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Distribution of Biomass in an Indiana Old-growth Forest from 1926 to 1992

MARTIN A. SPETICH AND GEORGE R. PARKER

Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana 47907

ABSTRACT.—We examined the structural and spatial distribution of woody biomass in relationship to disturbance in an Indiana old-growth deciduous forest over a 66-yr period. Analysis was done on the core 7.92 ha of a 20.6-ha forest in which every tree 10 cm dbh and over has been tagged and mapped since 1926. Five years are compared—1926, 1976, 1981, 1986 and 1992. Dry weight of living biomass for the 7.92-ha area for these 5 yr was 154 Mg/ha, 207 Mg/ha, 220 Mg/ha, 216 Mg/ha and 211 Mg/ha, respectively. Biomass of dead trees was 1 Mg ha^{-1} yr^{-1} from 1977 through 1981; 4 Mg ha^{-1} yr^{-1} from 1982 through 1986; and 3 Mg ha^{-1} yr^{-1} from 1987 through 1992. Biomass of trees that died between 1976 and 1992 was greatest for midseral species. Living biomass of dominant early to midseral species is declining while that of late seral species is increasing. In 1926 biomass of trees 10 to 25 cm diam consisted of 14% *Quercus* spp. and 12% *Acer saccharum.* By 1992 biomass in this diameter range consisted of 1% *Quercus* spp. and 43% *A. saccharum.*

Equilibrium patch size was estimated for biomass at each of the five inventory dates to determine if there was a change. Equilibrium patch size for biomass was estimated to be 0.64 ha during all five inventory dates based on the coefficient of variation (CV) of biomass for 16 different grid cell sizes. Grid cell size refers to the size of adjacent cells in a grid that covered the entire study area. The grid with the smallest cells had cells of 0.01 ha. This grid of 0.01-ha cells was aggregated to 15 additional grid cell sizes, where the largest grid cell size was 1.98 ha. CV for all grid cell sizes was highest in 1926 due to effects of prior grazing.

These data indicate an increase in deadwood biomass, a shift in stand composition, recovery from grazing by an increase in small diameter trees and no change in equilibrium patch size over the five inventory dates.

INTRODUCTION

While numerous studies have been published on the structure and composition of deciduous old-growth woodlands in midwestern U.S. (Cain, 1935; Schmelz and Lindsey, 1965; Jackson and Allen, 1968; Williamson, 1975; Runkle, 1982; Parker *et al.,* 1985; MacMillan, 1988; McCune *et al.,* 1988; Runkle, 1990, 1991) relatively few papers on biomass for such woodlands have been published (MacMillan, 1981; Morz *et al.,* 1985; MacMillan, 1988). Most studies of deciduous old-growth forests for the midwest have been confined to short time periods and none have examined spatial pattern of biomass over long time periods. These studies often used importance values, basal area and/or density to estimate the influence of trees in these communities (Wuenscher and Valiunas, 1967; Jackson, 1968; Jackson and Allen, 1968; Schmelz and Hodde, 1971; Schmelz and Lindsey, 1970; Johnson *et al.,* 1973; Jackson and Barnes, 1975; McCarthy *et al.,* 1987). Equations to calculate biomass were not available when many of these studies were implemented. Biomass gives a different perspective on species importance in these forests because biomass can be a more descriptive measure of a tree's ability to compete for and store resources. Biomass estimates take into account differences in wood density, upper stem dimensions and crown morphology (Bell *et al.,* 1984) that importance values and basal area do not. For example, 20 *Acer saccharum* and 20 *Populus deltoides* trees that are all 30 cm at dbh have the same basal area estimate. However, these same 20 *A. saccharum* and 20 *P. deltoides* trees would have biomass estimates of 45 Mg and 86 Mg, respectively.

The spatial scale at which the variability of biomass per unit area becomes stable has not been studied for midwestern forests. But, this measure is important to researchers designing studies to observe biomass dynamics through time and for a better understanding of the scale of effects of disturbance. It has been suggested that the scale at which equilibrium occurs is about 50 times the size of the average disturbance patch (Shugart, 1984). Busing and White's (1993) study tends to support this ratio. They found reduced variation of biomass at scales (subplot aggregation levels) >0.5 ha for an old-growth forest in Tennessee consisting of mostly shade-tolerant species, where most canopy gaps were <0.02 ha and averaged approximately 0.01 ha.

High rates of tree mortality have been noted in several midwestern old-growth forests (McGee, 1984; Barton and Schmelz, 1987; McCune *et al.,* 1988). The Barton and Schmelz (1987) study of a central Indiana old-growth forest from 1954 to 1984 indicated that mortality increased through time in almost every size class, with oaks and hickories contributing 79% of the mortality. Parker *et al.* (1985) found that mortality varied by species, size class and size class within a species. Their analysis of size-class distribution of all species suggested that early and midseral species were being replaced by more tolerant, late-seral species. McGee (1984) found that mortality was rapidly shifting an old-growth forest from oak-hickory (*Quercus-Carya*) to a sugar maple-yellow poplar (*Acer saccharum-Liriodendron tulipifera*) dominated forest. The reason for high rates of mortality is unknown but is likely due to multiple factors. Dieter Muller-Dombois (1987) reasoned that stand-level dieback in North America was caused mostly by indigenous pathogens.

Many old-growth woodlands in the midwest have overstories of *Quercus* species with understories of tolerant species such as *Acer saccharum* and *Fagus grandifolia* (Lindsey, 1962; Johnson *et al.,* 1973; Schlessinger, 1976; McGee, 1984, 1986; Ward and Parker, 1989; Parker, 1989; Boerner, 1991; Cho and Boener, 1991; Shotola *et al.,* 1992). Others have reported regeneration dominated by these understory species (Cain, 1935; Quarterman *et al.,* 1972; Abrams and Downs, 1990; Boerner, 1991). Fire, grazing and clearing for agriculture have a long history in the region and promoted domination of forests by seral species (Parker, 1993). Native Americans used fire for agricultural clearing and driving game which is a likely cause of the seral species in canopies of many old-growth forests in the region (DenUyl, 1954; Campbell, 1989; DeVivo, 1990; Reich *et al.,* 1990; Denevan, 1992). Presettlement, old-growth oak forests may have been maintained by fire, however modern fire suppression has been used in the midwest for nearly a century (Rusterholz, 1991). In a review of historical data dating back to the early part of this century McCune and Menges (1986) found that old-growth forests in the region had a strong successional trend toward shade-tolerant species such as sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*).

In this paper we examine the change in biomass of the cohort of trees that existed at Davis Research Forest in 1926, through 1976, 1981, 1986 and 1992. The objectives of this study were to determine the relationship of disturbance to: (1) long-term biomass dynamics and (2) the variability of biomass with spatial scale.

