

VERSAILLES STATE PARK REVISITED: TWENTY YEARS OF CHANGE IN OLD-GROWTH FORESTS OF LAUGHERY BLUFF AND DOGWOOD NATURE PRESERVES.

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INTRODUCTION

During the summer of 1968, the least disturbed sections of the old-growth beech-maple dominated forests located in Laughery Bluff and Dogwood Nature Preserves in Versailles State Park were examined by taking full-census data for all tree species. A detailed structural analysis based on those studies was reported by Jackson and Allen (1969). In that earlier study, the stands were referred to as Jackson Woods and Potzger Woods, respectively (Lindsey, *et al.*, 1969).

Following twenty growth seasons, the portions that were the subject of the original full censuses were re-measured and comparable stand attributes were calculated. Our objectives were: 1) to compare the 1988 stand measures of density, basal area, percent importance, size-class distribution, and diversity with those taken in 1968; and 2) to document composition changes, successional trends, and gap replacement patterns over a twenty-year period.

Laughery Bluff Nature Preserve, located on a high promontory, sustained moderately high losses of canopy trees (particularly mature beeches) to windthrow during the score of years. Wind damage was substantially less in Dogwood Nature Preserve, due in part to its more sheltered location.

The landscape and ecological setting of the study sites were described in full by Jackson and Allen (1969) and will not be repeated here. Both stands are on gently rolling topography, occupy well-drained Cincinnati silt loam soils derived from Silurian and Ordovician-aged limestone, respectively. Both tracts are within the section of the State Park located south of U.S. Highway 50. Neither is often visited, maintaining their overall natural condition and lack of human-induced disturbance.

METHODS

The 1968 full census areas were resurveyed in 1988 by using the same field procedures. Points outlining the perimeters of the two study sites were relocated as closely as possible. In Laughery Bluff, the study area consisted of 17.46 acres (7.96 ha) during both surveys. The Dogwood site increased slightly in area from 6.44 acres (2.61 ha) in 1968 to 6.80 acres (2.75 ha) in 1988 as a result of boundary adjustments. In both situations, stand margins were excluded from the tallies to avoid community transitions.

TABLE 1. Changes in community composition in Laughery Bluff State Nature Preserve, 1968-1988.

Species	Density/Acre		% Change		Basal Area/Acre		% Change		Percent Importance	
	1968	1988	1988	1968	1968	1988	1988	1968	1968	1988
As	42.33	58.99	+39.4	12.67	23.01	+81.6	25.88	37.29	+48.7	
Fg	14.32	8.88	-38.0	57.66	38.32	-33.6	32.38	21.45	-33.8	
Lt	11.68	10.65	- 8.8	19.53	27.29	+39.7	14.10	17.25	+22.3	
Ur	8.30	8.48	+ 2.1	2.67	2.05	-23.2	5.00	4.76	- 4.8	
Jn	3.78	2.86	-24.3	6.45	7.15	+10.9	4.63	4.55	- 1.7	
Fa-Fp	3.95	5.50	+39.2	2.63	4.43	+68.4	2.99	4.52	+51.2	
Cf	13.23	4.52	-65.8	2.18	0.71	-67.7	6.52	2.38	-63.5	
Ps	3.38	2.58	-23.7	1.19	1.30	+ 8.9	2.09	1.76	-15.8	
Ns	1.72	1.03	-40.0	1.61	1.74	+ 8.1	1.51	1.26	-16.6	
Sa	1.55	1.43	- 7.5	0.79	0.77	- 2.5	1.07	1.00	- 6.5	
Other Species*	4.75	5.00	+ 5.3	4.29	3.35	-17.7	4.15	3.79	- 8.7	
Total	108.99	109.29	- 0.3	111.67	110.12	- 1.4				

*Other species in descending order of 1988 importance: Coc, Ua, Qr, Ta, Vitis, Ccor, Ane, Ov, Ccar, Qa, Cov, At, Cg, Qmu, Ag, Ar, Aral. Three species recorded in 1968 (Jc, Fq, and Rp) were absent from the 1988 tally.

