FIFTY-FIVE YEARS OF ASSOCIATION AND DIVERSITY DYNAMICS IN AN OLD-GROWTH FOREST IN INDIANA: DAVIS-PURDUE RESEARCH FOREST 1926-1981[1/]

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Abstract.--All woody stems, ≥ 10 cm dbh, in an 8.5 ha study area were measured and mapped in 1926 and 1976-1981. Associations were analyzed using annuli density analysis. Diversity was calculated using species richness, Pielou's evenness index, and the Shannon-Weiner index. The association plexus for the canopy trees was less complex in 1981 than in 1926, possibly the result of greater stratification of species to their optimal sites. The association plexus for the subcanopy trees was more complex in 1981 than in 1926; in part the consequence of the large increase in ingrowth density. Diversity increased significantly from 1926 to 1981 in both size classes, primarily due to increased equitability.

Keywords: Shannon-Weiner index, equitability, transitional forest

INTRODUCTION

Although the literature on the central hardwoods is rich in detailed descriptions of the dynamics of stand structure (Leopold et al. 1985a, Nigh et al. 1985, Della-Bianca 1983, Muller 1982, Bormann and Likens 1981), there is little information on the dynamics of stand diversity and interspecific association in oak-hickory forests (Auclair and Goff 1971, Loucks 1970). State parks and recreation areas are often protected from man-induced exogenous disturbances such as harvesting and grazing as well as having active fire suppression programs. Information on the long term consequences of this management system on diversity and interspecific association is limited. The major objective of this study was to provide baseline information on the changes in associations and diversity of an old-growth oak forest managed as a forest preserve.

A criticism of many association studies is that they have not focused on associations at the interplant level, i.e. which species are the immediate neighbors of a plant (de Jong et al. 1983, Yarranton 1966). Our definition of association was limited to a neighborhood scale, up to 30 meters from any one plant. Associations were analyzed with annular association analysis.

This study also examined diversity within the forest. Whittaker (1965) designated within community diversity as alpha diversity. Alpha diversity is composed of two components: species richness and equitability (Stocker et al. 1985). Species richness indices examine the variety of species. Equitability indices examine the distribution of individuals among the species. Overall diversity was calculated using the Shannon-Weiner (1948) index. The number of species, S, was used as the measure of species richness; and Pielou's evenness index, J, was used to examine equitability.

STUDY AREA

The Davis-Purdue Research Forest is located in Randolph County in east-central Indiana. The 20.6 ha forest is considered one of the finest old-growth forests remaining on the Tipton Till Plain and is a Registered National Natural Landmark. It is likely that the forest was

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grazed prior to Purdue University ownership in 1917. The forest has subsequently been protected from grazing. Some dead and dying trees were harvested in the 1940's and 1950's. In 1971 there was a two to three hectare surface fire in the western part of the forest.

Topography is gently rolling with low relief. Elevation changes less than five meters over the study area. Areas of seasonal ponding are scattered throughout the forest. These areas are associated with Pewano and Brookston silty clay. Morley silt loams are found on the well-drained slopes. The somewhat poorly drained Blount silt loam is found on the level higher locations. Lindsey and Schmelz (1970) classified the forest as a lowland depressional forest due to an abundance of wet site tree species. Quercus spp. and Fraxinus americana accounted for 68% of the trees greater than 25 cm dbh (diameter at 1.37 m) in 1981 (table 1). Many of the oaks in the overstory are believed to be 150-200 years old with some individuals over 300 years (Parker et al. 1985). More extensive descriptions of forest vegetation, topography, and soils can be found in Parker et al. (1985), Leopold et al. (1985b), and Parker and Leopold (1983).

METHODS

Field Measurements

All trees over 10 cm dbh were first mapped, measured, and tagged in 1926 (Prentice 1927). In 1976 an inventory was taken of the woody vegetation in a central 8.5 ha study area. An interior study area was chosen to reduce edge effects on vegetation composition. All trees over 10 cm dbh were mapped, measured, and tagged. An inventory in 1981 recorded ingrowth and mortality since 1976 in the 8.5 ha study area. Survivors of the 1926 survey were identified by their original tags and/or the 1926 coordinates. Tree diameters were measured to the nearest inch (2.54 cm) in 1926, and to the nearest centimeter in 1976 and 1981. Stems were mapped to the nearest meter. For analyses all stems were divided into one of two size classes: canopy (> 25 cm dbh) and subcanopy (≤ 25 cm dbh). Twenty-five centimeters (10 inches) is the approximate diameter at which trees become part of the upper canopy. Nomenclature follows Kartesz and Kartesz (1980).