STUDY SITE

The Davis Research Forest (DRF) is a 20.6-ha, old-growth, deciduous forest located in Randolph County of E-central Indiana, in the SE ¼ of Section 23, Township 21 North, Range 12 East. The site is in the Blufton Till Plain Section of the Central Till Plain Natural Region (Homoya *et al.,* 1985). Topography of the area is gently rolling with 3.1 m of relief. The four soils in this forest are Blount (fine, illitic, mesic Aeric Ochraqualfs), Glynwood (fine, illitic, mesic Apuic Hapludalfs), Pewamo (fine, mixed, mesic Typic Argiaquolls) and

Saranac (fine, mixed, mesic Fluvaquentic Hapluquoll). The site is vegetatively classified as a lowland depressional forest (Lindsey and Schmelz, 1970) but is physiographically located on upland. In this forest, an elevation change of only 1 m can result in dramatic changes in species composition, from *Quercus macrocarpa* dominants to *Q. rubra* and *Q. alba* dominants (*i.e.* from wet to mesic site species for this portion of Indiana). The forest canopy is dominated by *Quercus-Carya* with a range of tree species that typically occur on mesic to wet mesic sites. Ward and Parker (1989) found that 80% of total area in canopy gaps in a 4-ha portion of this forest were gaps that were 0.005 ha or less and the largest gap was 0.0375 ha. Subcanopy species are dominated by *Acer-Ulmus*. For a detailed site description *see* Parker *et al.* (1985).

Davis Research Forest was privately owned until 1917 when it was donated to Purdue University. Livestock grazing occurred from the mid-1800s until 1917. Other human disturbances included the cutting of up to 50 dead, dying and storm-damaged trees in the 1940s and 1950s; and theft of 3–4 *Juglans nigra* trees in the 1960s. Dutch elm disease and phloem necrosis continue to alter the structural status of both *Ulmus americana* and *U. rubra*. Minor disturbances have occurred outside the portion of forest examined during this research.

METHODS

Both living and deadwood biomass was determined for each tree within the study area. A curve of coefficient of variation vs. grid cell-size was produced to look at the scale of biomass equilibrium for living trees and its relationship to disturbance. These values were then compared with inventory date and disturbance regime.

Past inventories and layout of the study area.—This research is based on the core 7.92 ha of the forest where location of all five inventories overlap and edge influence is minimized (Fig. 1A). Measurement of trees began in 1926 when Professor Bur N. Prentice inventoried the forest by dividing it into 55 quadrats (most 1 acre in size). Every tree 4 inches (10.2 cm) or larger in diam was measured for diameter to the nearest inch at 4.5 ft (1.37 m) above ground level, a metal ID tag was placed on each tree and each tree was located on a large-scale map. Additionally, species, quadrat number, tree height, crown position, estimated growth rate, attached vines and forking were recorded for each tree (Bur M. Prentice, 1927, unpublished report, Purdue University Department of Forestry).

In 1976, the 1926 quadrat corners were relocated. All trees over 10 cm in diam were identified by species, tagged and their diameters were measured to the nearest centimeter at 1.37 m above ground level in the core 7.92-ha study area. North-south and E-W coordinates for each tree were determined to the nearest meter. In 1981 ingrowth trees, less than 10 cm diam in 1976 but $\geq$10 cm by 1981, were measured. In 1986 the study area was gridded into 10 × 10 m grid cells and trees, including ingrowth, were remeasured and referenced to each 10 × 10 m grid cell (Fig. 1B). In 1992, the study area was inventoried on the same 10 × 10 m grid including ingrowth. The 1926, 1976, 1986 and 1992 inventories were a 100% census of trees in the study area. Because only ingrowth trees were measured in 1981, diameters of all other trees within the study area for that year were calculated by using an annual growth rate specific to each tree. Growth rates were derived from the differences of the 1986 and 1976 diameters for each tree as follows:

$$(1986 \text{ dbh } - 1976 \text{ dbh})/10 \text{ years} = \text{Growth rate (cm/year)}$$

For trees that died after 1981 and before 1986, we used average growth rate by species. Due to their physical similarity, *Quercus rubra* includes *Q. shumardii.*

Biomass equations.—Only recently have equations for calculating biomass been available for the midwest (Smith, 1985; Hahn and Hansen, 1991). These equations were used to

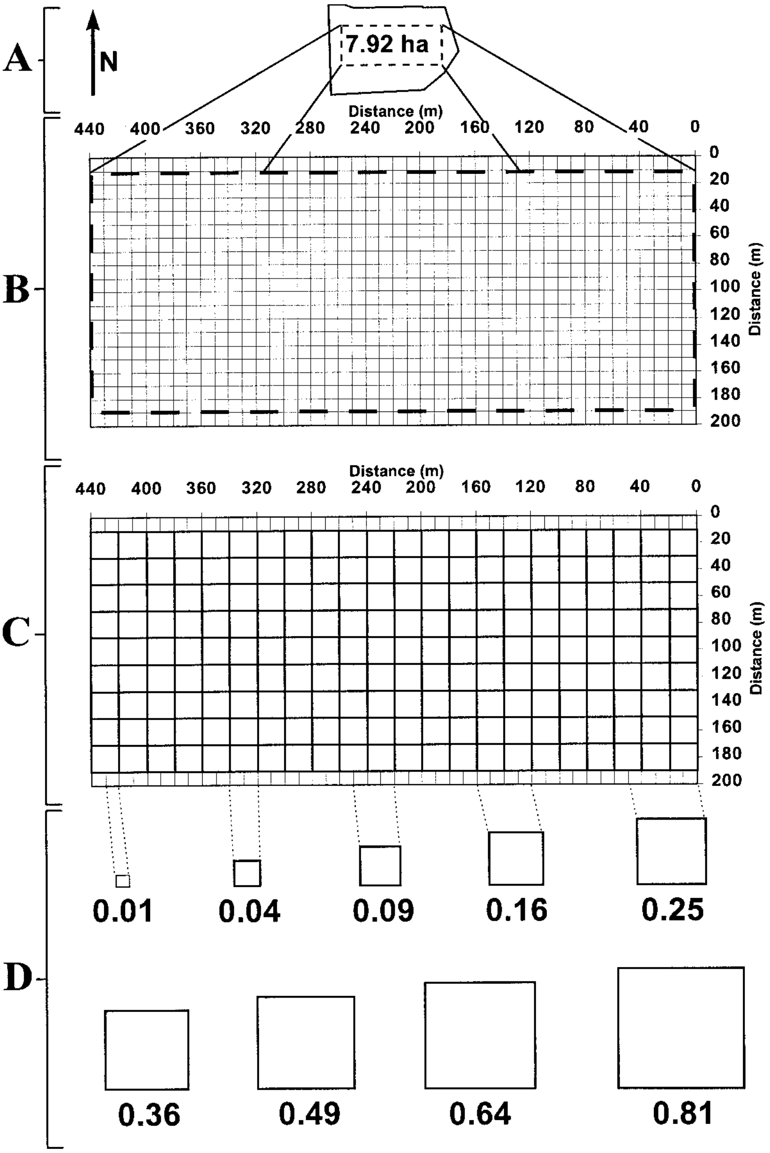

FIG. 1.—(A) Map of Davis Research Forest showing boundaries of the old-growth forest as solid lines and the study area as dashed lines. (B) The study area (dashed lines) divided into a grid of 10 × 10 m (0.01 ha) grid cells. (C) An example of how the study area was aggregated to a grid of 20 × 20 m grid cells (0.04 ha). (D) Nine of the 16 gird cell sizes used to aggregate the original 10 × 10 m grid into grids of larger grid cell size

determine dry weight biomass of each tree within the study site for the years 1926, 1976, 1981, 1986 and 1992. Two sets of equations were used to calculate biomass for each tree in this forest, one for the bole of each tree and one for the tree top and branches excluding leaves. These equations use a modified Wiebull model that is based on tree species, diameter and site index. Volume equations for the tree bole are based on over 50,000 observations (Hahn and Hansen, 1991) and take into account loss of biomass due to interior decay and other defects. A few trees in Davis Research Forest exceed the dbh range of the equations. This bole volume was combined with the tree top and branch volume from biomass equations in Smith (1985) to compute overall dry weight biomass for each tree.

