VEGETATIONAL ASSOCIATES AND SITE CHARACTERISTICS OF KENTUCKY COFFEETREE, *GYMNOCLADUS DIOICUS* (L.) K. KOCH

M. Leslie McClain[1] and Marion T. Jackson
Department of Life Sciences
Indiana State University
Terre Haute, Indiana 47809

Abstract.--The dispersed distribution of the Kentucky coffeetree has contributed to the paucity of information concerning its ecological life history. We examined the phytosociology of tree species associated with the coffeetree as related to topographic position and successional development. Lesser emphasis was given to edaphic conditions, growth habits, and phenology.

The coffeetree was encountered regularly in a wide range of successional development on five topographic units (upland flats, slope-ravines, stream terraces, floodplains and depressions). Lighter textured alluvial soils seemed to be the optimum sites for the species.

The coffeetree was its own nearest-neighbor in 61% of the samples, confirming a strong tendency for vegetative reproduction and limited dispersal of the heavy seeds. Hackberry, in early successional sites, and black walnut in more mature sites, were the next most common associates.

Ordination separated 69 maturing coffeetree sites along gradients in moisture and species composition. The sites segregated primarily into depressional, floodplain-terrace, and slope-ravine groups. Hackberry predominated in hydric depressions; well-drained floodplains and terraces were dominated by black walnut and coffeetree; while sugar maple was most important on mesic slopes and ravines; red oak was more common at dry mesic sites. Coffeetree reached its maximum importance at mesic and wet mesic sites (particularly on floodplains) near the center of the ordination space.

Additional keywords: Kentucky coffeetree, Indiana forest communities, forest ordination, ecological life history of trees.

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[1]Present address: Department of Biology, St. Catharine College, St. Catharine, Kentucky 40061.

INTRODUCTION

Although the geographic range of the Kentucky coffeetree, (*Gymnocladus dioicus* (L.) K. Koch), extends from the Oklahoma panhandle to the Finger Lakes region of New York, and from eastern South Dakota to northern Alabama, nowhere is it a common tree. It is typically distributed as widely-separated single trees or small groves (presumably clonal), a pattern that is missed by most forest sampling other than full stand inventories. The species grows in habitats ranging from fencerows to virgin forests, and in a variety of topographic situations and moisture conditions. The ecological life history is largely unknown, with most previous research being concerned primarily with morphology and physiology (List 1963; McDougall 1921; Pammel 1899; Raleigh 1930; Wiesehugel 1935).

In this study, we examined the site characteristics of the species as related to topographic position, soils and successional development. Of particular interest was the phytosociology of associated tree species.

THE STUDY AREA

Most sample sites were located in Vigo, Parke and Sullivan Counties in west-central Indiana, plus adjacent Clark and Crawford Counties in Illinois. Scattered samples were taken throughout Indiana, and at some other sites in Illinois and Kentucky. This general area is approximately the center of the geographic range of the species.

The majority of the study area is located in the Wabash Lowland physiographic unit (Malott 1922). Illinoian age glacial till and alluvium overlie sandstone and shale of Pennsylvanian age throughout most of this region. Early Wisconsinan age glacial till covers most of Parke County to the north, with Wisconsinan valley train deposits filling the broad Wabash River Valley (Wayne 1966). Deposits of windblown sand blanket the slopes immediately east of the river, with loess caps extending over much of the upland eastward.

The Wabash River system moderates the regional climate, permitting several southern tree species such as bald cypress (*Taxodium distichum* (L.) Richard), pecan (*Carya illinoensis* (Wangenh.) K. Koch), and sugarberry (*Celtis laevigata* Willd.) to extend their range northward (Lindsey *et al*. 1961). Precipitation averages about 45 inches annually.

The study area lies between the prairie border section of the oak-hickory forest and the beech-maple forest regions (Braun 1950). Most of the original vegetation has been cleared or strongly modified by cutting and/or grazing, but a number of representative old-growth forests which contain coffeetrees were intact.

METHODS

Sampling sites were located visually during the winter, since this was the period for most easily identifying coffeetrees from a distance. Mature trees

in winter are easily recognized by the coarse "naked" (gymnos) branches (klados), and rough scaly gray-pink bark. Additionally, female trees retain stout, leguminous pods until spring. Some locations were obtained from the literature. The majority of the sites encountered were sampled due to the relatively low total number of suitable locations. Highly disturbed sites were rejected.

Circular 0.04-ha (0.1-acre) sample plots were used because of their efficiency (Lindsey, Barton and Miles 1958). Plots were deliberately centered at individual coffeetrees or near the center of small groves. Where more than one plot could be obtained at a particular location, the plots were situated in nonoverlapping fashion to include as much of the grove as possible. Since our aim was to obtain as much information as possible about coffeetree growth sites, we chose not to sample forested areas randomly. With the widely scattered distribution pattern of the coffeetree, efficient use of field time dictated that we locate our samples where the trees occur. Species-area curves (Cain and Castro 1959) were used to determine sampling adequacy, however, we were concerned more with obtaining sufficient data rather than with obtaining too much.

At each plot the following data were recorded: 1) diameter, density, condition, and species of all trees 4.0 inches (10 cm) or greater diameter at breast height (dbh); 2) density by species of all saplings 2.0 to 3.9 inches (5-10 cm) dbh; 3) dbh of the nearest neighbor tree to each coffeetree 4.0 inches dbh and over, its species and the distance between their centers; 4) age and height of coffeetrees under 1 inch (2.5 cm) dbh, if possible; 5) an increment core taken 2 feet (0.6 m) above ground from one coffeetree in each available four-inch (10 cm) size class (first midpoint = six inches (15 cm); 6) one 100-gram soil sample each from topsoil and subsoil (0-4 inches (0-10 cm) and 4-8 (10-20 cm) inches depth); 7) kind, extent, and recency of disturbance; and 8) general location and topographic position.