All trees 2.0 inches (5.1 cm) dbh (diameter at breast height) and greater were included in both tallies. Trees from 2.0 to 3.9 inches (5.1-9.9 cm) were counted and recorded by species. All trees 4.0 inches (10.2 cm) and larger were measured to the nearest 0.1 inch (0.25 cm) with diameter tapes. Stand attributes were calculated as follows: density per acre; relative density; basal area per acre; and relative basal area. Percent importance is the average of the relative values of density and basal area.

Species nomenclature follows Little (1953) and Gleason and Cronquist (1963) for trees and other species, respectively. Species symbols usually represent the first letters of the respective genus and species names. Variations in measures between the two studies were tested for significance by using Chi-square analysis.

RESULTS

Laughrey Bluff attribute changes. Changes in community composition during the 20-year period are summarized in Table 1. Overall, density per acre for trees > 4" (10 cm) dbh remained static (109.0 stems in 1968 *versus* 109.3 stems in 1988); total basal area per acre declined only 1.4% (111.7 ft² in 1968 *versus* 110.1 ft² in 1988). (Metric equivalents are 269.2 *versus* 270.0 stems/ha and 25.64 *versus* 25.27 m²/ha).

Many individual tree species experienced marked changes in density, basal area, and percent importance (Table 1). Sugar maple (*Acer saccharum* Marsh.) increased 40% in density ($\chi^2 = 6.56^*$, 1 df) to 59 stems per average acre and nearly doubled (82% increase) in basal area per acre ($\chi^2 = 8.43^{**}$, 1 df). American beech (*Fagus grandifolia* Ehrh.) decreased 38% in density ($\chi^2 = 2.07$, 1 df) and 34% in basal area ($\chi^2 = 6.48^*$, 1 df). These approximately equal but opposing changes resulted in an essentially unchanged combined percent importance for the two dominant species (57.5% in 1968 *versus* 58.7% in 1988). Sugar maple increased in density through accessions; that is, gains in basal area resulted primarily from growth of small to medium-sized surviving trees. Changes in beech attributes were due largely to windthrow and other mortality of medium-sized to large canopy individuals.

Late-seral but intolerant species (*e.g.*, tulip tree (*Liriodendron tulipifera* L.), slippery elm (*Ulmus rubra* Muhl.), black walnut (*Juglans nigra* L.), black cherry (*Prunus serotina* Ehrh.), black gum (*Nyssa sylvatica* Marsh.), and sassafras (*Sassafras albidum* (Nutt.) Nees)) decreased in density from lack of replacement of dying trees, while these species increased in basal area through the growth of remaining stems. White and green ashes combined (*Fraxinus americana* L. and *F. pennsylvanica* Marsh.) increased in density, basal area, and percent importance. None of these changes was significant.

Among the most interesting and least explicable changes were the 66% decline in density ($\chi^2 = 13.23^{**}$, 1 df) and the 68% drop in basal area ($\chi^2 = 0.99$, 1 df) for flowering dogwood (*Cornus florida* L.; Table 1). Sixteen minor species collectively increased slightly in density (due largely to ingrowths of grapevine (*Vitis* spp.), oaks (*Quercus* spp.), and paw paw (*Asimina triloba* (L.) Dunal) but declined slightly in overall importance.

Dogwood Nature Preserve attribute changes. Stand attributes values for Dogwood Nature Preserve are shown in Table 2. Total stand density and overall basal area values are somewhat higher than those for Laughrey Bluff (126.9 stems

TABLE 2. Changes in community composition in Dogwood Nature Preserve, 1968-1988.