Biomass equations are not without error. However, estimating error in a series of biomass equations that combine several sources of information is very problematic and generally not a practical exercise (Chojnaky, 1988, and Chojnaky, pers. comm., 1997). For instance, these equations combine equations of bole volume, bole bark volume, tree top and branch biomass, and estimates of wood density and bark density. Under these circumstances, calculating error would require destructive sampling of the study site. Despite this limitation these equations have been accepted as a standard in the midwest (Smith, 1985; Hansen and Hahn, 1991; Jose and Gillespie, 1997a, 1997b; Kaczmarek *et al.,* 1995). As the only equations available for the lower midwest, they provide relative biomass estimates for the region. Three input parameters are used in the equations: diameter at 1.37 m above groundlevel, tree species and site index. These equations are very sensitive to changes in diameter and species and least sensitive to changes in site index.

Site index (SI) values were obtained from three sources. The first was a statewide inventory done by Nick Bush (site index forester for the Indiana Department of Natural Resources) from 1981 to 1982. The data for that inventory were in the Soil Conservation Service's Integrated Resource Information System (dated 16 January 1985 and were obtained from the SCS Indianapolis Office in 1985). The second source was the Randolph County Soil Survey (Neely, 1987). The last source is from Carmean (1979) used to cross-reference known SI values for one species to species for which SI values were not available from other sources. SI values were then assigned to each tree and used as one of the three independent variables in the biomass equations as stated above.

Spatial scale of biomass variation.—All trees in the 7.92-ha study area were referenced to one of the 792 (10 × 10 m) grid cells, in which the tree was located (Fig. 1B). Data for the 10 × 10 m grid was then aggregated to 15 additional grid cell sizes (Fig. 1C and 1D). Biomass for each grid cell at all 16 grid cell sizes was referenced to each grid cell. Then the grids of the study area were used for comparisons of biomass variation; the grid cell size for each grid was: 0.01, 0.04, 0.09, 0.16, 0.25, 0.36, 0.49, 0.64, 0.81, 0.90, 1.08, 1.26, 1.44, 1.62, 1.8 and 1.98 ha. From 0.01 to 0.81 ha, grid cells were aggregated by increasing x and y axis for each successive increase in area by 10 m (Fig. 1C and 1D). The 10 m increment was used due to the constraint of the 10 × 10 m grid layout of the study area. Because the dimensions of the area were x = 440 m, y = 180 m (Fig. 1B and 1C) and a maximum number of grid cells were desired for each aggregation of cells, the y dimension (N–S) was held constant at 180 m while the x dimension (E–W) increased from 50 to 60, 70, 80, 90, 100 and 110 m for grid cell sizes from 0.90 to 1.98 ha.

This range of grid cell sizes was used to increase the probability of encompassing equilibrium patch size. Quasi-equilibrium landscape theory holds that vegetation attributes are consistent when averaged over a sufficiently large area (Shugart, 1984). To determine equilibrium patch size, coefficient of variation (CV) is plotted against grid cell size (Busing and White, 1993). The point at which CV levels off is the equilibrium patch size. However, to graphically determine this leveling off, one must have patch size (grid cell size) values larger

TABLE 1.—Biomass of living trees in the 7.92-ha study area, from a 100% census

Year	Biomass of all trees >10 cm dbh (Mg/ha)	Biomass of all trees from 10 to 25 cm dbh (Mg/ha)
1926	154	4
1976	207	14
1981	220	16
1986	216	17
1992	211	17

than the equilibrium value. Without a range of values that goes beyond the equilibrium patch size, determination of this leveling off would be impossible.

Shugart (1984) found that an area 50 times larger than the typical disturbance patch is required for equilibrium and Ward and Parker's (1989) data indicated that 80% of gaps in a 4-ha portion of this forest (the eastern ½ of our study area) were less than 0.005 ha, with the largest gap 0.0375 ha. We used the largest gap of 0.0375 ha and magnified it over 50 times to 1.98 ha to increase the probability of encompassing the equilibrium patch size. The coefficient of variation (CV) of biomass was calculated for each of the 16 grid cell sizes. Maximum number of grid cells were used for each grid cell size to encompass as much of the 7.92-ha study area as possible. Because the study area was 180 × 440 m, some grids covered less than the entire 7.92-ha study area. Trying to encompass the entire 7.92-ha area would have resulted in edge grid cells of unequal dimensions or sizes in these cases. CV was plotted against grid cell size to help determine equilibrium patch size at which CV showed only minimal changes for each additional increase in grid cell size.

Standing deadwood.—The entire forest was inventoried for tree mortality in 1976, 1978, 1981, 1983, 1984, 1986, 1987, 1988, 1989, 1991 and 1992. Trees that died during noninventory years were tallied during the following inventory. Biomass of tree mortality was grouped into three time intervals: 1977 to 1981, 1982 to 1986 and 1987 to 1992. Mortality for 1976 was not used due to the long time interval from 1926.

RESULTS

Biomass of the interior 7.92 ha increased from 1926 to 1976, peaked in 1981; then decreased in 1986 and continued to decrease to 1992 (Table 1). Biomass by tree diameter and year shows the bulk of biomass steadily moving towards larger diameter classes and expanding over a wider range of diameters over time (Fig. 2).

There was a total of 34 species in the core area over the five inventory periods (Table 2). *Morus rubra* existed only in 1926. *Cercis canadensis* existed as a gap species in 1976, 1981 and 1986 but was shaded out by other species by 1992 (Table 2). By 1976 *Acer saccharinum* had begun seeding in from larger trees in wet areas outside of the core area with some individuals reaching >10 cm dbh by 1986 (Table 2).

In 1926, the 10–25 cm diam trees had the lowest biomass of any year and continued to increase throughout the study (Fig. 3 and Table 1). In 1926, relative biomass was *Ulmus* spp. > *Fraxinus americana* > *Quercus* spp. > *Carya ovata* > *Acer saccharum* > *Juglans nigra* > *Gleditsia triacanthos* > *Celtis occidentalis* > *Aesculus glabra* > *Fagus grandifolia*. The remaining trees consisted of mostly early to midseral species (Fig. 4). By 1992 biomass of *A. saccharum* had increased over threefold and biomass of all *Quercus* spp. had decreased by a factor of >11 (Fig. 4).