Sampling sites were grouped into two major developmental stages (maturing and early successional) and five topographic positions (depression, floodplain, terrace, slope, and upland). Maturing sites were those at which the canopy was closed in the tree stratum. Depressional positions were those at which water stands for at least one month on part of the site. Each set of samples for each developmental stage and topographic position was considered to be a stand. Species attributes tables including density, basal area, frequency, percent importance and size class distribution were constructed for each such stand.

The 69 sample sites in the maturing forest groups were analyzed by ordination. Importance percentages for each species were determined by averaging the relative density and relative basal area for each species at each site. This method is a slight modification of the procedure advanced by Curtis and McIntosh (1950). Coefficients of similarity between the sample sites were based on the 21 most important species. The ordination procedure used was a modification of the Bray-Curtis (1957) technique. Ordination patterns were compared by arranging sample site locations into spatial cells on the basis of species co-domination at a minimum level of 15 percent importance.

Flood susceptibility continuum indices were computed for each stand following the method of Lindsey et al. (1961). Nearest-neighbor determinations were made for 533 different coffeetrees, including tabulations of frequency of species associations and mean area per tree (computed by using half the distance to the nearest-neighbor as the radius of a circle).

Soil texture was determined by the hydrometer method (Bouyoucos 1936). Soil texture data for each topographic position were plotted on separate soil texture triangles. Soil pH was determined by Fisher Accumet electronic pH meter. Soil nutrients were extracted in acetate buffer solution (Wolf and Ichisaka 1947). Potassium concentrations were determined by flame spectrophotometry. Calcium and magnesium concentrations were determined by EDTA titration.

Continuous air temperature data were recorded from mid-February to mid-May at one site by a Bendix-Friez hygrothermograph. The instrument was housed in a standard U.S. Weather Bureau instrument shelter located within a grove of mature Kentucky coffeetrees at a forested upland ravine site in Vigo County, Indiana. Cumulative running temperature summations were computed to flowering date of the trees for three physiological thresholds of 40, 45 and 50° F (4.4, 7.2 and 10° C).

RESULTS AND DISCUSSION

Site Characterization

Coffeetrees were encountered regularly on each of the five landform units. The method of sample site selection resulted in artificially high importance percentages for coffeetree in the sites sampled, as compared to its very low incidence in forest vegetation generally. However, these values do reflect the species' high importance at sites where it is found.

Most sampling sites were located on soils with sandy loam, loam, and silty loam textures (Fig. 1). Pure sands were encountered on all topographic sites except uplands. Pure silts were rarely represented and no sample location had heavy clay soil. Upland sites tended to higher silt content and several depression soils had increased clay. Topsoil concentrations of three nutrients averaged 72 ppm for potassium, 4,500 ppm for calcium, and 1,500 ppm for magnesium and were higher than subsoil concentrations (Fig. 2) (McClain 1973).

Overall soil pH values ranged from strongly acid 5.4 to somewhat alkaline 8.2 (Fig. 2). Mean pH values for each physiographic sample grouping ranged from 6.1 to 7.8. Upland, slope and terrace groupings were slightly acid and the lowland units slightly basic. The distribution of soil pH values (and, therefore, coffeetrees) was bimodal with peaks at 6.0 and 8.0 (Fig. 2). This pattern suggests that bottomland sites are more favorable locations for coffeetree growth since the availability of most metabolic nutrients is greatest within a pH range of 6.0-8.0. Overflow of circumneutral Wabash River water

and tributary streams plus the leaching of cationic nutrients from agricultural lands in these watersheds keeps the floodplain and terrace soils slightly basic and near optimum for coffeetree success.