Association Analysis

To study association at the interplant level we developed a technique to discern which species have high relative densities in close proximity to other species- annuli density analysis. All trees inside of a twenty meter buffer strip around the perimeter of the study area were used as focal trees. All species with a minimum of twenty trees inside the buffer strip were used in the analysis. Using each tree's coordinates as a focal point the density (stems/ha) of other (associative) species in successive discrete annuli determined. Density measurements extended out fourteen meters using annuli widths of two meters. Mean densities (by focal species) were plotted against distance from focal trees. We used the following subjective criteria for association: 1) density of associative species peaked with a minimum mean value of 140% stand average density within 14 m of focal trees, or 2) density of associative species was 120% of stand average density for three consecutive annuli within 14 m of focal trees.

An implicit assumption of annuli density analysis is that species dispersion in a forest are dependent on edaphic, historic, or biotic factors. Reciprocally high density of each species in the proximity of the other species would strongly suggest both species have similar niches in the forest community, i.e. they are associated. The advantage of using relative densities in studying associations is changes in absolute densities should have limited effect on the detection of associations allowing any changes in associations to be related to biotic and/or abiotic mechanisms of association.

Diversity Analysis

One of the most widely used measures of species diversity is the Shannon-Weiner index of diversity, $H' = -\Sigma\, p_i \log(p_i)$; where p_i is the proportion of total individuals in the ith species (Shannon 1948). This index has been used to study diversity in central hardwoods (Auclair and Goff 1971, Loucks 1970), and in southern hardwoods (Christensen 1977, Monk 1967). The Shannon-Weiner index of diversity is sensitive to changes in the number of species and the distribution of individuals among the species. For a given number of species and individuals, the index has the highest value when all species have the same number of individuals. A t-test described in Zar (1974, p115) was used to determine when populations had significantly different diversities. Species number, S, was used as the index of species richness. Stocker et al. (1985) reported species number was as satisfactory as other, more complex, indices. Equitability was calculated using an index, $J = H'/H'_{max}$, described in Pielou (1969).

To examine the influence of canopy trees on subcanopy diversity the study area was partitioned into 84-0.1 ha plots. Within each plot the following canopy parameters were determined: 1926 density (n/ha), 1926 basal area (m^2/ha), 1926 stocking (%), 1981 density, 1981 basal area, 1981 stocking, change in density from 1926 to 1981, change in basal area from 1926 to 1981, and change in stocking from 1926 to 1981. Percent stocking was calculated

Table 1.--Stand density and stocking by species and diameter class of trees ≥ 10.0 cm dbh in the interior 8.5 ha of the Davis-Purdue Research Forest.

Species	(Abbreviation)	Canopy[1/] 1926	Canopy[1/] 1981	Subcanopy[2/] 1926	Subcanopy[2/] 1981
Acer negundo	(Ane)	--	--	--	21
Acer saccharinum	(Asn)	6	3	--	15
Acer saccharum	(Asa)	49	69	16	531
Aesculus glabra	(Agl)	6	6	4	144
Amelanchier arborea	(Aar)	--	--	--	13
Carpinus caroliniana	(Cca)	--	--	--	93
Carya cordiformis	(Cco)	3	4	--	44
Carya glabra	(Cgl)	--	1	1	8
Carya ovata	(Cov)	48	49	30	179
Celtis occidentalis	(Ceo)	1	8	8	46
Crataegus spp.	(Csp)	--	--	1	46
Fagus grandifolia	(Fgr)	6	14	1	62
Fraxinus americana	(Fam)	220	102	39	65
Fraxinus nigra	(Fni)	46	5	1	13
Fraxinus quadrangulata	(Fqu)	3	2	--	8
Gleditsia triacanthos	(Gtr)	6	9	15	2
Juglans nigra	(Jni)	40	46	37	22
Ostrya virginiana	(Ovi)	--	--	1	42
Platanus occidentalis	(Poc)	4	4	4	--
Prunus serotina	(Pse)	1	4	3	37
Quercus alba	(Qal)	105	83	6	3
Quercus bicolor	(Qbi)	48	39	2	4
Quercus macrocarpa	(Qma)	76	66	4	3
Quercus muehlenbergii	(Qmu)	31	26	1	2
Quercus palustris	(Qpa)	32	25	3	1
Quercus rubra	(Qru)	292	181	9	6
Tilia americana	(Tam)	1	3	3	12
Ulmus americana	(Uam)	44	18	137	608
Ulmus rubra	(Uru)	8	2	1	53
Other species[3/]		3	1	2	5
Total (8.5 ha)		1079	770	327	2117
Stocking (%)		73	81	4	19

