SUCCESSION IN AND COMPOSITION OF A CENTRAL ILLINOIS PRAIRIE GROVE

DAVID L. COX, R. MICHAEL MILLER, AND JOHN A. HOSTETLER
Illinois Central College, East Peoria, Illinois 61611;
Department of Biological Sciences, Illinois State University, Normal, Illinois 61761;
Biology Department, Lambuth College, Jackson, Tennessee 38301

ABSTRACT.—The composition and succession of a mature stand in Funk Forest, McLean Co., Illinois were examined by standard ecological methods during June and July of 1970. Tree density in a sample from this prairie grove is 202 trees/ha (> 10 cm dbh) with a basal area of 28.5 m^2. Succession is tending to a maple climax. Sugar maple (*Acer saccharum*) is the dominant tree species, followed by oaks and ashes. Maples and oaks are randomly distributed. A sugar maple-pawpaw (*Asimina triloba*) understory of 4890 saplings/ha has an aggregated dispersion. Pawpaw and sugar maple saplings are negatively associated. Herb density is 83 stems/m^2. The herb dominants, in order of importance, are wild ginger (*Asarum reflexum*), wood nettle (*Laportea canadensis*), and large waterleaf (*Hydrophyllum canadense*). A nettle-ginger association is common. The large waterleaf is negatively associated with ginger and most other herbs. Other analyses include coefficient of community and Simpson's diversity index.

Funk Forest is a remnant of a prairie grove that once occupied a five-square-mile area along Timber Creek in McLean Co., Illinois. These groves, a striking feature of the Illinois prairie, are isolated from main bodies of timber and found on uplands along watercourses or on rough morainal land. Most of these formerly numerous prairie groves have now been cleared for agriculture.

Several workers have studied the ecology of this unique type of woods. Gleason (1912) made the first phytogeographical study of a prairie grove. Telford (1926), Boggess (1964), and Boggess and Bailey (1964) analyzed the woody vegetation of two similar stands in central Illinois. Clark (1947), Calef (1953), and Boggess and Geis (1966) have done the only previous vegetational studies of the Funk Forest area. Clark reported tree percentages from transect data. Calef, Boggess, and Geis worked in the 60-acre University of Illinois' Funk Forest Natural Area. Calef's data on the woody vegetation was based on a strip transect survey. Boggess and Geis examined the woody vegetation of the same area twelve years later, and also presented data on soil profiles.

Prior to our work, no comprehensive ecological study had been done in Funk Forest. The primary objective was to quantitatively and qualitatively determine the floristic composition of this woodland community. A second objective was to investigate the interrelationships among the herbs, saplings, and trees. The final objective was to discover the successional trends in this prairie grove.

Funk Forest is located in McLean Co., Illinois (89° 08′ W Long; 40° 21′ N Lat). Much of the original forest area was cleared for agriculture, and presently only several hundred hectares of woods remain, much of which has been heavily grazed and selectively cut in the past. Timber Creek is the most notable topographic feature of the forest. The relief of the area varies from 195 m to 210 m above sea level. Funk Forest is more mesic than the typical oak-hickory woods of central Illinois. Our study area has flat, fairly moist, upland topography, and was selected because it is one of the few mature, undis-

turbed tracts available. Subjectively we noted that our plot has a homogenous distribution of tree species. There are drier tracts in the forest that have a higher oak frequency.

The forest is in the Till Plains Section of the Central Lowland physiographic province and is on a loess deposit covering the LeRoy moraine, which is of the Tazewell Substage of the Early Wisconsin glaciation, formed during the Late Pleistocene (Wascher *et al.*, 1960). In a study of a similar prairie grove, Vestal and Heermans (1945) suggested that the groves developed 400 to 600 years ago on uplands occupied by prairie; however, Gleason (1912) proposed that fires spreading from the adjacent prairies isolated the groves from pre-existing main bodies of timber.

The Funk Forest climate is classified as the humid continental type. Great variations in temperature and precipitation are typical. A climatological summary of the area shows that annual precipitation averages 36.7 inches (Illinois State Water Survey, 1964), annual temperature averages 11-12 C, with a mean growing season of 171 days extending from April to September (Fehrenbacher and Wascher, 1967).