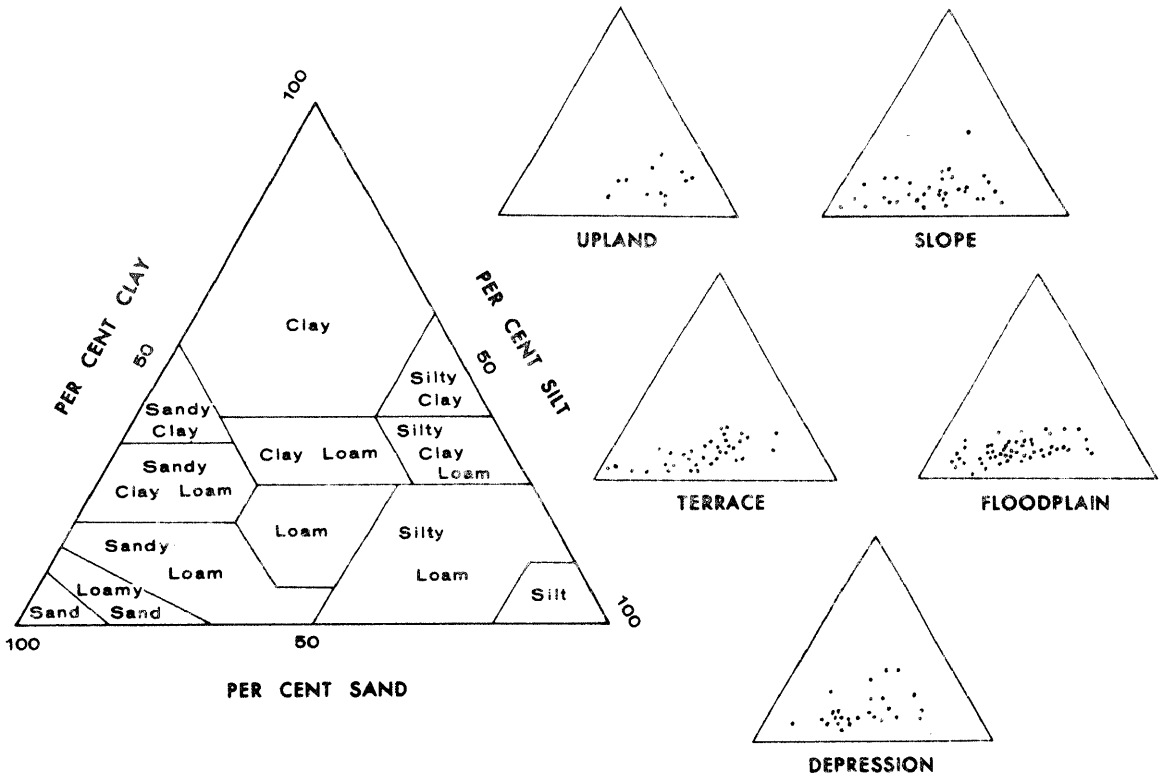

Figure 1. Distribution of sample sites for both early successional and maturing forest communities by soil texture classification and topographic position.

Hedrick (1933) and Curtis (1959) suggested that to some extent Kentucky coffeetree distribution in New York and Wisconsin, respectively, is correlated with sites of former Indian encampments. Presumably many Indian tribes used the large seeds in a kind of dice game, inadvertently planting the species near their villages in the process. In the area of this study, many of the sample locations on well-drained floodplains are in the vicinity of former Indian camp or village sites. Streams were natural corridors of movement for the Indian, which may account in part for the frequency of coffeetrees in many stream valleys.

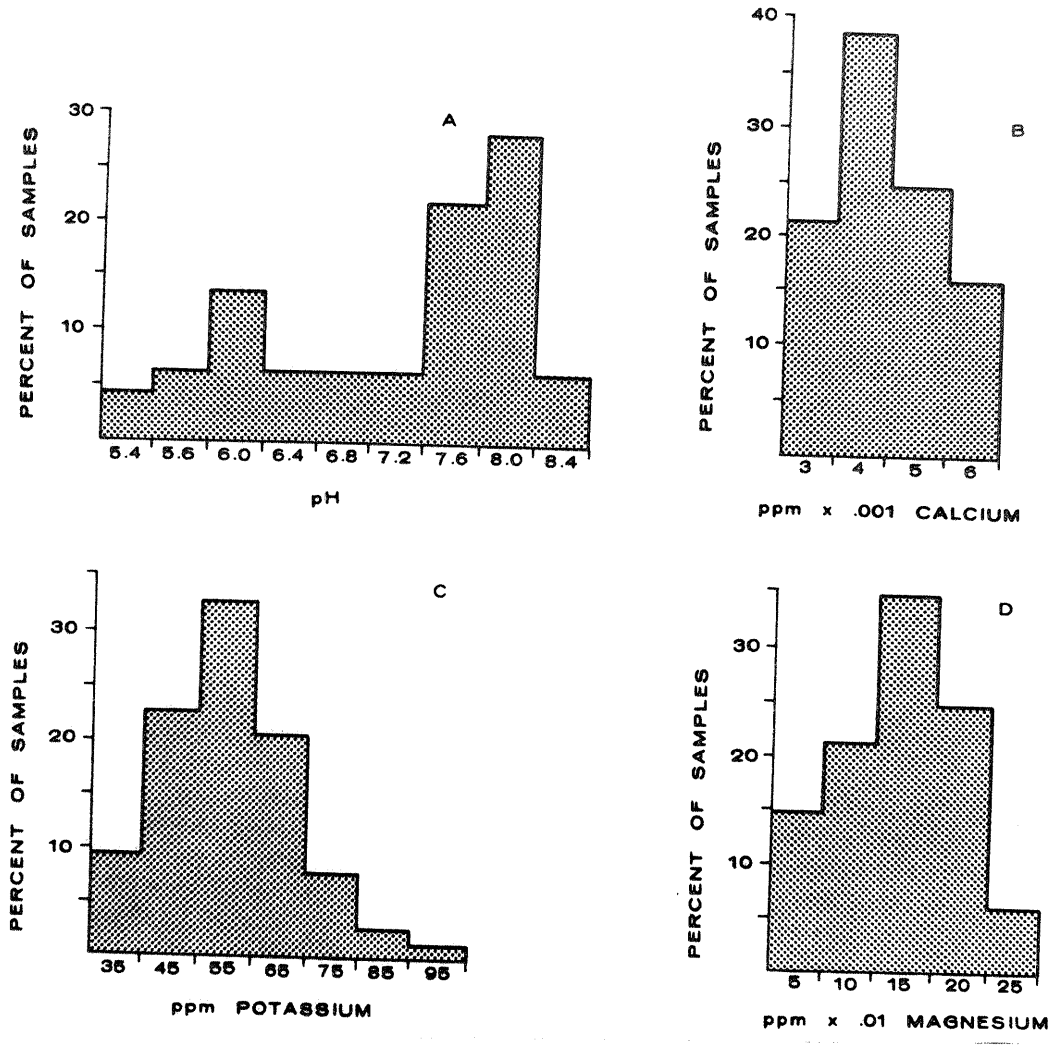

Figure 2. Chemical properties of soils at 85 sites representing all topographic positions and both early successional and maturing forest communities.

Sample Attributes

A total of 61 woody species greater than 2 inches (5 cm) dbh were associated with coffeetree in the 141 sites (Table 1). Of the 2,551 trees recorded, 758 (29.7%) were coffeetrees. The mean values of 6.7 coffeetrees per site in the seral group and 4.0 in the maturing group indicates the strong clumping tendency of the species. Contagion is the result of both vegetative reproduction by root suckering and the relative lack of effective dispersal agents for the heavy fruits.