[1/] All stems > 25 cm dbh.
[2/] All stems ≤ 25 cm dbh.
[3/] Includes Cercis canadensis, Cornus florida, Morus rubra, and Populus deltoides.

using the tree-area equation of Ginrich (1967). Procedures outlined in Zar (1974) were used to calculate and assign significance to simple correlation coefficients for each of the canopy parameters with 1981 subcanopy diversity (H').

RESULTS

Association

Positive associations between species with greater than four stems per hectare are shown in plexus diagrams (fig. 1-2). Species were arranged for clarity. Area of inscribed circles in proportional to each species stand density. Only positive associations are shown. Line length is unrelated to the strength of the association. Assignment of specie hydric/mesic associations was based on s tolerance to periodic inundation (Teske Hinckley 1977). Hydric species are species found primarily on depressional which periodically have ponded water duri year.

In 1926 a complex association plexus distinct hydric to mesic gradient cou observed for the canopy trees (fig. 1). species was associated with an average other species. The largest component hydric association was Quercus macrocarpa with Quercus bicolor, Fraxinus nigra, and americana. The mesic association was dom by Quercus rubra with lesser componen Quercus alba and Acer saccharum. Associ

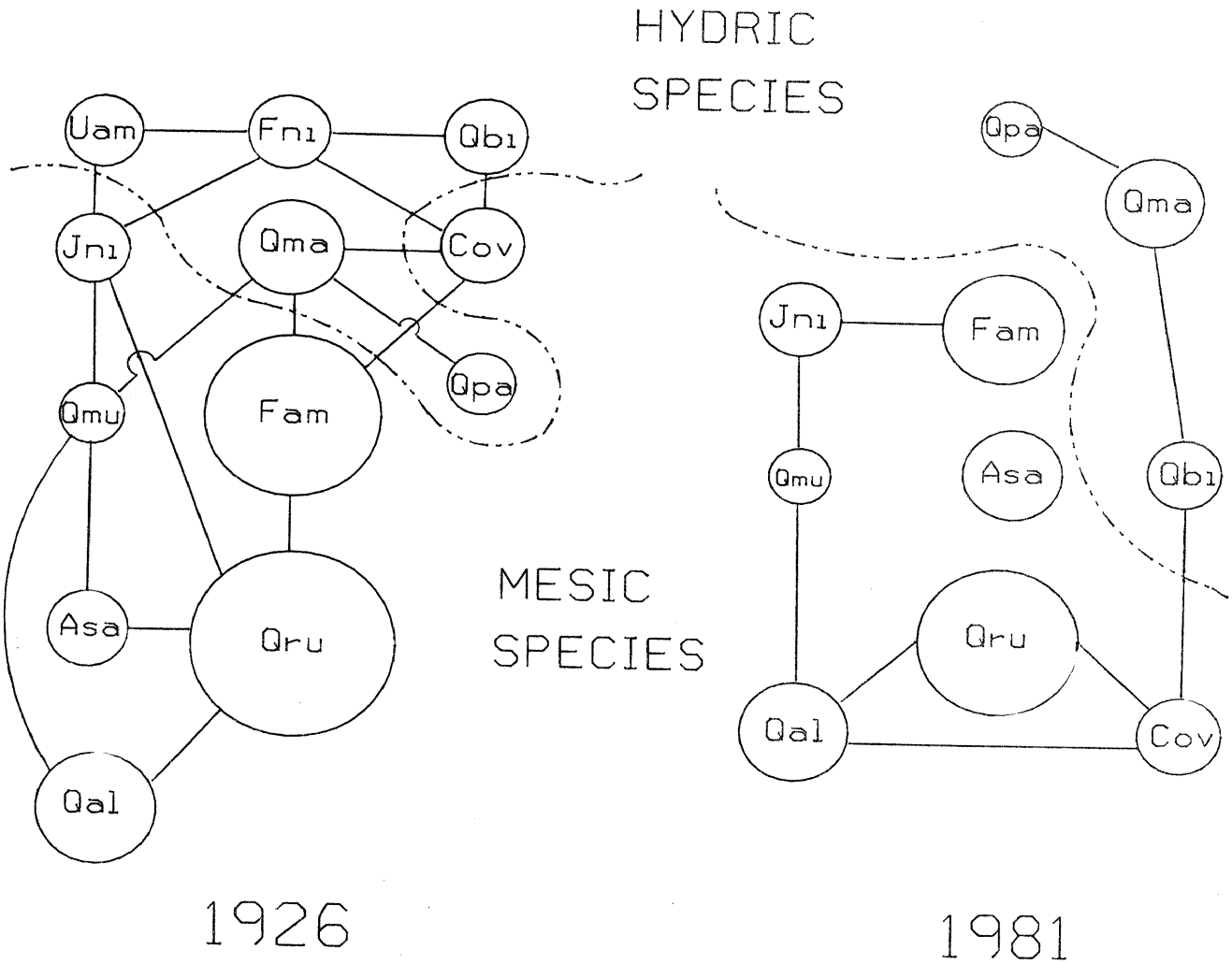

Figure 1.--Association plexus for canopy trees at the Davis-Purdue Research Forest. Species were arranged for clarity. Area of inscribed circles in proportional to each species stand density. Only positive associations are shown. Line length is unrelated to the strength of the association. See Table 1 for species abbreviations.