A detailed soil survey of the forest has not yet been undertaken. Recent surveys of Odell (1957) and Fehrenbacher and Wascher (1967) described this soil as Grey-brown Podzolic, Alfisoil order, Birkbeck soil association M. This association typically has a silt loam A horizon, a heavy silty-clay loam B, and a glacial till C. Boggess and Geis (1966), working in a similar area of Funk Forest, found the A horizon to be 30 cm deep and encountered C at 1.5-2.0 m. Organic matter of the A horizon was 5%, and pH was 6.0.

Methods and Procedures

The field study was carried out from Mid-June through July 1970. A 1-hectare area was used as the study plot, and was subdivided into 676 quadrats. Quadrats were randomly selected when sampling from the entire hectare proved impractical.

Trees were classified into three groups based on diameter at breast height (dbh): trees, > 10 cm; saplings, 2.5 to 10 cm; and seedlings, < 2.5 cm. We recorded species and dbh for all trees in the hectare. Density, relative density, dominance, and relative dominance were calculated from standard formulas (McIntosh, 1957). We modified the importance value of Curtis and McIntosh (1951), as did McIntosh (1957) and Boggess (1964), to calculate the importance value index (IVI = 200). Using the same class sizes and methods as Boggess and Geis (1966), we calculated basal areas by diameter class.

Saplings were studied by transect and line interception methods. We modified the transect methods of Calef (1953) by using a 2 m transect width along 189 m of grid lines. A sapling stem count was taken at 3 m intervals, and density and frequency were calculated. We graphed number of individuals per interval against transect length to show relationships between the two dominant sapling species. The line interception method of Buell and Cantlon (1950) was used to obtain sapling dominance. The intersect lengths over a 150 m hectare diagonal were measured, and cover area calculated. The importance value (Curtis and McIntosh, 1951) was obtained by adding the relative density and frequency values computed from the transect intervals with the relative dominance value

calculated by line-intercept (IV = 300).

The frequencies and densities of herbs and seedlings were measured in 15 randomly selected 1-m^2 quadrats. Another 150 m line intercept was used to find herb dominance. We graphed meters of herb cover against intercept line length to show relationships that the quadrat method does not emphasize. Importance values were calculated by adding the relative dominance value from the intercept method to the relative density and frequency figures from the quadrat technique (IV = 300).

An intrapopulation dispersion analysis (Bray, 1956, 1962) was done on each dominant tree species, and evaluated by a Chi-square test. Sapling dispersion was calculated using the variance to mean ratio method based on the Poisson distribution (Curtis and McIntosh, 1950; Cottam, Curtis, and Hale, 1953).

Dice (1945) and McIntosh (1957) described the contingency table method for calculating interspecific association, and Cole (1949) described the Chi-square test used to determine the significance level. This method was used to verify suspected negative associations between the two dominant sapling species and among the herb dominants.

The Simpson's index of diversity (Simpson, 1949) was calculated from our tree data and also from the earlier data reported for the Funk Forest Natural Area by Boggess and Geis (1966). Likewise the community similarity coefficients (Bray and Curtis, 1957) for these areas were calculated.

Plant nomenclature is that of Jones (1963).

Results

The hectare contained a total of 202 trees (> 10 cm) with a total basal area of 28.5 m^2 (Table 1). Total sapling density was 4890 per hectare (Table 2). The total herb density was 83 stems per m^2 (Table 3).

The intrapopulation dispersion analyses done on sugar maple (*Acer saccharum*) and oak trees showed no significant differences from random distribution at the .05 level. Dispersion analyses on saplings showed they have contagious distributions: the variance to mean ratios calculated for pawpaw (*Asimina triloba*) and sugar maple saplings were 2.19 and 2.92 respectively, which were significant at the .05 level.

Transect data (Fig. 1) illustrate the negative association between pawpaw and sugar maple saplings, and show their contagious distributions. The interspecific association between pawpaw and maple saplings calculated by the contingency table method was −.295. A Chi-square test showed this to be significant at the .05 level.