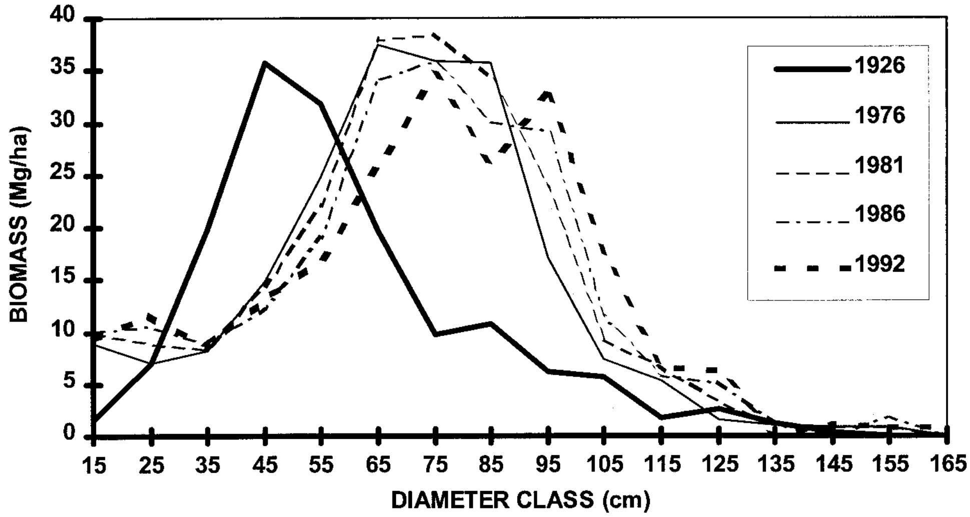

FIG. 2.—Living biomass by 10-cm diam classes for each inventory year. The 1926 trees were measured in 1-inch diam classes but were converted to metric values for graphical presentation

Most individuals of *Ulmus* spp., *Fraxinus americana, Juglans nigra, Quercus* spp. and the category listed as "other spp." in the 10–25 cm dbh range that were present in 1926 died by 1992 (Fig. 4). *Carya ovata* had the greatest percentage of the 1926 trees that remained in the same dbh range through 1992. Species with the most outgrowth (grew beyond this 10 to 25 cm diam range by 1992) were *Acer saccharum, C. ovata, J. nigra,* all *Quercus* spp. and *Fraxinus americana.*

In 1926 biomass of trees ≥100 cm in diam was 12 Mg/ha and consisted of five species (the ≥100 cm diam range was chosen because of the large drop in both living biomass and number of species at ≥100 cm). Relative biomass was *Quercus macrocarpa,* > *Q. rubra* > *Q. alba* > *Q. bicolor* > *Ulmus americana.* By 1992 biomass of trees ≥100 cm was 33 Mg/ha and consisted of six species. Relative biomass was *Q. rubra* > *Q. macrocarpa* > *Q. alba* > *Q. palustris* > *Q. bicolor* > *Quercus muehlenbergii.*

Stand biomass of midseral species (*Quercus rubra, Q. alba, Fraxinus americana* and *Q. palustris*) is either leveling off or decreasing, whereas the late seral species (*Acer saccharum*) is steadily increasing in biomass (Fig. 5). *Ulmus americana* was represented mainly in the smaller diameters by 1992, however biomass remained at nearly the same level from 1926 to 1992 (Fig. 5).

The coefficient of variation (CV) of the 16 grid cell sizes decreases rapidly from grid cell sizes of 0.01 to 0.04 ha for all five inventory dates (Fig. 6). From 0.04 ha to 0.09 ha the 1926 CV is higher than the other four dates with a CV of 41% at 0.09 ha and an average CV of 26% for the other inventory dates. At 0.16 ha the last four inventory dates are beginning to diverge into two groups based on similar CVs (one-way ANOVA showed significant differences between the two groups, $P < 0.001$, df = 51): (1.) 1976 and 1981 and (2.) 1986 and 1992. CVs for all inventories levels off at 0.64 ha, with average CVs for grid cell size from 0.64 ha to 1.98 ha of: 23.44, 11.33, 10.11, 6.44 and 6.11 for the years 1926, 1976, 1981, 1986 and 1992, respectively. There are three ranges of grid cell size that decrease in rate of CV decline; they are: 0.04 to 0.09 ha, 0.09 ha to 0.25 ha and 0.25 to 0.64 ha.

TABLE 2.—All species at each inventory date for the core 7.92 ha of Davis Research Forest, from a 100% census. For each year and species combination #/ha is the number of trees per hectare and avg. dbh (cm) is the average diameter at breast height (1.37 m). Note that *Q. rubra* includes *Q. schumardii*

	Year									
	1926		1976		1981		1986		1992	
Species	#/ha	Avg. dbh (cm)	#/ha	Avg. dbh (cm)	#/ha	Avg. dbh (cm)	#/ha	Avg. dbh (cm)	#/ha	Avg. dbh (cm)
Acer negundo	0.0	0.0	2.0	14.4	2.4	15.8	2.9	16.4	3.3	17.0
A. rubrum	0.6	46.7	2.5	23.1	2.8	24.8	2.9	24.5	2.7	27.0
A. saccharinum	0.0	0.0	0.0	0.0	0.0	0.0	0.3	11.1	0.3	13.7
A. saccharum	7.6	30.6	56.3	17.7	69.3	17.9	84.5	18.2	96.5	18.6
Aesculus glabra	0.9	26.1	16.5	14.0	17.9	14.4	17.3	14.9	17.0	15.6
Amelanchier arborea	0.0	0.0	0.1	11.0	0.1	11.6	0.0	0.0	0.0	0.0
Carpinus caroliniana	0.0	0.0	12.4	11.6	12.4	12.0	6.1	12.1	3.2	12.7
Carya cordiformis	0.4	38.1	4.0	18.1	4.5	18.2	3.9	19.5	4.0	19.7
C. glabra	0.3	21.6	1.1	19.1	1.3	19.5	1.3	20.8	1.1	22.6
C. ovata	8.7	30.0	23.6	19.5	24.7	20.0	23.5	20.3	22.9	20.6
Celtis occidentalis	0.8	19.9	9.3	16.3	10.9	16.9	11.7	17.7	11.2	18.1
Cercis canadensis	0.0	0.0	0.4	14.0	0.3	12.0	0.1	14.2	0.0	0.0
Cornus florida	0.0	0.0	0.4	10.7	0.4	11.0	0.4	10.8	0.4	10.7
Crataegus spp.	0.0	0.0	5.3	12.3	5.7	12.4	4.9	12.8	4.2	13.3
Fagus grandifolia	0.9	38.1	9.1	19.6	9.5	21.1	9.2	23.2	9.5	25.0
Fraxinus americana	30.6	35.7	19.1	39.8	19.1	41.0	15.5	42.5	13.3	43.2
F. nigra	5.7	35.8	1.4	27.8	1.4	29.4	0.9	26.5	0.6	22.6
F. quadrangulata	0.4	47.4	1.5	25.8	1.8	21.4	2.0	19.1	1.6	15.9
Gleditsia triacanthos	2.5	22.1	1.4	36.1	1.1	39.8	0.6	44.4	0.5	41.6
Juglans nigra	9.3	27.6	8.0	37.2	7.8	39.2	6.9	43.0	6.7	44.9
Morus rubra	0.5	22.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ostrya virginiana	0.1	10.2	4.5	12.3	4.9	12.6	4.3	12.4	2.7	13.2
Platanus occidentalis	0.8	28.8	0.5	41.0	0.5	43.4	0.5	45.2	0.4	52.1
Populus deltoides	0.1	27.9	0.1	53.0	0.1	55.7	0.1	58.4	0.1	62.0
Prunus serotina	0.5	19.7	4.5	17.0	5.1	17.9	4.4	18.5	4.3	18.4
Quercus alba	12.9	47.6	11.0	64.6	10.2	67.9	9.7	70.1	9.1	72.0
Q. bicolor	6.7	49.7	5.8	59.1	5.8	61.7	5.2	65.9	4.9	68.5
Q. macricarpa	9.2	55.3	8.1	71.5	8.1	73.8	8.1	76.1	7.8	78.4
Q. muehlenbergii	4.2	43.3	3.5	59.8	3.4	62.6	3.4	64.8	3.4	67.4
Q. palustris	3.9	49.4	3.3	70.0	3.4	68.2	2.8	76.0	2.4	81.9
Q. rubra	35.5	48.8	22.5	67.9	21.5	70.9	17.7	73.5	14.9	76.6
Tilia americana	0.5	24.8	1.8	19.6	1.8	22.1	1.6	25.0	1.8	25.1
Ulmus americana	20.8	21.4	62.9	15.4	61.6	16.2	55.6	17.3	46.0	17.7
U. rubra	1.0	40.6	16.8	15.8	18.3	16.6	20.2	17.3	15.3	18.8