Species	Density/Acre		Basal Area/Acre		Percent Importance	
	1968	1988	1968	1988	1968	1988
As	68.63	89.71	23.93	40.30	38.53	51.54
Fg	14.29	11.76	57.84	47.05	30.69	23.54
Jn	4.50	4.41	7.44	8.80	5.05	5.28
Fa-Fp	7.30	5.00	5.17	7.74	5.23	5.08
Lt	2.48	2.21	4.13	4.31	2.79	2.63
Ns	2.64	1.47	5.24	3.96	3.33	2.17
Ps	3.57	1.91	2.44	2.66	2.52	1.83
Ur	3.88	2.21	3.12	2.06	2.94	1.73
Ta	1.24	1.62	0.90	1.50	0.90	1.23
Ua	1.55	1.32	1.00	1.23	1.07	1.02
Other Species*	11.35	5.30	5.37	4.83	7.61	4.01
Total	121.43	126.92	116.58	124.44		
		+ 4.52		+ 7.7		

*Other species in descending order of 1988 importance: Coc, Ccor, Cf, Sa, Vitis, Qr, Ag, Qa, Ar, Cg, Ov. Two species recorded in 1968 (Fg, Qmu) were absent from the 1988 tally.

in 1988 *versus* 109.3 in 1968 and 124.4 ft²/acre in 1988 *versus* 110.0 in 1968, respectively). (Metric equivalents are 313.4 and 270.0 stems/ha and 28.55 and 25.27 m²/ha). Changes in total density and basal area were greater (4.5% and 7.7%) than found for Laughery Bluff, but neither difference was significant ($\chi^2 = 0.25$ and 0.53, 1df, respectively).

Sugar maple increased its dominance with a 31% increase in density ($\chi^2 = 6.47^*$, 1 df) plus a 68% increase in basal area ($\chi^2 = 11.20^{**}$, 1 df). Beech declined in both density (18%) and basal area (19%), but neither change was significant ($\chi^2 = 0.45$ and 2.01, respectively). The two species combined strengthened their co-dominance from 69.2 to 75.1 percent importance during the 20 years, the 13% gain for sugar maple more than offsetting the 7% decline in beech. As is typical in many beech-maple dominated forests, young sugar maples are rapidly entering this stand, along with relatively rapid growth in size of surviving sub-canopy trees. Declines in beech resulted from the deaths of a few canopy trees.

All of the subdominant species except American basswood (*Tilia americana* L.) and the minor species collectively declined in density, none significantly. Changes in basal area were less predictable, depending upon mortality losses in comparison with growth. The subdominant walnut and ashes increased substantially in basal area through growth, despite losses in density. All subdominant species declined in percent importance, except walnut and basswood, with the minor species collectively suffering the greatest loss, due largely to mortality in understory species.

Laughery Bluff size class changes. A size-class comparison by species reveals modest recruitment of entry-sized trees (2.0-3.9" dbh) into the stand by both of the co-dominant species (Tables 3). Sugar maple gained 48 individuals for a 5% increase, while the 20 new beeches represent a 111% increase in young saplings. The populations of all other species sustained substantial losses from the 2.0-3.9" size class except hackberry (*Celtis occidentalis* L.) and the minor species collectively.

For the size classes greater than 4.0" dbh, sugar maple and beech experienced contrasting changes (Table 3). Subcanopy sugar maples (4.0-11.9" dbh) increased in number by 30%. Subcanopy beech remained unchanged at only 8 individuals, compared to 904 similar-sized sugar maples in the 1988 census. Sugar maple increased threefold in the 12-19.9" dbh class and by fivefold in the 20-27.9" dbh class. Medium-sized and large beech declined by 59%, 41%, and 40% in the 8-inch size classes, respectively, ranging from 12-36" dbh.

In 1968, beech represented 65% (220 of 329) of the canopy trees greater than 20" dbh. By 1988, beech represented only 45% (138 of 306), for a net loss of 82 canopy trees (4.6/acre) in 20 years ($\chi^2 = 19.72^{**}$, 1 df). An average loss of one canopy tree per acre every four years released many of the existing trees of other species.

In addition to the gains in sugar maple mentioned above, tulip tree increased by 57% (from 61 to 96 individuals; $\chi^2 = 20.08^{**}$, 1 df) and black walnut by 60% (from 20 to 32 individuals; $\chi^2 = 7.20^{**}$, 1 df) in size classes greater than 20" dbh. Both of these intolerant species lost individuals in all size classes below 20" dbh as the light gaps created by beech mortality began closing above them. Tulip tree declined from 169 to 108 small trees (36% loss; $\chi^2 = 22.02^{**}$, 1 df), while black walnut dropped from 48 to 18 (63% loss; $\chi^2 = 18.75^{**}$, 1 df). All other species

TABLE 3. Size-class comparison for Laughery Bluff Nature Preserve, 1968 versus 1988.