The distribution of the three herb dominants, wild ginger (*Asarum reflexum*), wood nettle (*Laportea canadensis*), and large waterleaf (*Hydrophyllum canadense*), is illustrated by a graph of a portion of line intercept (Fig. 2). The intercept data also revealed that appendaged waterleaf (*H. appendiculatum*) and wild ginger often occurred under wood nettle, but rarely under large waterleaf. Most other species also occurred with wood nettle rather than large waterleaf, and oak seedlings showed no relationship with herb distribution, but were dispersed around parent oaks. Interspecific association analyses of the wild ginger-large waterleaf and wild ginger-wood nettle relationships showed the former to have a nega-

TABLE 1.—Number of Trees and Basal Area (m^2) per hectare by Diameter Class and Importance Value Index

	Diameter Classes (cm)												
	10-15		16-30		31-61		62-91		92 +		Total		
Species	N	B.A.	N	B.A.	N	B.A.	N	B.A.	N	B.A.	N	B.A.	IVI
Acer saccharum	28	0.38	46	2.10	60	8.99	5	1.72	—	—	139	13.19	115.5
Quercus rubra	—	—	1	0.03	2	0.48	4	1.56	3	2.59	10	4.66	19.7
Q. alba	—	—	—	—	2	0.26	4	2.31	1	0.85	7	3.42	16.7
Fraxinus americana	1	0.02	1	0.07	2	0.44	4	1.58	—	—	8	2.11	11.4
F. quadrangulata	1	0.02	3	0.12	4	0.77	2	0.71	—	—	10	1.62	10.6
Ulmus rubra	8	0.08	2	0.09	1	0.26	—	—	1	0.80	12	1.23	10.2
Celtis occidentalis	3	0.04	1	0.05	2	0.36	1	0.36	—	—	7	0.81	6.3
Q. macrocarpa	—	—	—	—	3	0.53	—	—	—	—	3	0.53	3.4
Carya ovata	—	—	—	—	1	0.22	1	0.44	—	—	2	0.66	3.3
Juglans nigra	—	—	—	—	1	0.22	—	—	—	—	1	0.22	1.3
Tilia americana	2	0.02	—	—	—	—	—	—	—	—	2	0.02	1.1
Carya tomentosa	1	0.01	—	—	—	—	—	—	—	—	1	0.01	0.5
Total	44	0.57	54	2.46	78	12.53	21	8.68	5	4.24	202	28.48	200.0

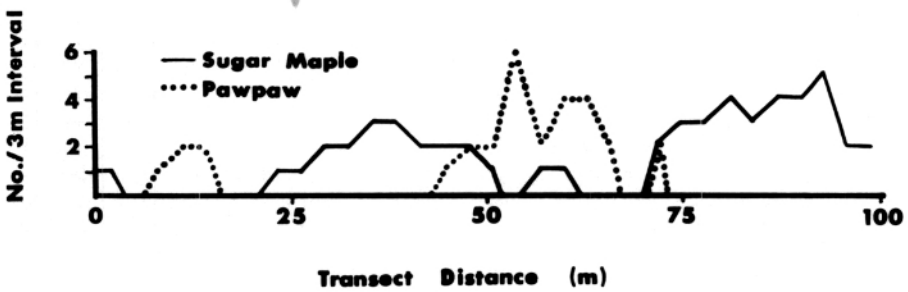

FIGURE 1.—Sapling distribution of sugar maple (*Acer saccharum*) and pawpaw (*Asimina triloba*) along a line intercept, showing their aggregated dispersion and negative association.