Deadwood biomass additions increased from 1976 to 1992 with peak additions from 1982 to 1986 (Table 3). *Quercus rubra, Q. alba* and *Fraxinus americana* consistently contributed the most biomass (Fig. 7). The number of species contributing more than 0.1 Mg ha^{-1} yr^{-1} of deadwood during each time period was: 1977 to 1981 = four species; 1982 to 1986 = seven species; and 1987 to 1992 = five species (Fig. 7). *Ulmus americana* was the fourth largest contributor in 1977 to 1981 with 11% of total deadwood and in 1987 to 1992 with 7% of total deadwood. From 1982 to 1986 *Q. bicolor* with 6% of total deadwood, *Q. palustris*

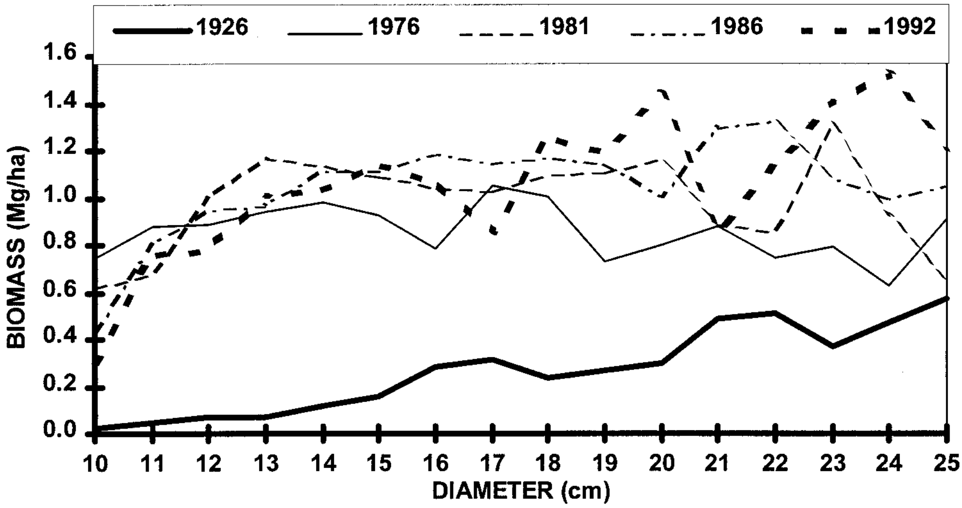

FIG. 3.—Total living biomass for the 10 to 25 cm range of diameters for each inventory year

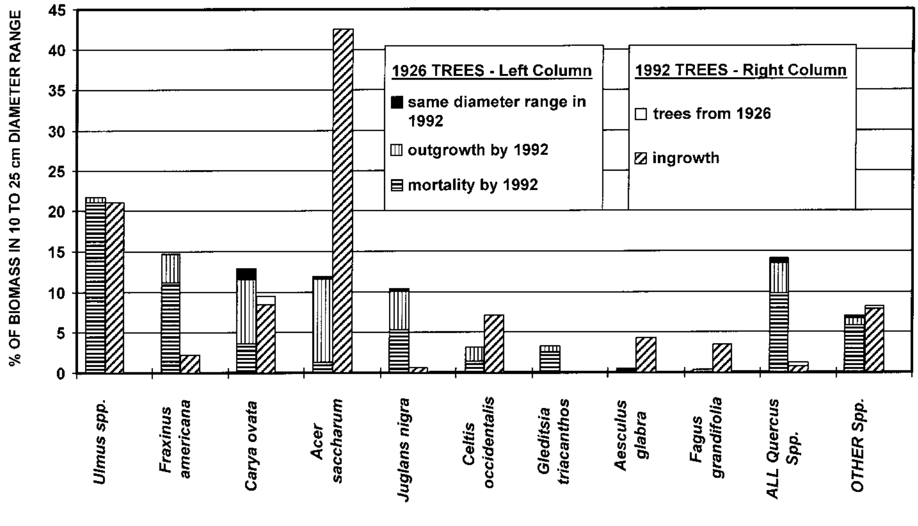

FIG. 4.—Percent biomass for trees ranging in diam from 10 to 25 cm dbh, by species, for 1926 and 1992. Individual species were shown when biomass was >3% in either year. Column categories for 1926 are: same diameter range in 1992 (trees that remained in this diameter range through 1992); outgrowth by 1992 (trees that were >25 cm dbh by 1992); mortality by 1992 (trees that died by 1992). Column categories for 1992 are: trees from 1926 (original 1926 trees that survived but did not grow out of this size class). Note that there was more biomass in 1992 (*see* Fig. 3) and that percent of biomass in this figure is relative to the year in question. *Acer saccharum* increased from 12% in 1926 to 43% by 1992. All *Quercus* spp. combined decreased from 14% in 1926 to 1% by 1992. Mid-seral species have decreased in importance while the late seral *Acer saccharum* increased in importance. *Fagus grandifolia* also increased but is not likely to become a major component of this forest