Species	Year	Size Classes							Total > 4"	Total > 2"
		2-3.9	4-11.9	12-19.9	20-27.9	28-35.9	36-43.9			
As	68	976	699	38	2	—	—	739	1715	
	88	1024	904	114	10	—	—	1030	2054	
Fg	68	18	8	22	107	100	13	250	268	
	88	38	8	9	63	60	15	155	193	
Lt	68	26	73	70	49	11	1	204	230	
	88	18	35	55	59	32	5	186	204	
Jn	68	2	11	35	20	—	—	66	68	
	88	—	3	15	29	3	—	50	50	
Fa-Fp	68	59	51	14	3	1	—	69	128	
	88	23	65	21	8	2	—	96	119	
Ur-Ua	68	155	151	11	7	—	—	169	324	
	88	82	141	15	2	1	—	159	241	
Ns	68	7	20	5	4	1	—	30	37	
	88	1	7	6	2	3	—	18	19	
Ps	68	41	53	5	1	—	—	59	100	
	88	20	40	3	2	—	—	45	65	
Cf	68	79	231	—	—	—	—	231	310	
	88	67	79	—	—	—	—	79	146	
Coc	68	18	10	3	2	—	—	15	33	
	88	43	13	4	2	—	—	19	62	
Other Spp.	68	188	53	12	6	1	—	72	260	
	88	271	68	7	4	1	81	352		
Total	68	1569	1360	215	201	114	14	1904	3473	
	88	1587	1363	249	181	104	21	1918	3505	

collectively remained essentially constant (26 *versus* 28) in the larger size classes (an 8% overall gain). The minor species collectively lost 190 individuals (1166 *versus* 976) from their populations for a 16% decline ($\chi^2 = 30.96^{**}$, 1 df). Many of these losses resulted from the high mortality of elms (*Ulmus rubra* Muhl. and *U. americana* L.) and flowering dogwood (*Cornus florida* L.) from the smallest size classes.

When comparing totals for all species, the size classes below 12" dbh increased by only 21 stems (2929 *versus* 2950). Sugar maple increased from a total of 57% to 65% of all small individuals from 1968 to 1988. All species collectively increased by only 11 stems (544 *versus* 555) in size classes above 12" dbh, for a remarkably constant overall stand density. Sugar maples' contribution to that total increased from 7.4% in 1968 to 22.7% in 1988. Meanwhile, beech declined from 44.5% to 26.5% of the canopy trees.

Dogwood Nature Preserve size class changes. Sugar maple experienced a 32% loss in young saplings (2-3.9" dbh ($\chi^2 = 59.04^{**}$, 1 df), while beech doubled its modest number of two individuals (Table 4). The collective population of all species other than the two dominants sustained an even greater loss of 63% (182 *versus* 68), primarily from mortality in understory species, which never reach canopy size.

In size classes greater than 4.0" dbh, sugar maple increased 39% from a total of 442 to 616 ($\chi^2 = 68.49^{**}$, 1 df), while beech declined slightly (13%) from 92 to 80 stems ($\chi^2 = 1.57$, 1 df). Subcanopy sugar maples (4.0-11.9" dbh) increased 31% whereas canopy maples increased 177% (from 26 to 72 stems) due to advancements from smaller size classes. Canopy beeches (> 12" dbh) sustained little windthrow and only minor mortality for a net loss of 9 trees (84 *versus* 75), only 1.3 per acre during the 20-year period.

Collectively, black walnut, the ashes, and tulip tree increased modestly in numbers of canopy trees from a total of 48 in 1968 to 58 in 1988 (a 21% change). All three species collectively declined in number of subcanopy individuals from 55 to 21 ($\chi^2 = 21.01^{**}$, 1 df). All minor species had a combined gain of only 11 individuals (28% increase) in the canopy size classes, while populations of subcanopy species were reduced from a total of 286 to only 112, a 61% decline. Dogwood declined precipitously from a total of 84 to only 26 stems in 1988, a 69% loss ($\chi^2 = 40.05^{**}$, 1 df).