Basal area per acre and mean diameter were lower for both coffeetrees and all species in seral than in maturing groups (Table 1). The mean dbh of 12.3 inches (31.2 cm) for coffeetrees in maturing groups is about average for old-growth

stands in Indiana (Schmelz and Lindsey 1970). Densities were higher in seral groups. The maximum age of any cored coffeetree within the sample sites was 133 years for a 25.6-inch individual in Dobb's Park Nature Preserve in Vigo County, Indiana. The largest individual coffeetree encountered was a 56-inch dbh monarch at an Allen County, Indiana farmstead, a new state champion tree.

Table 1. Stand attributes of developmental units sampled.

Characteristic	Seral Stands	Maturing Stands	All Stands
Number of 0.04-ha Samples	72	69	141
Total Tree Species >5 cm dbh	48	54	61
Mean No. Species/Stand	27.3	28.6	28.0
Total Trees - Gymnocladus	484	274	758
Total Trees - All Species	1,336	1,215	2,551
Density/ha - Gymnocladus	166.0	98.1	132.9
Density/ha - All Species	458.4	435.0	446.8
Basal Area/(m^2/ha) - Gymnocladus	6.96	7.55	7.25
Basal Area/(m^2/ha) - All Species	19.35	32.30	25.69
Mean Diameter (cm) - Gymnocladus	23.1	31.2	26.4
Mean Diameter (cm) - All Species	23.1	30.7	26.9

Vegetation Associates

Among maturing sites the coffeetree reached its greatest importance (28%) in the upland grouping; its lowest importance (14%) occurred in the slope grouping (Table 2). The coffeetree was the leading dominant at all maturing groupings except on mesic slopes where sugar maple (*Acer saccharum* Marsh.) exceeded it.

At seral sites the coffeetree was even more prominent, contributing 30% or greater importance on all topographic units except depressions where it comprised one-fifth of the importance. Too few suitable upland seral sampling sites were located for analysis although occasional individual coffeetrees or clonal clumps were found isolated in lawns, fencerows, or field borders. The coffeetree was the leading dominant at all seral groupings except depressions where hackberry (*Celtis occidentalis* L.) was slightly more important (Table 2). The coffeetree was regularly found in floodplain forests, beech-maple stands, and in upland depressional communities. Oak-hickory stands contained coffeetree much less commonly.

Species found to associate with the coffeetree were common at similar sites where the coffeetree was absent. Overall, black walnut (*Juglans nigra* L.), sugar maple, hackberry, elms and ashes were the most important associates at the maturing sites. Disregarding coffeetree, the mesic upland and slope groupings were dominated by the usual mesic-site species of sugar maple, white ash (*Fraxinus americana* L.), red oak (*Quercus rubra* L.), beech (*Fagus*

Table 2. Importance percentages for major tree species at coffeetree sample sites. Stands were grouped according to seral development and topographic position.

Species	Maturing Forest Stands					
	Upland	Slope	Terrace	Floodplain	Depression	Mean
Gymnocladus dioicus	28	14	21	20	21	21
Juglans nigra	.87	10	7.6	19	4.6	8.4
Acer saccharum	3.9	23	3.8	4.7	6.6	8.4
Celtis occidentalis	.70	2.7	13	10	11	7.5
Ulmus americana	5.8	4.3	10	8.3	4.8	6.6
Fraxinus americana	11	4.2	5.5	1.4	1.2	4.7
Quercus rubra	4.1	9.7	1.8	4.4	--	4.0
Platanus occidentalis	--	--	--	1.2	12	2.6
Quercus macrocarpa	6.0	1.4	1.2	<1	3.1	2.4
Aesculus glabra	--	2.8	1.7	2.6	4.6	2.3
Prunus serotina	1.6	1.0	6.0	<1	2.6	2.3
Ulmus rubra	2.4	3.5	2.4	<1	2.2	2.2
Other Species[1]	36(17)	23(19)	26(13)	27(25)	26(14)	27

Species	Early Successional Forest Stands				
	Slope	Terrace	Floodplain	Depression	Mean
Gymnocladus dioicus	31	33	30	20	28
Celtis occidentalis	14	15	20	21	18
Juglans nigra	5.5	10	6.0	5.5	6.8
Ulmus americana	6.0	4.2	7.1	9.3	6.6
Acer negundo	4.4	5.0	11	5.7	6.5
Acer saccharinum	1.8	--	2.0	12	4.0
Cercis canadensis	<1	1.1	4.3	1.9	2.0
Fraxinus pennsylvanica	1.8	3.5	1.0	1.3	1.9
Prunus serotina	1.0	6.6	--	--	1.9
Aesculus glabra	<1	<1	3.6	2.7	1.8
Other Species[1]	34(24)	21(25)	15(14)	21(8)	23

[1] Number of other species is shown in parentheses.

grandifolia Ehrh.), and black walnut. Similarly, on wet mesic terraces and floodplains, more typical wet-site species, such as hackberry, black walnut, and American elm (Ulmus americana L.) predominate. The hydric depressions had high values for hackberry, sycamore (Platanus occidentalis L.), and green ash (Fraxinus pennsylvanica Marsh.).

At seral sites hackberry was the consistent co-dominant, with black walnut, American elm, and box-elder (Acer negundo L.) as consistent subdominants. On well-drained terrace soils, wild black cherry (Prunus serotina Ehrh.) became more prominent. In the hydric seral depressional grouping, silver maple (Acer saccharinum L.) was the second most important associate with coffeetree.