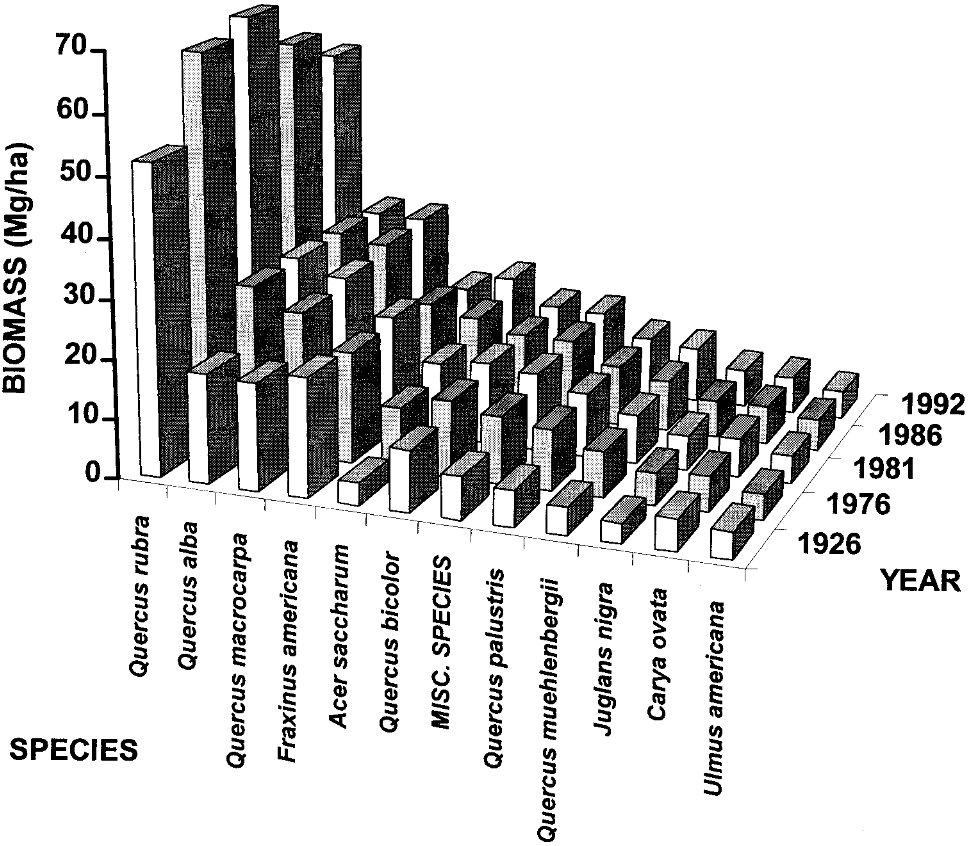

FIG. 5.—Living biomass of the 11 most important species, by year. There are 23 miscellaneous species (*see* Table 2). Note that *Fagus grandifolia* is included in the miscellaneous species group

with 5% of total, *Carya ovata* with 4% of total and *U. americana* with 3% of total were fourth, fifth, sixth and seventh contributors, respectively. Proportion of deadwood biomass additions from trees ≥70 cm dbh was: 1977 to 1981 = 25%, 1982 to 1986 = 45% and 1987 = 58%. The ≥70 cm dbh range was chosen because this is approximately the maximum diameter of deadwood in Indiana second-growth forests, thus quantifying a unique feature of old-growth forest.

DISCUSSION

Davis Research Forest (DRF) biomass estimates are greater than mean biomass estimates reported for other mature temperate deciduous forests. In a summary of 36 studies, Cole and Rupp (1981) found the mean biomass of mature temperate deciduous forests was 151.9 Mg/ha (SD ± 58.1). However, it is not clear what components were measured at each site. The DRF values ranged from a low of 154 Mg/ha in 1926 to a high of 220 Mg/ha in 1981 (Table 1). Note that the 1926 and 1976 values fall within one SD of the Cole and Rupp mean. However, if grazing had not occurred at DRF during the mid-1800s through 1917, these biomass values might have been greater. Lack of grazing would have allowed regen-

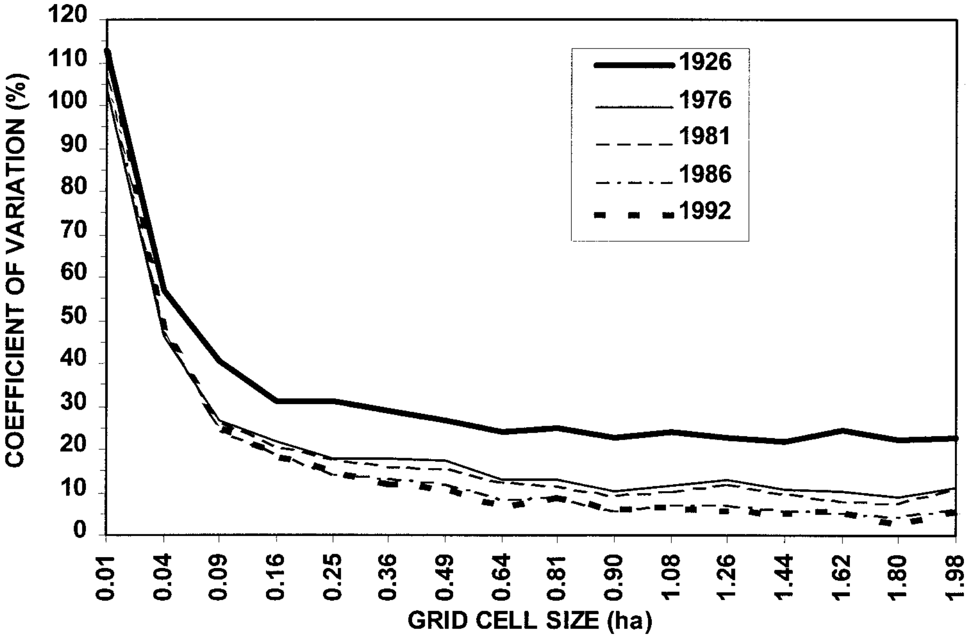

FIG. 6.—Coefficient of variation at 16 grid cell sizes and five time periods. The 7.92-ha study area was gridded by each grid cell size. The site had a 100% inventory of trees at each date

erating trees to fill in canopy gaps and these trees would have been approximately 60 to 125 yr old by 1976.

Even with the lack of grazing it is unlikely that DRF will ever reach biomass levels associated with old-growth forests of the Great Smoky Mountains (GSM). The average branch and bole biomass of six old-growth deciduous stands in the GSM was 401 Mg/ha (Busing *et al.,* 1993). These estimates included all trees >2 cm. Average basal area was 47 m^2/ha compared to DRF's 23.7 m^2/ha in 1926 and 31.0 m^2/ha in 1976 (Parker *et al.,* 1985). White and Peet (1994) gave the diameter range for GSM's old-growth cove hardwoods as 2 to 3 m compared to DRF's largest tree ever recorded at 1.6 m and most below 1 m (Fig. 2). Greater biomass in the GSM is attributed mostly to larger diameters and differences in species morphology. Individual *Platanus occidentalis* trees in Indiana bottomlands in 1870 to 1890 have been recorded to range in diam from 2.4 to 4.6 m (DenUyl, 1957). However, a 1930 study of 22 old-growth forests in Ohio, Indiana and Illinois found only one tree >1.2 m (Auten, 1941).