In 1968, beech and sugar maple totaled 88 of 116 canopy trees (76%) in sizes greater than 20" dbh. By 1988, they represented 77 of 117 canopy trees (68%) for a net loss of only 11 stems ($\chi^2 = 1.38$, 1 df). Increased combined dominance from 69 to 75% resulted primarily from small maples entering the stand, plus net growth of larger trees.

When totals for all species are compared (on an acreage-adjusted basis), subcanopy individuals declined 24% from 210.1 per acre to 159.7 per acre ($\chi^2 = 12.09^{**}$, 1 df). Smaller canopy trees (12-19.9" dbh) increased 63% from 12.7 to 20.7 stems per acre ($\chi^2 = 5.04^{**}$, 1 df). Large canopy trees over 20" dbh remained essentially static (18.0 *versus* 16.9 per acre).

Size class changes by species group. Examination of size class changes for selected groups of species reveals some interesting patterns (Table 5). Xerophytic species (mostly *Quercus* and *Carya*) declined in number in most size classes

TABLE 4. Size-class comparison for Dogwood Nature Preserve, 1968 versus 1988.

Species	Year	Size Classes							Total	Total	Total
		2-3.9	4-11.9	12-19.9	20-27.9	28-35.9	36-43.9	> 4"			
As	68	586	416	12	10	4	—	442	1028		
	88	400	544	58	6	8	—	616	1016		
Fg	68	2	8	10	30	36	8	92	94		
	88	4	5	12	30	23	10	80	84		
Jn	68	—	2	20	7	—	—	29	29		
	88	—	1	19	10	—	—	30	30		
Fa-Fp	68	9	33	11	3	—	—	47	56		
	88	—	15	9	9	2	—	35	35		
Lt	68	2	9	3	2	2	—	16	18		
	88	—	5	5	2	1	1	14	14		
Ns	68	2	7	2	7	1	—	17	19		
	88	—	1	3	2	3	—	9	9		
Ur-Ua	68	10	25	7	3	—	—	35	45		
	88	—	10	15	—	1	—	26	26		
Ps	68	1	15	8	—	—	—	23	24		
	88	—	1	10	2	—	—	13	13		
Cf	68	64	20	—	—	—	—	20	84		
	88	17	9	—	—	—	—	9	26		
Coc	68	4	4	—	—	1	—	5	9		
	88	—	2	1	1	1	—	5	5		
Other Spp.	68	89	45	9	1	1	—	56	145		
	88	51	21	9	2	1	—	33	84		
Total	68	769	584	82	63	45	8	782	1551		
	88	472	614	141	64	40	11	870	1342		

except for entry-sized trees in Laughery Bluff. Overall these species lost half of their stems in Dogwood Preserve. Hydrophytic species likewise dropped substantially in Dogwood Preserve and slightly in Laughery Bluff in most size classes. Conversely, mesophytic species (not shown in Table 5) collectively changed very little in most size classes or in overall totals. These changes reflect the mesic conditioning that is widespread in beech-maple stands in the Midwest.

Understory species declined significantly overall in both stands, primarily due to high losses of flowering dogwood. Increases in 2-4" stems in Laughery Bluff resulted from invasion of paw paw into mesic light gaps and large sinks. Lianas (predominantly *Vitis* sp.) increased only slightly in Dogwood Preserve through growth of existing stems, while rapid invasion into canopy openings doubled the vine population in the Laughery Bluff stand.

Yearly changes for key species. Table 6 summarizes the average annual percentage change in stems and basal area for key species during the 20-year period. Sugar maple increased more than any other species in both stands. At an average compounded increase in density in Laughery Bluff of 1.8%/year, sugar maple would be expected to double in numbers in less than 40 years; at a sustained basal area increase of 4.1%/year, the species would double in that measure in about 16 years. Beech declined in density and basal area at nearly 2%/year in Laughery Bluff and at about 1% per year in Dogwood Preserve. These opposing changes for the co-dominants, if continued at these rates for another 20 years, would result in predominately sugar maple stands with beech relegated to a subdominant species.