must be qualified since Quercus shumardii, Fraxinus pennsylvanica, and Carya laciniosa were not separated from Q. rubra, F. americana, and C. ovata, respectively. The former species tend to occupy wetter sites than their counterparts.

The association plexus for canopy trees had become less complex by 1981 (fig. 1). Each species was associated with an average of 1.8 other species. Only five of the eighteen interspecific associations observed in 1926 were still present in 1981. Five of the 1926 associations not observed in 1981 were the result of F. nigra and U. americana not being included in the plexus because their density dropped below the threshhold of four stems per hectare (table 1). This left a hydric association dominated by three species of oaks: Q. macrocarpa, Q. bicolor, and Quercus palustris. On the best drained sites there was a Q. rubra-Q. alba association and the intermediate sites supported Juglans nigra, F. americana, and C. ovata. Acer saccharum was found on all but the most poorly drained sites. Stable associations were generally between species with similar flooding tolerances such as Q. macrocarpa and Q. palustris on the wettest sites and Q. rubra and Q. alba on the better drained sites.

Four species had sufficient density in the subcanopy trees in 1926 to be included in the association analysis (fig. 2). Each species was associated with an average of 1.5 other species. U. americana was the only hydric site species. The mesic association included F. americana, J. nigra, and C. ovata. Following a release from