TABLE 3.—Deadwood biomass for three time intervals in a 7.92-ha core area of Davis forest. Based on trees that died during each period, values do not include residual deadwood from previous dates

Time period	Deadwood biomass ($Mg\ ha^{-1}\ year^{-1}$)
1977 to 1981	1
1982 to 1986	4
1987 to 1992	3

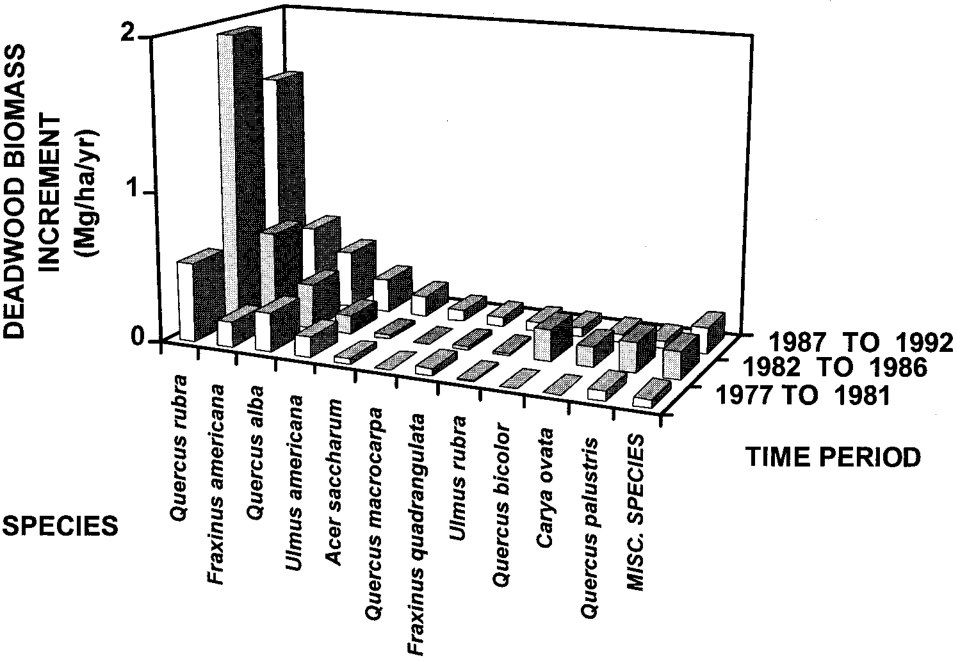

FIG. 7.—Deadwood biomass increment in Mg ha^{-1} $year^{-1}$ for three time intervals. The miscellaneous category includes 19 species

Species dynamics and disturbance.—Which tree species will regenerate in forest gaps depends on gap size and state of the understory (Runkle, 1982, 1990). At the DRF, most gaps are too small for shade-intolerant trees to reach maturity (Parker and Sherwood, 1986) and sugar maple dominates the understory advanced regeneration pool in all but wet, seasonally ponded areas. This results in the regeneration of late seral, shade-tolerant trees in most gaps. In 1976 *Acer saccharum* accounted for 20% of all trees within a 5-m radius of dead dominant or codominant trees (Parker *et al.,* 1985). Visual observations in 1992 indicated the same pattern of species regeneration. Since 1926, biomass of the 10 to 25-cm diam class has included an increasingly larger proportion of *A. saccharum,* indicating its increasing importance in the regeneration pool. However, overall biomass is still dominated by earlier seral species.

In this forest, midseral species accounted for most biomass and overall biomass levels increased until 1981 (Table 1). From 1981 through 1992, biomass was decreasing. Biomass of some midseral species was decreasing, whereas biomass of other midseral species was leveling off (Fig. 5). Late seral *Acer saccharum* was increasing in overall biomass (Fig. 5) and total number (Table 2). Parker and Ward (1987) obtained similar results by looking at importance of late seral species. The increase of *A. saccharum* is likely due, in part, to fire supression.

However, other disturbance factors have also affected dynamics of this forest. For instance; Dutch elm disease and release from grazing have contributed to the biomass change of *Ulmus americana* and *U. rubra.* The relatively level biomass of *U. americana* (Fig. 5) supports the predicition for the replacement and maintenance of this tree as a subcanopy species

(Parker and Leopold, 1983). Grazing ended in 1917 (Parker and Leopold, 1983), making establishment of young trees possible. Dutch elm disease spread into this part of Indiana by the late 1940s and early 1950s (Schuder, 1955). By the late 1960s the *U. americana* at DRF were dying. This disease eliminated dominant trees in the forest, creating more canopy gaps in which regeneration could occur. In 1992 trees ≥100 cm diam were 100% *Quercus*. The only year when another species existed in this diameter range was 1926 when *U. americana* was 5% of the biomass. In 1976 Parker, *et al.* (1985) found 30% of all trees growing within a 5 m radius of dead dominant or codominant trees were *U. americana*. Although total biomass has remained relatively level, biomass distribution has shifted to mainly small diameter trees. Without protection from livestock grazing, *U. americana* would not have been able to re-establish itself in these small-diameter trees.

Protection from grazing and fire began in 1917. In 1926 the 10 to 25-cm diam trees consisted of 14% *Quercus* species and 12% *Acer saccharum* (Fig. 4). After more than 75 yr of disturbance suppression, in 1992 subcanopy trees were 43% *A. saccharum* with all *Quercus* species representing only 1%. Similar shifts in species composition of midwestern old-growth forests have been found (Johnson *et al.,* 1973; Cho and Boerner, 1991; and Shotola *et al.,* 1992). The low biomass of *Fagus grandifolia* in 1926 (Fig. 4) could have been due in part to soil compaction by livestock before 1917. Additionally, while a specific limiting factor has not been identified, this site doesn't appear to be favorable to the regeneration of *F. grandifolia* (Parker and Ward, 1987).

Carya ovata showed little response to release from grazing in overall biomass (Fig. 5), but did increase in number of trees (Table 2). In addition, a relatively large proportion of the original 1926 *C. ovata* individuals remained in the 10 to 25 cm dbh range throughout the 66-yr inventory period (Fig. 4). This is likely due to its relatively slow growth rate and relatively good survival. Of trees in this dbh range, percent survival of *C. ovata* was high, second only to *Acer saccharum.*

The major factor influencing changes in tree regeneration in this forest has been grazing. This is supported by the increase in the biomass-diameter curves for 10 to 25 cm diam trees (Fig. 3) after 1926. In fact, the forest was described as open and parklike in 1926 due to grazing (Parker and Leopold, 1983). This forest is now closed and dense in comparison.