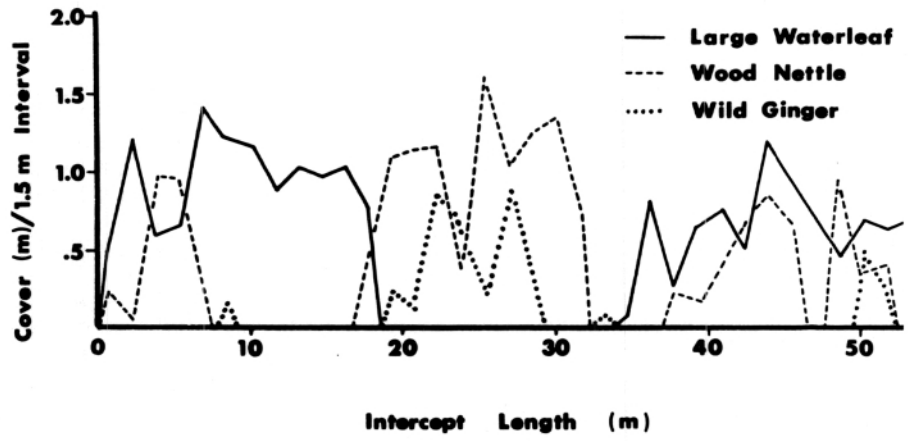

FIGURE 2.—Distribution of herb cover for the three dominant herbs, large waterleaf (*Hydrophyllum canadense*), wood nettle (*Laportea canadensis*), and wild ginger (*Asarum reflexum*), along a line intercept, showing their associations.

tive association and the latter a positive one, both significant at the .05 level.

The Simpson's diversity index calculated for our area was 2.04, and for the Funk Forest Natural Area (Boggess and Geis, 1966), 5.30. The coefficient of community between our area and Boggess and Geis' total area was .575, but between our area and their sugar maple community, .740.

DISCUSSION

Funk Forest is a mesic forest and *Acer saccharum* is the dominant species. Beech (*Fagus grandifolia*), characteristic of the Western Mesophytic Forest, is missing. Gleason (1912) in his study of several central Illinois prairie groves suggested that, in the past, burr oak (*Quercus macrocarpa*) was the leading dominant and that these forests had gone through three successional stages: oak-hickory to burr oak to red oak. He predicted the final stage of succession would be a maple-basswood type. Using Whittaker's (1953) definition of the term "climax", we concluded that the Funk Forest

area is now headed for a maple climax.

Few *Acer saccharum* seedlings were observed on the forest floor, and these were found where there were gaps in the canopy. In the matrix surrounding the gaps, *Quercus rubra* seedlings were more numerous than the *A. saccharum* seedlings. These findings are similar to those of Bray and Curtis' (1957) study of a maple-beech forest in Wisconsin. Our intrapopulation dispersion analysis of *A. saccharum* saplings indicated clumping, which further supports the observation that sugar maples arise in response to gaps in the canopy. Sugar maple does not establish seedlings extensively in the dense shade of a stable forest in which it is the dominant tree. The ability of *A. saccharum* to take advantage of canopy openings and to remain the dominant member of the forest community seems to depend on seed production and the ability of seedlings to grow rapidly in gaps and overtop those species already present (Bray, 1956.)

Sugar maples have replaced oaks as the dominant species. Table 1 shows that the majority of oak species are in the larger size classes, while sugar maple is present in all but the largest diameter class. As Gleason (1912) suggested, oaks were apparently the pioneer climax species, but as canopy space opens, they are being replaced by sugar maple. A diameter class comparison with Calef's (1953) and Boggess and Geis' (1966) data further shows the increase in sugar maple and decrease in oaks over the last two decades. Sugar maple has been increasing in all diameter classes, while oaks are decreasing in the larger diameter classes due to mortality and are not being replaced. Though *Quercus rubra* seedlings are prevalent in the stand, they persist only a year and usually do not develop into saplings (Table 2). The future status of the oaks suggests a decreasing importance as the forest approaches a sugar maple climax.

In 1953 Calef reported a maple-elm association in the area. Boggess and Geis (1966) noted a decrease in the importance of American elm (*Ulmus americana*) twelve years later. By 1970, we found no live American elm in our study area, though it was present in very limited numbers in the stand. Dead trees indicated its former presence. Dutch elm disease and phloem necrosis have caused the mortality of *U. americana*, and may also explain the decline of *U. rubra* in the stand.

The dispersion of sugar maple and oak trees was close to random, whereas the saplings were strongly clumped. Goodall (1952) pointed out that random distribution of individuals is less common than aggregation in natural vegetation. Whitford (1949) found that for

TABLE 2.—Sapling Analysis from Transect and Intercept Methods[a]

Species	Dens. (No./ha)	Rel. Dens.	Rel. Freq.	Rel. Dom.	Imp. Val.
Acer saccharum	3280	67.1	55.6	62.9	185.6
Asimina triloba	1100	22.5	22.2	11.0	55.7
Ulmus rubra	180	3.7	8.6	21.4	33.7
Carya ovata	210	4.3	8.6	3.3	16.2
Others[b]	120	2.4	5.0	1.4	8.8

[a]Density and frequency computed from transect intervals, and dominance from line intercept.

