develop quickly and are very shade-tolerant. Based on unpublished pre-tornado data, Bailey & MacMillan (1977) described

Table 10.—Changes in structure of the Happy Valley forest over 25 years. Pre-tornado conditions (based on unpublished 1973 class data) were: Mean point-to-tree distance = 4.4 m, Mean area/tree = 19.56 m², Density of trees = 512/ha. Reference citations (a) Bailey & MacMillan 1977, (b) Martin & MacMillan 1982, (c) MacMillan 1996, (d) Lindsay Betz unpublished.

	1974 (a)	1981 (b)	1989 (c)	1994 (d)	1999 (d)
Transect 1					
Mean point-to-tree distance (m)	5.1	3.1	2.9	2.9	3.2
Mean area/tree (m ²)	25.64	9.60	7.83	8.41	10.24
Density (trees/ha)	391	1041	1180	1231	983
Transect 2					
Mean point-to-tree distance (m)	4.7	3.5	3.0	3.5	3.5
Mean area/tree (m ²)	21.78	12.30	9.21	12.25	12.25
Density (trees/ha)	460	813	1091	864	819
Transect 3					
Mean point-to-tree distance (m)	3.9	3.7	3.4	3.3	3.2
Mean area/tree (m ²)	15.24	13.70	11.57	10.89	13.69
Density (trees/ha)	652	730	857	946	746
Transects 1 & 2					
Mean point-to-tree distance (m)	4.9	3.3	2.9	3.3	3.4
Mean area/tree (m ²)	23.70	11.00	8.51	10.33	11.24
Density (trees/ha)	425	926	1186	1047	901

the middle portion of Happy Valley as a sugar maple/Ohio buckeye sub-climax forest. At that time, Ohio buckeye was a significant component in small- and large-diameter classes, indicating that saplings were being recruited into the "tree" category and that some large trees survived the tornado. In the combined data from Transects 1 and 2, Ohio buckeye ranked a distant second in 1981, ninth in 1989, and fourth in 1994 and 1999. The decrease found in 1989 was due to loss of several large-diameter trees that were damaged in the tornado, managed to survive through 1981, but succumbed by 1984. In 1994 and 1999 the importance of Ohio buckeye was due to many small stems (relative density and frequency). As predicted, the importance value of Ohio buckeye has increased following canopy closure (MacMillan 1996).

American basswood is a fast-growing, long-lived tree common in sugar maple forests (Elias 1980). It grows best in low, moist, well-drained areas, although it grows well on the mesic east-facing slopes of Happy Valley. Following the tornado of 1974, most of the damaged basswood trees coppiced, meaning they sent up several stems from the root crown. In this most damaged portion of the valley, American basswood ranked fourteenth in 1974, seventh in 1981, ninth in 1989, and fifth in 1994 and 1999. These importance values were due to higher relative density and frequency values during the first 20 years. After 25 years, as predicted (MacMillan 1996), the relative dominance (basal area) of basswood is now a significant factor in its importance, indicating the growth of smaller stems into larger diameter classes.

White ash is found across the eastern United States in deep, well-drained soils (Elias 1980). It often grows near streams and along lower slopes of hills and mountains. It grows slowly during the sapling stage and increases in growth rate over the next 50 years. In this most damaged portion of the valley, white ash ranked a distant second in 1974 (based on its relative frequency and dominance), fifteenth in 1981 (based on a very small relative dominance), twelfth in 1989 (with a larger relative dominance), and sixth in 1994 and 1999 based more on relative density and frequency than dominance. These results suggest that a few large white ash trees were damaged but survived the tornado and spread many seeds. The

older trees then died, and many saplings were recruited into the smaller diameter classes before the canopy closed, as MacMillan (1996) suggested. There is still a large white ash seedling population in the understory.

Tulip tree (or yellow poplar) is an invader of disturbed sites. It was not found in the most disturbed region of the valley in 1974. Two stems were recorded in 1981, 1 stem in 1989, none in 1994, and 1 stem in 1999. After the 15-year census, MacMillan (1996) predicted that this rapidly growing species would increase in importance over the next 5 years. That has not happened, probably because the canopy closed and few disturbed sites remain.

Changes in forest structure.—Sorenson's quotient of similarity (Brower et al. 1990) suggests that Transects 1 & 2, and Transects 1 & 3 became more similar between 1989 and 1994, and decreased in similarity in 1999 (Table 9). Transects 2 & 3, and 1 + 2 & 3 increased in similarity over the past 10 years. These data suggest that the more damaged northern and central portions of the valley are becoming similar to the less damaged southern portion. The Bray & Curtis (1957) similarity index indicates that Transects 1 & 2 became more similar, Transects 1 & 3 became less similar, and Transects 2 & 3, and 1 + 2 & 3 became slightly more similar over the past 10 years (Table 9). Differences between the two measures of similarity may be due to the factors they compare. Bray and Curtis compare importance values, and Sorenson compares the number of species common to both sites. The trend toward increasing similarity was expected due to the proximity of the sites, the similar soils, seed sources, exposure and climate. This trend of increasing similarity throughout the valley forest is predicted to continue.