Rate of biomass accumulation.—Not only has biomass distribution and regeneration changed within this forest, but the rate of biomass accumulation has increased even though 47% of the trees originally tagged in 1926 had died by 1976 (Parker *et al.,* 1985). From 1926 to 1976, the average annual rate of accumulation was 1 Mg ha^{-1} $year^{-1}$. Between 1976 and 1981, the average annual rate of biomass accumulation was 3 Mg ha^{-1} $year^{-1}$. This is due, in part, to biomass accumulation on larger diameter trees. For instance, in 1926 the diameter range of trees containing most of the biomass was 25–65 cm, while in 1976 this range was 40–90 cm. Additionally, there were nearly twice as many trees in 1976 (1926 = 1309, 1976 = 2533). This higher density of trees has also influenced the spatial variability of biomass.

Spatial and temporal scale of biomass.—Scaling in space and time is an important issue in ecology (Wiens, 1989). In studies of tree dynamics, knowledge of the scale at which processes take place is important to understanding the pattern and role of disturbance. It can also be useful when determining quadrat or relevé size to use for a study. DRF data give both spatial and temporal scales of biomass. The 1926 CV values were greater than all other inventory dates at all 16 grid cell scales (Fig. 6). This is attributed to suppression of tree regeneration by livestock from the 1800s to 1917 which resulted in patchiness of biomass distribution. After the stand began recovery from grazing, gaps filled in with new trees and biomass became more evenly distributed.

Grazing can be considered exogenous disturbance destroying mainly understory trees. However, tree mortality is endogenous disturbance throughout the forest strata. *Quercus rubra,* a spatially uniformly distributed spp. (Leopold *et al.,* 1985), accounted for 40% of deadwood from 1977 to 1981, 52% from 1982 to 1986 and 46% from 1987 to 1992. Increased mortality after 1981 was probably responsible for the 1976 and 1981 CVs and the 1986 and 1992 CVs diverging into two groups of similar values (Fig. 6). This divergence shows how both mortality of an evenly distributed species and subsequent regeneration may have combined to lower CVs. CVs are decreasing with time at all scales. CVs for all inventories level off at grid cell sizes ≥0.64 ha, indicating an equilibrium patch size for biomass. Busing and White (1993) found similar results for an old-growth forest in the Great Smoky Mountians National Park. In their study, spatial variation at scales >0.5 ha was low for both biomass and total basal area. Their study suggested that biomass may have reached equilibrium between 0.5 and 1.0 ha due to reduced spatial variation and prompted them to support Shugart's *et al.* (1981) ratio of patch size.

Using a forest simulation model that looked at gap size vs. biomass, Shugart *et al.* (1981) estimated a 50:1 ratio was needed to stabilize variance. Our design considered disturbance patch size to be equal to the canopy gap size of approximately 0.005 ha (Ward and Parker, 1989). Therefore, our estimate of 0.64 ha for equilibrium patch size was 128 times greater than the disturbance patch size.

Although our equilibrium patch size was much larger than expected for a canopy gap it may not be as large for the effective gap. We define canopy gap as the land surface directly under a canopy opening (Runkle, 1991) and effective gap as the surface area in which biomass is significantly influenced by the canopy opening. It is likely that the effective gap includes both canopy gap and understory gap. Belsky and Canham (1994) pointed to evidence indicating that understory patches are not the same size or shape as the canopy gap. These patches can be considerably larger than the canopy gap. This difference could be more pronounced for some factors when the gaps are small, since the proportion of canopy edge to gap area becomes larger.

Care should be taken when applying our results for equilibrium patch size to other forests, especially younger forests. Competitive sorting of species may be more advanced in old-growth forests (Muller, 1982) than in younger stands. Because species aggregate to different degrees in DRF, species-specific mortality can influence the variability of stand biomass. For instance, Busing and White (1993) found more variation of biomass when individual species were considered in an old-growth forest in the Great Smoky Mountains National Park. Therefore our results for equilibrium patch size at DRF probably do not apply to younger stands.

Deadwood.—Lang and Forman (1978) found that large decaying boles represented 10% of aboveground biomass and 9% of total detritus in an undisturbed oak forest in New Jersey. McCarthy and Bailey (1994) found biomass of deadwood for three managed forests, 100–200 yr old, was 33 Mg/ha (diam range ≥2.5 cm). Muller and Liu (1991) estimated the range of coarse woody debris for warm, temperate deciduous forests to be 22 to 32 Mg/ha (diam range ≥20 cm). In a southern Indiana old-growth forest, MacMillan (1988) estimated biomass of dead and downed *Quercus* sp., *Carya* sp., *Fraxinus grandifolia* and *Acer* sp. to be 15.083; 2.333; 0.203; and 0.366 Mg/ha, respectively (diam range ≥5 cm).

We can consider only periodic additions of deadwood biomass at DRF because decomposition rates are unknown, thus the residual amount of deadwood biomass from previous periods is unknown. *Quercus rubra, Fraxinus americana, Q. alba* and *Ulmus americana* are the greatest contributors of deadwood biomass (Fig. 7). *Ulmus americana* is now distributed in small diameters and is 4th to 7th in deadwood contribution (Fig. 7), but still has relatively level living biomass from 1926 to 1992 (Fig. 5). Therefore, it is rapidly cycling energy and nutrients through this forest. This cycling is implied in Figure 4 where nearly all 10–25 cm dbh *U. americana* trees that existed in 1926 died by 1992 but percent biomass in 1992 was nearly equal to the 1926 value. Many more large diameter *Q. rubra, Q. alba* and *F. americana* died from 1982 to 1992 than from 1977 through 1981.

The increase of deadwood biomass in 1982 to 1992 indicates a higher frequency of canopy gap formation than in 1977 to 1981 (Table 3). Percent of deadwood from trees ≥70 cm has increased from 25% to 45% to 58% for each successive time period. This indicates that the largest trees are either past maturity, under stress or both. In a mortality study of a virgin mixed mesophytic forest in Tennessee, McGee (1984) found the average age of mortality for *Quercus rubra* = 135 yr and for *F. americana* = 172 yr. These two species contribute the most deadwood biomass at DRF. This corresponds to average ages of dominant *Q. rubra* = 147 yr and *F. americana* = 154 yr, based on a pilot study of tree ages at DRF in which cross sections of randomly selected, recently dead trees were collected to determine age. The DRF mortality rates were useful in estimating the future trajectory of this forest.

Future trajectory.—Based on this time series of biomass accumulation and shifts in distribution, we predicted the future trajectory of this forest. In this scenario there are no exogenous events and biomass continues to decline until it reaches the end of the transition phase. In the transition phase, biomass declines, gap formation increases and there is a shift from mid- to late seral species (Borman and Likens, 1979). Based on the mortality rate of midseral species from 1986 to 1992, the earliest that an *Acer*-dominated phase would begin is the year 2070, excluding exogenous events. Using published data of Petty and Lindsey (1961), we calculated biomass of an old-growth site with late seral, shade-tolerant trees in central Indiana at 160 Mg/ha. We would expect biomass to vary around this value (the estimated mean) over time.

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