[b]*Cercis canadensis, Celtis occidentalis, Morus rubra, Carya tomentosa, Fraxinus quadrangulata,* and *Quercus rubra.*

many species young plants are aggregated but older ones approach random distribution. Curtis and McIntosh (1950) reported similar findings: mature trees tend to be randomly distributed, particularly in large size classes; saplings are more clumped; and seedlings show maximum aggregation.

Presently pawpaws (*Asimina triloba*) are the only saplings that approach maple saplings in importance (Table 2). The negative association between pawpaw and sugar maple saplings could be explained by interspecific competition. However, since *Asimina* is an understory tree which does well under minimum light and dense canopy, and reproduces primarily vegetatively; and *Acer* is found where there are canopy openings, and reproduces by seed, it is likely that this negative association reflects their different environmental requirements and their growth habits.

The dominant herbs were wild ginger (*Asarum reflexum*), wood nettle (*Laportea canadensis*), large waterleaf (*Hydrophyllum canadense*), and appendaged waterleaf (*H. appendiculatum*) (Table 3). Both Cain (1939) and Gleason (1926) pointed out the ambiguity of the term "association". Here we use the word to mean the coincident occurrence of the dominants. The wood nettle-wild ginger-appendaged waterleaf association was common throughout the area. McDougall (1922) reported this association to be typical of sugar maple forests: he used the term "symbiosis" to explain their interrelationships, but his definition of the term is no longer in current usage. Rowe (1956) found herbaceous undergrowth to be an accurate indicator of the tree climax in his area. Daubenmire (1968, p 221) suggested that forest undergrowth is commonly a rich mixture of species that persists indefinitely, so the present association may represent the dynamic equilibrium for the area.

Wild ginger is found throughout the stand, but due to its growth habit is not conspicuous. In spring the large waterleaf forms dense patches and does not regularly associate with the other herb dominants; in fact, it is negatively associated with wild ginger, appendaged waterleaf, and most of the less important herbs. In summer, wood nettle is found abundantly in moist areas of the woods except in areas of heavy canopy. A preliminary study has shown that light intensity is an important factor in the distribution of these herb dominants (manuscript in preparation).

The community similarity coefficients showed that our study area

TABLE 3.—Analysis of Herbs with an Importance Value over 5.0[a]

Species	Dens. (No./m²)	Rel. Dens.	Rel. Freq.	Rel. Dom.	Imp. Val.
Asarum reflexum	43.1	51.8	15.9	16.8	84.5
Laportea canadensis	14.7	17.6	15.9	45.9	79.4
Hydrophyllum canadense	8.6	10.3	2.1	28.4	40.8
H. appendiculatum	3.2	3.8	9.5	3.3	16.6
Smilacina racemosa	2.5	3.0	8.4	0.7	12.1
Osmorhiza longistylis	1.1	1.4	7.5	0.1	9.0
Quercus rubra (seedlings)	2.1	2.6	3.2	2.2	8.0
Cystopteris fragilis	1.6	1.9	5.3	0.5	7.7
Phryma leptostachya	1.9	2.3	5.3	—	7.6
Viola affinis	1.2	1.4	5.3	—	6.7
Others	3.0	3.9	21.6	2.1	27.6

[a]Density and frequency calculated by quadrant method, dominance by line intercept.

was most similar to the maple stand in the Funk Forest Natural Area (Boggess and Geis, 1966). The fact that the coefficient is not even higher reflects the continued loss of American elm and oaks during the intervening years. The low Simpson's diversity index supports our observation that the study area has a rather homogenous composition and was largely sugar maple. The Funk Forest Natural Area has a higher index value because it is a larger area and includes several different successional stages.

Acknowledgments

We wish to thank Dr. John D. Buffington for his continuing encouragement and guidance, and Dr. Birkenholz, Dr. Haines, and Dr. Liberta for their helpful suggestions in preparing the manuscript.

Literature Cited

Boggess, W. R. 1964. Trelease Woods, Champaign County, Illinois: woody vegetation and stand composition. Trans. Ill. State Acad. Sci. 57:261-271.