Ashes are increasing in basal area in both stands at rates approaching that of sugar maple. Tulip tree and black walnut are both declining in numbers but increasing in basal area through incremental growth of medium-sized and larger trees. Elms are rapidly losing basal area as diseases afflicting larger individuals of those species continue to exact their toll. Flowering dogwood, with declines of around 3% for both measures in both stands, has limited tenure in these nature preserves, if these trends continue. Such loss rates would essentially extirpate that species within another 20 years.

Diversity changes. Species richness of large woody plants in Laughery Bluff was 33 in all size classes in 1968. Five of these were present only in the 2-3.9" class. Six species from the 1968 survey were not encountered at sizes > 2" dbh in 1988: butternut (*Juglans cinerea* L.), blue ash (*Fraxinus quadrangulata* Michx.), black locust (*Robinia pseudo-acacia* L.), poison-ivy (*Rhus radicans* L.), red mulberry (*Morus rubra* L.), and rock elm (*Ulmus thomasi* Sarg.). Species new to the area in 1988 include: green ash (*Fraxinus pennsylvanica* Marsh.), red maple (*Acer rubrum* L.), and devil's walkingstick (*Aralia spinosa* L.). The species richness now stands at 30.

Dogwood Preserve contained 27 large woody species in 1968 and 24 in 1988. The three species absent in 1988 were: blue ash, chinkapin oak (*Quercus muehlenbergii* Engelm.), and paw paw (*Asimina triloba* (L.) Dunal.). No species new to the stand was encountered.

DISCUSSION

Although the two stands under consideration are geographically close, occur on similar topography and soils, and have the same co-dominant species, their

TABLE 5. Comparison of size-class changes for selected groups of species 1968 versus 1988.

Species Group	Size Class							Total >4"	Total >2"
	2-4	4-12	12-20	20-28	28-36	>36			
Xerophytic Species									
Dogwood 1968	9	13	7	—	—	—	20	29	
1988	3	4	5	2	—	—	11	14	
Laughery 1968	4	6	5	4	1	—	16	20	
1988	11	7	2	3	1	1	14	25	
Hydrophytic Species									
Dogwood 1968	22	40	10	10	2	—	62	84	
1988	10	16	21	3	4	—	44	54	
Laughery 1968	217	184	19	14	1	—	218	435	
1988	202	179	25	6	4	—	214	416	
Understory Species									
Dogwood 1968	97	36	—	—	—	—	36	133	
1988	23	10	—	—	—	—	10	33	
Laughery 1968	155	245	—	—	—	—	245	400	
1988	172	95	—	—	—	—	95	267	
Lianas									
Dogwood 1968	35	—	—	—	—	—	0	35	
1988	31	5	—	—	—	—	5	36	
Laughery 1968	82	6	—	—	—	—	6	88	
1988	139	13	—	—	—	—	13	152	

TABLE 6. Average yearly percentage change in stem density and basal area for key species.

Species	% Change in Stems		% Change in Basal Area	
	Laughery	Dogwood	Laughery	Dogwood
As	+1.83	+1.54	+4.08	+3.42
Fg	-1.90	-0.89	-1.68	-0.93
Lt	-0.44	-0.54	+1.99	+0.22
Jn	-1.21	-0.10	+0.53	+0.91
Fa-Fp	+1.96	-1.58	+3.43	+2.49
Ur-Ua	-0.29	-1.75	-1.73	-1.01
Cf	-3.29	-2.88	-3.38	-3.10
All Species	+0.04	+0.23	-0.07	+0.34

bedrock geology, history of disturbance, and present-day composition are somewhat different.

Laughery Bluff occurs on Silurian limestone, which is subject to karst formation, creating frequent sinks of varying size and configuration. These sinks, with unstable slopes and internal drainage create thinner canopy along their rims and accumulate fertile alluvium in their bottoms. Improved light availability and soil conditions favor establishment and thrifty growth of such species as tulip tree, black walnut, white and green ash, and slippery elm. The stand attributes values (Table 1) reflect the improved conditions for these subdominant species. The collective percent importance for these five species is 31.1% (up from 26.7% in 1968). Beech and sugar maple are definitely co-dominant but total only 58.7 percent importance. Minor cutting of canopy trees in the 1930's (Jackson and Allen, 1969) has also favored the continuance and growth of subdominant species, as the stand is still adjusting to that disturbance and the stress of windthrow of several canopy beeches during the past twenty years.