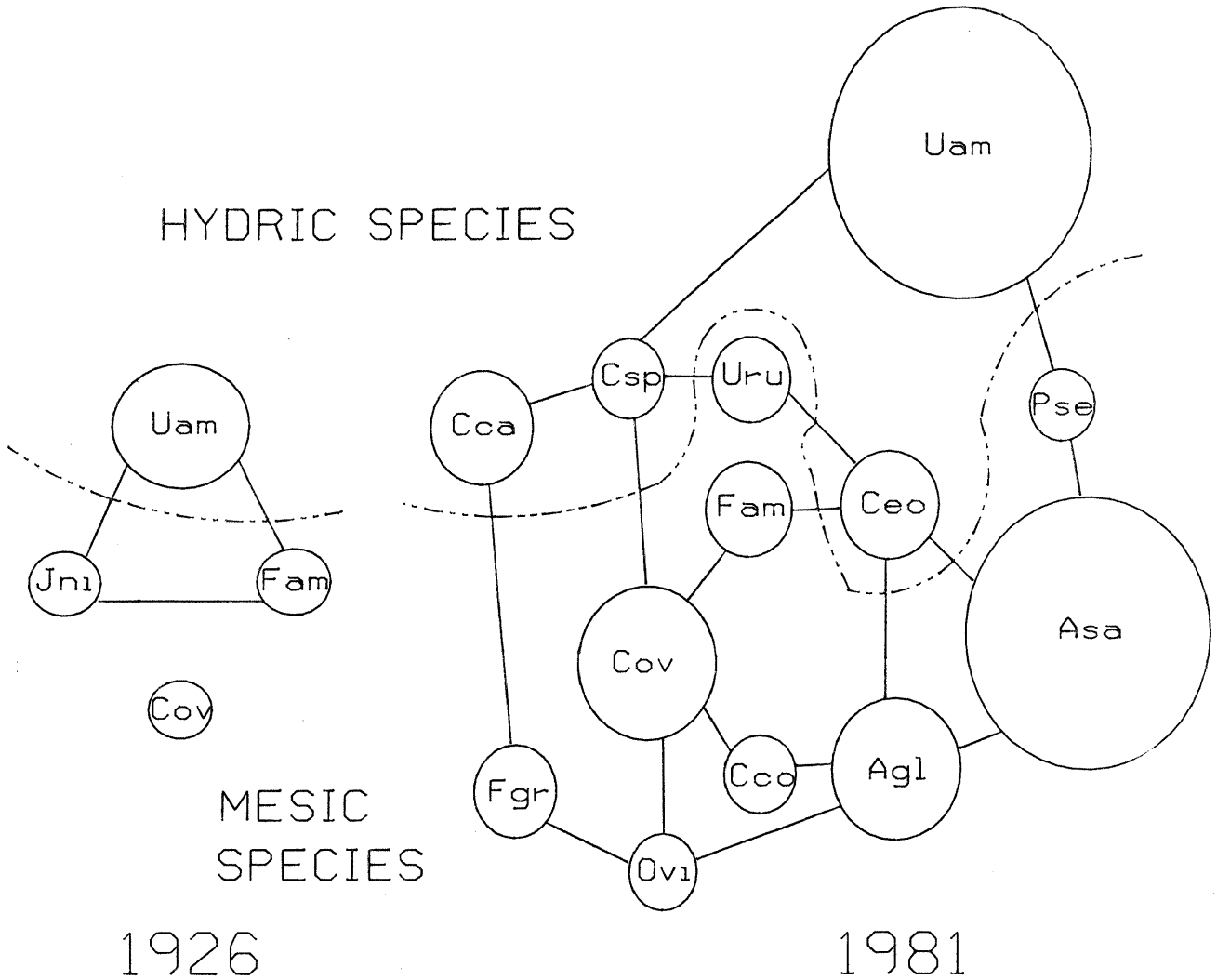

Figure 2.--Association plexus for subcanopy trees at the Davis-Purdue Research Forest. Species were arranged for clarity. Area of inscribed circles in proportional to each species stand density. Only positive associations are shown. Line length is unrelated to the strength of the association. See Table 1 for species abbreviations.

exogenous disturbance subcanopy density increased from 327 trees in 1926 to 1079 trees in 1981 (table 1). Thirteen species were included in the 1981 association plexus for the subcanopy trees (fig. 2). Each species was associated with an average of 2.8 other species. U. americana still dominated the subcanopy trees on the hydric sites and was associated with Carpinus caroliniana, Celtis occidentalis, Ulmus rubra, and Crataegus spp. The most numerous species of the mesic association was A. saccharum. Other species included in the mesic association were C. ovata, Aesculus glabra, Fagus grandifolia, and F. americana. No identifiable association of gap colonizing species (e.g. Prunus serotina, F. americana, etc.) was observed. This could be due in part to the low density of stems within a gap by the time they have reached subcanopy size. Many of the canopy oaks appear to decline gradually before dying further reducing the chance of 'gap' species successfully colonizing any holes in the upper canopy.

Diversity

Species richness for the canopy stratum remained constant at 25 species. One species, Morus rubra, was lost and one species Carya glabra was gained. Equitability increased from 0.73 in 1926 to 0.78 in 1981. The increase in

equitability accounted for the significant ($p \leq 0.01$) increase in species diversity over the fifty-five years from 2.35 to 2.50. The increase in equitability and species diversity was in large part due to the decreased importance of Q. rubra and F. americana (table 1).