Boggess, W. R., and L. W. Bailey. 1964. Brownfield Woods, Illinois: woody vegetation and changes since 1925. Amer. Midland Natur. 71:392-401.

Boggess, W. R., and J. W. Geis. 1966. Funk Forest Natural Area, McLean County, Illinois: woody vegetation and ecological trends. Trans. Ill. State Acad. Sci. 59:123-133.

Bray, J. R. 1956. Gap phase replacement in a maple-basswood forest. Ecology 37:598-600.

Bray, J. R. 1962. Use of non-area analytic data to determine species dispersion. Ecology 43:328-333.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27:325-349.

Buell, M. F., and J. E. Cantlon. 1950. A study of two communities of the New Jersey Pine Barrens and a comparison of methods. Ecology 31:567-586.

Cain, S. A. 1939. The climax and its complexities. Amer. Midland Natur. 21:146-181.

Calef, R. T. 1953. Flora and ecological analysis of the vegetation of the Funk Forest Natural Area, McLean County, Illinois. Trans. Ill. State Acad. Sci. 46:41-55.

Clark, H. R. 1947. A study of the deciduous forest at Funk's Grove, Illinois. MS Thesis. Ill. State Univ., Normal, Ill. 58 p.

Cole, L. C. 1949. The measurement of interspecific association. Ecology 30: 411-424.

Cottam, G., J. T. Curtis, and B. W. Hale. 1953. Some sampling characteristics of a population of randomly dispersed individuals. Ecology 34:741-757.

Curtis, J. T., and R. P. McIntosh. 1950. The interrelations of certain analytic and synthetic phytosociological characters. Ecology 31:434-455.

Curtis, J. T., and R. P. McIntosh. 1951. An upland forest continuum in the prairie forest border region of Wisconsin. Ecology 32:476-493.

Daubenmire, R. 1968. Plant communities: a textbook of plant synecology. Harper and Row, New York. 300 p.

Dice, L. R. 1945. Measures of the amount of ecological association between species. Ecology 26:297-302.

Fehrenbacher, J. B., and H. L. Wascher. 1967. Soils of Illinois. USDA Bull. 725:1-47.

Gleason, H. A. 1912. An isolated prairie grove and its phytogeographical significance. Bot. Gaz. 53:38-49.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53:7-26.

Goodall, D. W. 1952. Quantitative aspects of plant distribution. Biol. Rev. 27:194-242.

Illinois State Water Survey. 1964. Local climatological data, 1901-1962, Bloomington, Illinois. Ill. Dep. Regist. Educ., Springfield, Illinois. 5 p.

Jones, G. N. 1963. Flora of Illinois. Amer. Midland Natur. Monogr. 7. 401 p.

McDougall, W. B. 1922. Symbiosis in a deciduous forest. Bot. Gaz. 73:200-212.

McIntosh, R. P. 1957. The York Woods, a case history of forest succession in southern Wisconsin. Ecology 38:29-37.

Odell, R. T. 1957. Soils of McLean County, Illinois. Dep. Agron., Univ. Ill. Mimeo., Agr. 1744. 3 p.

Rowe, J. S. 1956. Uses of undergrowth plant species in forestry. Ecology 37: 461-473.

Simpson, E. H. 1949. Measurement of diversity. Nature 163:688.

Telford, D. J. 1926. Brownfield Woods: a remnant of the original Illinois forest. Ill. Nat. Hist. Surv. Forestry Circ. No. 3. 16 p.

Vestal, A. G., and M. F. Heermans. 1945. Size requirements for reference areas in mixed forests. Ecology 26: 122-134.

WASCHER, H. L., J. D. ALEXANDER, B. W. RAY, A. H. BEEVERS, and R. T. ODELL. 1960. Characteristics of soils associated with glacial tills in northeastern Illinois. Ill. Agr. Exp. Sta. Bull. 665. 155 p.

WHITFORD, P. B. 1949. Distribution of woodland plants in relation to succession and clonal growth. Ecology 30: 199-208.

WHITTAKER, R. H. 1953. A consideration of climax theory: the climax as a population and pattern. Ecol. Monogr. 23:41-78.

Manuscript received August 27, 1971.