Differences between seral and mature stands generally reflect the responses of the component species to changes in the light and moisture regimes and to the moderation of microclimatic conditions. The large number of species which were present at low importances was often attributable to local topographic or soil moisture variations at the site such as small streams, slightly elevated mounds, depressions, etc. For example, at most sites classified as depressional the coffeetrees were actually growing at the edge of the depression and, therefore, in a slightly less hydric situation than the classification would indicate even though the bulk of the sites were depressional. Examples of this situation included such species as rock elm (Ulmus thomasii Sarg.), black ash (Fraxinus nigra Marsh.) and swamp chestnut oak (Quercus michauxii Nutt.). Historical or land use differences such as fencerows, cutting practices or grazing also contributed to this. Several sites which had coffeetrees growing at the base of the abandoned Wabash and Erie Canal levee also had xeric species such as shagbark hickory (Carya ovata (Mill.) K. Koch) growing at the crest. Species such as apple (Malus sp.) and black locust (Robinia pseudoacacia L.) are attributable to land use practices. A number of these species which were present at relatively low importance percentages are not listed individually in Table 2, but collective importances are given.

Recurring ensembles of several of the top ten species such as black walnut with American elm and hackberry with box-elder typify sites which contain the sporadically-occurring coffeetree. Frequencies of species occurring with the coffeetree are listed in Table 3.

Nearest-Neighbors

The high frequency and the low mean area per tree of the coffeetree as its own nearest-neighbor reflects the cloning habit of the species (Table 4). The coffeetree occurred as its own nearest-neighbor in about three of five comparisons (61%). The mean area occupied by coffeetrees with other coffeetrees as nearest-neighbors transposes to a density of about 440 trees per acre (1,087 per hectare) (roughly twice the average density expected for similar but non-cloning species in both seral and mature situations). In opposition to this, the mean area occupied by coffeetrees with other species as nearest-neighbors transposes to a density of 150 trees per acre (370 per hectare) (somewhat less than expected, considering the variation in topographic position and age). The most common nearest-neighbor species were also the most important associates of coffeetree (Tables 2, 3 and 4).

Table 3. Frequencies of occurrence of species associated with Kentucky coffeetree in various stand types. Numbers in parentheses represent the number of sample plots.

Species[1]	Maturing Floodplain Stand (23)	All Maturing Stands (69)	All Successional Stands (72)	All Stands (141)
Gymnocladus dioicus (L.) K. Koch	100	100	100	100
Juglans nigra L.	83	55	44	50
Celtis occidentalis L.	74	54	71	62
Ulmus americana L.	61	59	44	52
Quercus rubra L.	30	36	4.2	20
Acer saccharum Marsh.	26	48	11	29
Cercis canadensis L.	26	14	19	17
Aesculus glabra Willd.	17	20	17	18
Acer negundo L.	17	13	46	30
Crataegus spp.	17	8.7	8.3	8.5
Fraxinus americana L.	13	26	2.8	14
Sassafras albidum (Nutt.) Nees.	13	8.7	2.8	5.7
Fraxinus pennsylvanica Marsh.	8.7	16	14	15
Platanus occidentalis L.	8.7	10	8.3	9.2
Acer saccharinum L.	8.7	4.3	17	11
Acer nigrum Michx. f.	8.7	12	2.8	7.1
Carya ovata (Mill.) K. Koch	8.7	5.8	2.8	4.3
Cornus florida L.	8.7	2.9	--	2.1
Ulmus rubra Muhl.	4.3	20	13	16
Prunus serotina Ehrh.	4.3	18	18	18

[1]Other species encountered at lower frequencies and arranged in decreasing order include: Q. macrocarpa Michx., Gleditsia triacanthos L., C. cordiformis (Wangenh.) K. Koch, Carpinus caroliniana Walt., Q. alba L., Liriodendron tulipifera L., Fagus grandifolia Ehrh., Q. muehlenbergii Engelm., Tilia americana L., C. glabra (Mill.) Sweet, Populus deltoides Bartr., Catalpa speciosa Warden, Nyssa sylvatica Marsh., C. laciniosa Michx. f. Loud, F. nigra Marsh., Morus rubra L., Malus sp., Asimina triloba L. Dunal., C. ovalis (Wang.) Sarg., Maclura pomifera Raf. Schneid., Q. velutina Lam., Q. bicolor Willd., Q. palustris Muench., Q. imbricaria Michx., Prunus sp., U. thomasii Sarg., A. rubrum L., C. tomentosa Nutt., Ostrya virginiana (Mill.) K. Koch, Q. shumardii Buckl., Robinia pseudoacacia L., C. illinoensis (Wangenh.) K. Koch, U. alata Michx., Ailanthus altissima (Mill.) Swingle, Betula nigra L., Q. michauxii Nutt., Pinus sylvestrix L., Diospyros virginiana L., Q. marilandica Muench.

Table 4. Nearest-neighbor analysis. Species are listed in decreasing order in terms of the number of times the second tree was the nearest-neighbor to the sampled coffeetrees.

Species	Number of Comparisons	Percent of Comparisons	Mean Area (Square Meters)
Gymnocladus dioicus	327	61	9.3
Celtis occidentalis	49	9.2	34.4
Juglans nigra	26	4.9	22.3
Ulmus americana	18	3.4	16.7
Acer negundo	16	3.0	35.3
Acer saccharum	15	2.8	21.4
Fraxinus pennsylvanica	7	1.3	7.8
Acer saccharinum	6	1.1	76.2
Quercus rubra	5	.94	6.0
Cercis canadensis	5	.94	8.6
Carya glabra	5	.94	10.2
Aesculus glabra	5	.94	30.7
24 Other Species	49	9.2	28.8
Total Comparisons	533		$\bar{X}$ = 16.7[1]

[1]Mean area of coffeetrees with other species as nearest-neighbors was 27.0 square meters.