The structure of the Happy Valley forest has not continually changed in one direction over the past 25 years (Table 10). Between 15 and 20 years after the tornado (1989–1994) the trend of decreasing values of mean point-to-tree distance and mean area per tree, and the increasing values of tree density (number of trees per hectare), reversed on all three transects. Forest recovery had reached a turning point. After 20 years, the mean point-to-tree distance began to increase suggesting that some trees had died. Likewise, the mean area per tree began to increase suggesting that the

canopy had closed and canopy trees were increasing in diameter. On the more-damaged Transects 1 & 2, the density of trees in 1974 (immediately following the tornado) was lower than on the less damaged Transect 3, as expected due to wind damage. By 1981 (7 years after the tornado) the density of trees on Transects 1 & 2 was higher than on the less-damaged Transect 3, and it remained higher for 25 years. This is explained by the rapid growth of saplings once the canopy had been removed. By 1999 (25 years after the tornado) the density of trees had decreased on all three transects (Table 10). We predict that the mean point-to-tree distance and mean area per tree will continue to increase, and the density of trees will continue to decrease, as the valley forest matures. We attempted to use size structure analysis (Parker 1992; Ziegler 1995) to evaluate the structural dynamics of the most abundant species on each transect. However, our samples were too small, 79% of the stems sampled were less than 25 cm dbh, and historically most of the trees were less than 25 years old due to the tornado of 1974.

In conclusion, we predict that the damaged and undamaged areas of Happy Valley will continue to change in structure and composition and that they will continue to become more similar. Sugar maple will continue to be the dominant tree throughout the valley. If Ohio buckeye continues to increase in importance and establish itself in the canopy, the valley forest may grow back to the same type of community it was before the tornado of 1974.

LITERATURE CITED

- [Anonymous]. 1974. Death toll climbs to 9 from tornado. *The Madison Courier* 126(278):15c. (April 5). Madison, Indiana.
- Bailey, J.B. 1974. A tree census of post-tornado conditions of Happy Valley. Biology Department, Hanover College, Hanover, Indiana. 27 pp.(unpubl.)
- Bailey, J.B. & P.C. MacMillan. 1977. A tree census of pre- and post-tornado forest conditions of Happy Valley, Jefferson County, Indiana. *Proceedings of the Indiana Academy of Science* 86: 199–202.
- Betz, Lindsay. 1999. Twenty-five years of forest succession in Happy Valley, Jefferson County, Indiana. Biology Department, Hanover College, Hanover, Indiana. 35 pp. (unpubl.)
- Bray, J.R. & J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27:325–349.
- Brower, J., J. Zarr & C. von Ende. 1990. *Field and Laboratory Methods for General Ecology*. Wm. C. Brown Publishing Co., Dubuque, Iowa. 237 pp.
- Cottam, C. & J.T. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451–460.
- Cox, G.W. 1990. *Laboratory Manual in General Ecology*. Wm. C. Brown Publishing Co., Dubuque, Iowa. 237 pp.
- Elias, T.S. 1980. *The Complete Trees of North America*. Times Mirror Magazine, New York. 948 pp.
- Larking, L. 1974. Tornado strips away famed beauty of Hanover College campus in Indiana. *The Courier Journal*: A56. (April 5). Louisville, Kentucky.
- MacMillan, P.C. 1996. Fifteen years of forest succession in Happy Valley, Jefferson County, Indiana. *Proceedings of the Indiana Academy of Science* 105:159–168.
- Martin, C.J. & P.C. MacMillan. 1982. Seven years of forest succession in Happy Valley, Jefferson County, Indiana. *Proceedings of the Indiana Academy of Science* 92:197–206.
- Nickell, A.K. 1985. *Soil survey of Jefferson County*. United States Department of Agriculture, Soil Conservation Service.
- Parker, A.J. 1992. Spatial variation in diameter structures of forests in Lassen Volcanic National Park, California. *Professional Geographer* 44: 147–160.
- Ziegler, S.S. 1995. Relict eastern white pine (*Pinus strobus* L.) stands in southwestern Wisconsin. *American Midland Naturalist* 133:88–100.

Manuscript received 8 August 2002, revised 23 January 2003.