From 1926 to 1981 both species richness and equitability increased for the subcanopy stratum. Species richness increased from 24 species to 30 species. Two species were lost and eight species were gained. Equitability increased from 0.66 in 1926 to 0.68 in 1981. Predictably, species diversity increased along with it's components; from 2.10 in 1926 to 2.31 in 1981. The increase was significant ($p \leq 0.01$). Subcanopy diversity (H') in 1981 was negatively correlated with most canopy parameters (table 2). The 0.1 ha plots with low level of canopy stocking, such as canopy gaps, were associated with high levels of subcanopy diversity. However, 1981 subcanopy diversity was not found to be significantly correlated with changes in the levels of canopy parameters from 1926 to 1981.

Table 2.--Correlation coefficients of canopy parameters with 1981 subcanopy diversity (H').

Year	Parameters Density (n/ha)	Basal area (m^2/ha)	Stocking (%)
1926	-0.246*[1/]	-0.264*	-0.274*
1981	-0.144	-0.224*	-0.219*
1981-1926[2/]	0.152	0.021	0.044

[1/] * = significant at $p \leq 0.05$.
[2/] Difference between 1981 value and 1926 value.

DISCUSSION

Species in the 1981 canopy plexus were associated with an average of 40% fewer species than in 1926. We believe the decreased levels of association were the result of stratification of the early and mid-seral species to sites where each species has a competitive edge. If species were areally segregated by some site characteristics then each species would be aggregated in those sites where it has the competitive edge. Leopold et al. (1985b) found most species at the Davis-Purdue Forest had aggregated distributions and concluded soil drainage was the most important factor controlling species distribution. As the original colonizers die and are not replaced each becomes more isolated from and less associated with other species.

Much of the shift from early and mid-seral to late seral species reported by Parker et al. (1985) appears to be occurring in the mesic association where A. saccharum is the predominant species. The future tree composition on hydric sites is less certain. Late seral species, including A. saccharum and F. grandifolia, have been unable to establish on hydric sites allowing successful recruitment of less shade tolerant species such as U. americana, C. occidentalis, Carya cordiformis, Acer negundo, and Acer saccharinum. While U. americana had the highest density of any species in the hydric association, few individuals are able to reach the upper canopy because of Dutch elm disease (Ceratocystis ulmi) and phloem necrosis (Parker and Leopold 1983).

Early studies reported diversity increased throughout succession in eastern hardwoods (Monk 1967, Whittaker 1965). More recent papers suggest diversity peaks early in succession on mesic sites (Metzger and Schultz 1984, Hibbs 1983, Christensen 1977). The peak in diversity occurs during succession when early, middle, and late seral species coexist in roughly equivalent proportions. Periodic disturbances (flooding/drought) associated with hydric and xeric sites may prevent diversity from reaching a maximum (Adams and Anderson 1980, Bell and del Moral 1977).

We found diversity of the canopy stratum has been remarkably stable considering nearly fifty percent mortality of all 1926 canopy trees. Mortality rates ranged from 98.5% for U. americana to 20.6% for A. saccharum. The slight, though significant, increase in diversity has been largely the result of the decreasing density of Quercus spp. and F. americana causing an increase in equitability.

Breakup of the upper canopy may have been a factor contributing to the increase in subcanopy stratum diversity. Subcanopy diversity was higher in plots with low levels of canopy parameters than in plots with high levels of canopy parameters. The importance of canopy breakup in influencing subcanopy diversity should be qualified for two reasons. First, changes in the level of canopy parameters (gap formation- gap closure) were not correlated with subcanopy diversity. Second, canopy stocking increased from 1926 to 1981 along with the increase in subcanopy stratum diversity.

We believe much of the increase in diversity of the subcanopy stratum can be attributed to the release from disturbance, mostly grazing, following Purdue University's acquisition of the property in 1917. For twenty-three species subcanopy density has increased since 1926. Only for Quercus spp. and J. nigra has subcanopy density decreased. With 87% of the subcanopy stems concentrated in four species: A. saccharum, C. ovata, F. americana, and F. grandifolia, diversity of the canopy stratum may ultimately decrease in the absence of allogenic disturbance.

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