Flood Tolerance

Flood tolerance indices for the site groupings ranged from 650 to 850. These are generally within the intermediate group which contains species able to withstand infrequent flooding of rather short duration. Species behavior (as indicated by importance percentages when plotted along the flood tolerance continuum (Fig. 3) tended to substantiate previous work on floodplain trees along the Wabash and Tippecanoe Rivers (Lindsey *et al.* 1961). Importance percentages of the coffeetree peaked around 740 along the gradient, indicating an ability to withstand only infrequent flooding of short duration. Hackberry and a group of wet-site species (sycamore; silver maple; and cottonwood, *Populus deltoides* Bartr.) exhibited similar curves. Black walnut was more erratic, possibly due to local topographic influences, and was not plotted here. Sugar maple, although a frequently associated species in many floodplain samples reached its greatest importance at a continuum index of 850, and was observed on the floodplain most commonly on the coarser textured soils.

Growth Habits

Examination of size class structures revealed a much greater density of coffeetrees in the smaller size classes at successional sites than at maturing

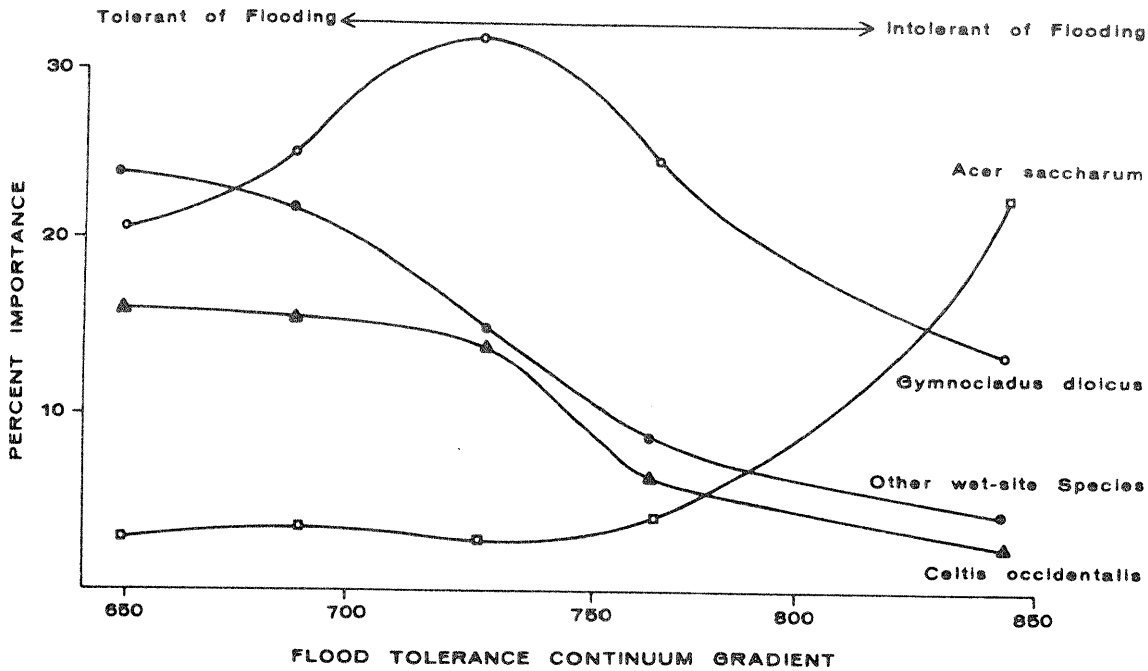

Figure 3. Distribution patterns of major tree species along the flood tolerance continuum gradient. Other wet-site species considered collectively are as follows: Acer saccharinum, A. negundo, Fraxinus pennsylvanica, Populus deltoides, Platanus occidentalis and Ulmus americana.

sites. This could be due to the relatively greater availability of light. Field observations suggest that most of the reproduction of the species in disturbed situations is vegetative. The ability to send up root sprouts allows individuals to maintain themselves over long periods of disturbance such as grazing or cutting without loss of root viability.

With disturbance, the coffeetree's root system sends up a number of suckers which can put on considerable growth due to the high root-shoot ratio. Examination of spatial patterns at coffeetree groves indicates that this clonal growth may persist into maturity of the site where several individuals may share interconnecting root systems. One interconnecting root system was noted connecting two coffeetree stems growing along an eroding ditch in Fontanet, Indiana. Both stems were about 10 inches (25 cm) dbh and about 5 feet (1.5 m) apart.

Development of a large taproot during the first season of growth was noted in a sample garden plot. Root biomass in dry weight of 25 seedlings ranged from two to four times the shoot weight in open grown conditions. This stored food may enhance the survival capacity of the individual by allowing juveniles to persist through adverse conditions. Furthermore, coffeetrees growing in fencerows or forest edges have shown exceptionally vigorous growth both in density and elongation (up to 1.5 m annually).

The lower densities of the coffeetree's reproductive size classes at maturing sites do not necessarily preclude an intolerance to shade. Curtis (1959) reported that seedlings of red elm (Ulmus rubra Muhl.) can give rise to rhizomes with erect stems which may persist under the canopy for long periods. Likewise, the coffeetree was found to possess a similar ability at some of the least disturbed sites.

Phenology

One of the problems faced by a species with such a widely-scattered low density distribution pattern is synchronization of phenological events such as flowering and pollination. Cumulative temperature summations exert a major control over spring flowering phenology of vascular plants (Lindsey and Newman 1956; Jackson 1966).