Dogwood Preserve, which is found on Ordovician limestone, has about the same relief as Laughery Bluff, but the drainage is external through surface ravines. Disturbance from cutting was slight and prior to 1930 (Stearns, 1956). Recent windthrows occurred at only one third the frequency (on a per acre basis) of those at Laughery Bluff. Consequently, the subdominant species discussed above total only 14.7 percent importance (down from 16.9% in 1968). Beech and sugar maple are overwhelmingly the co-dominant species at 75.1 percent importance. Interestingly, the co-dominant and subdominant species have combined totals of exactly 89.8 percent importance in each stand; 1968 totals were 84.2 and 85.2 percent, respectively. Adjustments among the relative contributions of these seven species have kept total stand density and basal area values remarkably constant during the past twenty years, despite substantial losses of canopy beeches. Perhaps this reflects the resilience of old-growth forest communities, a documented example of the concepts of dynamic equilibrium and interspersed of a mosaic of community dominants.

Rapid increases in sugar maple in beech-maple dominated stands, apparently at the expense of beech, has been frequently documented (*e.g.*, Abrell and Jackson, 1977; Dunn and Jackson, 1979; Lindsey, *et al.*, 1969). These two stands also follow

that pattern. During the past twenty years, the co-dominant species reversed positions at Laughery Bluff as a result of a gain in importance for sugar maple of 12.2%, while beech dropped 10.9% (Table 1). In Dogwood Preserve, sugar maple increased its dominance with a 13% gain, while beech decreased 7.2% (Table 2). These changes are a result of the rapid ingrowth of large numbers of sugar maple saplings into the 4-11.9" size class plus advancements of fewer survivors into large size classes (Tables 3,4) along with deaths of canopy beeches. Entry of sugar maple into the 2-4" size class has slowed or reversed; Laughery Bluff increased by only 5% (Table 3); Dogwood Preserve had a 32% decline. These numbers in part reflect differences in the size and number of canopy openings initially as well as differential survival rates of these young trees in low light conditions.

Prolific reproduction of sugar maple may be viewed as a biotic term insurance for maintaining canopy co-dominance for the species. Sugar maple sustains high mortality among smaller size classes, but survivors are also capable of reaching the canopy in a shorter time than can beech, if favorable conditions occur. Conversely, sugar maples apparently reach great age (> 200 years) much less frequently than do beeches. The slower growing beech have the potential for longer residence time as canopy individuals, once they reach large size. By employing contrasting life history strategies, the two species may co-dominate for long periods, each waxing and waning in response to change in the importance of the other and to environmental perturbations lasting a few decades to a century or more. In recent decades, beech has sustained heavy mortality from windthrow in many Midwestern stands, augmenting the natural tendency for sugar maple to increase.

The average yearly changes in density and basal area for certain species (Table 6) give reason for concern about the demography of some populations within these stands. Although such average yearly change rates are most likely not linear over long periods, consistent declines of even 1% per year would eliminate a species from the stand in less than a century. Flowering dogwood has decreased in both density and basal area at rates averaging more than 3% per year. These great population reductions were subjectively apparent to us upon first entering the stands for the 1988 study.

The authors have noted dieback and mortality of dogwood in a number of mesic stands in southern Indiana but had no quantitative documentation of population depletion before this study. Dogwood is well known to weather drought conditions poorly and as a species which concentrates calcium (Fowells, 1965). McCune, *et al.* (1987) have a monitoring study to determine the impact of mining activity surrounding Hemmer Woods on dogwood populations. More such studies on a long-term basis for a number of species are needed to determine causation of declines such as we noted for flowering dogwood from our twenty-year comparison. If the loss rates of past years are continued for another two decades, flowering dogwood will be essentially extirpated from both of these stands. Perhaps, Dogwood Nature Preserve should be renamed.

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