Correlations between bud break and flower anthesis with temperature summations in degree hours at three presumptive thresholds are shown below:

Phenological Event	Temperature Threshold in °F		
	40	45	50
Budding Date			
Year 1 - April 17	6,918	4,299	2,426
Year 2 - April 20	9,302	6,299	4,083
Flowering Date			
Year 1 - May 17	18,908	12,987	8,188
Year 2 - May 13	18,934	13,416	8,856

Flowering is a much more definite event than bud break, and according to these data, more precisely controlled by temperature summations. Variations in degree hour accumulations prior to budding ranged from 2,384 to 2,000 to 1,657 degree hours difference between the dates of bud break from year 1 to year 2 at the respective thresholds. Accumulations prior to flower anthesis varied only 26, 439 and 668 degree hours at the 40, 45 and 50° thresholds, respectively. Although these data do not cover a sufficient number of years to be conclusive, the remarkably close cumulative temperature sums for the two years suggest that the 40° F level closely approaches the temperature threshold leading to flowering.

For pollinators to be able to transfer pollen effectively within this widely spaced population, the variation in flowering phenology must be narrow. That pollination is effective is borne out by our observations that the great majority of all pistillate trees do set fruit in a given good fruiting year. Pollen vectors were not examined, but would be the subject of an interesting study.

Ordination

Coffeetree sites generally segregated into three major topographic positions as follows: floodplain-terrace, upland-depressional, and slope-ravine (Fig. 4). Coffeetrees were not found actually growing in wet depressions but

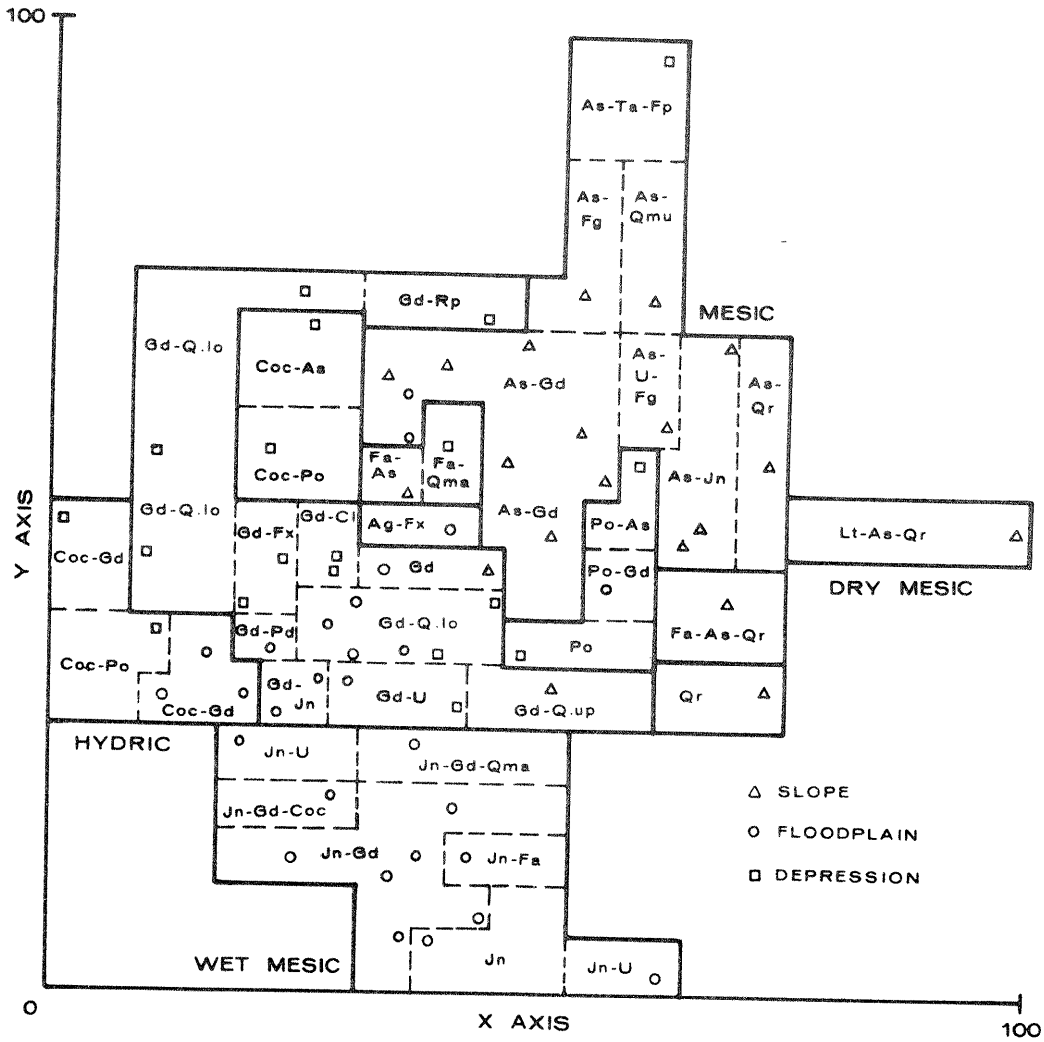

Figure 4. Two-dimensional ordination of the 69 individual sample sites located in maturing forest communities. Sample sites were designated according to three major topographic units as listed in the legend. Ordination cells enclose within solid lines those samples characterized by the same dominant species. Separations according to subdominant species are by dashed lines. Species codes are as follows: Aesculus glabra (Ag), Acer saccharum (As), Carya laciniosa (Cl), Celtis occidentalis (Coc), Fraxinus americana (Fa), F. pennsylvanica (Fp), F. pennsylvanica and nigra (Fx), Gymnocladus dioicus (Gd), Juglans nigra (Jn), Liriodendron tulipifera (Lt), Populus deltoides (Pd), Platanus occidentalis (Po), Quercus-low ground species (Q-lo), Q. macrocarpa (Qma), Q. muehlenbergii (Qmu), Q. rubra (Qr), Q.-upland species (Q-up), Robinia pseudoacacia (Rp), Tilia americana (Ta), and Ulmus species (U).

rather along the edge of depressional situations. Campbell (1978, personal communication) reported a similar distribution in swamp forests of central Kentucky. In addition, coffeetrees were frequently found growing along the lower reaches of slopes and ravines in somewhat wetter situations than the designation slope-ravine indicates. These transitional sites, between slope

and floodplain were difficult to categorize as to topographic position. Consequently, some interspersion of these three major topographic positions occurred near the center of the ordination space (Fig. 4). Associated tree species, which influence the ordination pattern, also range across topographic gradients, with some species being found in all three topographic positions.

Definite correlations between soil texture differences, pH or nutrient concentrations and species composition were not possible from the ordination, but sample locations deployed well diagonally across the ordination along moisture gradients from hydric and wet mesic to mesic and dry mesic sites (Fig. 4).

Sample locations characterized by identical or similar dominant species, at the 15% or greater importance level, were grouped by constructing cells within the ordination space. Cells encompassing sample sites having a common leading dominant species are enclosed by solid lines (Fig. 4). Variations in second or third dominants are separated by dashed lines.

Sites in the hydric sector of the ordination had hackberry (Coc) as the major influent on these largely depressional sites. Of lesser importance were lowland oaks (Q. macrocarpa and palustris), sycamore (Po), wet-site ashes (F. pennsylvanica and nigra), cottonwood (Pd) and shellbark hickory (Cl). Coffeetree (Gd) ranged from first to fourth or fifth in importance in the several hydric sites.

The wet mesic sector is characterized by well-drained floodplain and terrace sites dominated by black walnut (Jn) or coffeetrees. The most frequent associated species are American, red and cork elms (U), lowland oaks (Qma and Q. shumardii), hackberry and white ash (Fa). Coffeetrees thrive on these deep, fertile, neutral or slightly basic soils. Mesic slopes and ravines have sugar maple (As) as the predominant species, with a variety of mesic species as important associates (Fig. 4). Sites occupying transitions from slopes to terrace or floodplain topography have ashes (F. americana or pennsylvanica), Ohio buckeye (Ag), or sycamore (Po) at increased importance. Nine of the 69 sample sites were co-dominated by sugar maple and coffeetree, a type which included the largest amount of ordination space.

The cell dominated by sycamore at right center seemed misplaced within the ordination until the size class data were examined. Each of the three depression and floodplain sites within this cell had one or two large sycamores within the 0.1-acre sample, which skewed the importance percentage in their favor.

Red oak (Qr) as dominant or important influent characterizes the few dry mesic sites sampled. No xeric (for Indiana) maturing sites containing coffeetrees were encountered in our sample.

Interestingly, coffeetree is the first dominant most consistently at sites in the wet mesic sector near ordination center. Coffeetree was the sole dominant at lower slope and floodplain sites near the exact center of ordination space.

In general, the ordination shows a close affinity of the upland and depressional sites with both the floodplain and slope-ravine sites. This affinity indicates rather narrow soil moisture and drainage regimes when one considers the actual spatial distribution of the individual coffeetrees at each site, i.e., on the periphery of depressions and along the lower reaches of slopes. If this is true, then the chances of ecotypic variation being responsible for the coffeetree growing in three quite different habitats would be small.

It would be interesting to ordinate the same sample sites, but omitting coffeetree from the computations. Such an ordination would reflect the community matrix at the sample locations, but would avoid the influence of the artificially high coffeetree importance created by sampling only at sites where coffeetree was present.

CONCLUSIONS

The coffeetree was encountered regularly in a wide range of successional development on five topographic units (upland flats, slope-ravines, stream terraces, floodplains and depressions). However, at many of the slope-ravine and depressional sites, the individual coffeetrees were located spatially along the mesic periphery of these two landform units. The coffeetree was found most commonly on lighter textured soils.

Hackberry, black walnut, and American elm each occurred in half or more of the sample sites. Hackberry was more often found at successional sites while black walnut and American elm were somewhat more frequently found at more mature sites. Sugar maple was found at 29% of all sites, occurred at about half of the mature sites and was conspicuously prominent on slope-ravine topography. Box-elder with a frequency of 30% overall was more prominent at successional sites.

The coffeetree was its own nearest-neighbor at 61% of the comparisons. Hackberry, at early successional sites, and black walnut at more mature sites were the next most common associates at 9.2% and 4.9% of the comparisons, respectively.

The tendency of the coffeetree to clump is due to vegetative reproduction and limited dispersal of the heavy seeds. Seedlings tended to build up a reserve of food in the roots. One interconnecting root system was found but it is not known how widespread this phenomenon is. Rhizome-like runners were discovered at several of the least disturbed sites.

Importance percentages plotted along a flood tolerance gradient indicated that the coffeetree has the ability to withstand only infrequent flooding of short duration.

Ordination separated 69 maturing coffeetree sites along gradients in moisture and species composition. The sites segregated primarily into depressional, floodplain-terrace, and slope-ravine groups. Hackberry predominated in hydric depressions. Well-drained floodplains and terraces were

dominated by black walnut and coffeetree. Sugar maple was most important on mesic slopes and ravines, with red oak becoming more common at dry mesic sites. Coffeetree reached its maximum importance at mesic and wet-mesic sites (particularly on floodplains) near the center of ordination space indicating that the floodplain is the optimum site for coffeetree.

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