PATTERNS OF TREE SPECIES DIVERSITY AND COMPOSITION IN OLD-FIELD SUCCESSIONAL FORESTS IN CENTRAL ILLINOIS

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ABSTRACT.—Tree species diversity increases and dominance decreases with proximity to forest border in two 60-year-old successional forest stands developed on abandoned agricultural land in Piatt County, Illinois. A regression equation allowed us to quantify an increase in diversity with closeness to forest border for one of the forest stands. Shingle oak is the most dominant species in both stands. While other oak species importance values are lower in the stand with less forested border, shingle oak's importance value is higher, suggesting it has a seed dispersal mechanism that is different than the other oaks. Other dominant trees in the 60-year-old stands include American elm, slippery elm, and black walnut.

In agricultural regions of the Midwest there are few examples of undisturbed old-field succession to forest. Continuing disturbances such as mowing, grazing, and selective tree cutting during forest succession are common, and they disrupt natural successional patterns. At Allerton Park in Piatt County, Illinois, old agricultural fields set aside in the 1930s have reverted to forest without such disturbances. The configuration of these fields allows not only an opportunity to describe the woody species composition and forest structure of the approximately 60-year-old successional forests, but also to examine the effect of surrounding forest and old-field configuration on the composition and diversity of the successional forests.

Surrounding vegetation influences tree invasion during old-field succession (Bazzaz 1968, Myster 1993), and species found invading old-fields are often found in adjacent forest stands (Ashby and Weaver 1970, Buell and others 1971, Crowder and Harmsen 1998). The ability of a tree species to disperse seed onto a successional area is thought to be as important as other factors, such as competition, in determining species composition on old-fields (De Steven 1991a, 1991b). Density of trees on fields is greater near forest borders during the earlier periods of succession (Myster and Pickett 1992), and this relationship is more pronounced on smaller fields, which also exhibit greater species richness when in close proximity to forest border (Crowder and Harmsen 1998).

Differing seed dispersal mechanisms (wind, bird, or mammal) of trees are also important in determining the ability of trees to invade an old-field. These mechanisms affect the timing of invasion for individual species (Buell and others 1971, McDonnell and Stiles 1983, Christensen and Peet 1984, Burton 1989, Myster and Pickett 1992), and thus influence diversity by determining which species can become successfully established.

If forest border influences the species composition and densities of successional forests on old-fields, then different amounts of forest border along the perimeter of an old-field and the extent to which the forest surrounds the old-field should have an effect on tree species composition and diversity of successional forests. At Allerton Park, we studied two forest stands that developed on old-fields abandoned approximately 60 years ago with differing original amounts of forest border.

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We hypothesized that a forest stand that developed on a narrow field almost completely surrounded by forest would have greater species diversity than a forest stand that developed on a wider field that had forest border only along certain portions. We further hypothesized species diversity would decrease and dominance of the most common species would increase with increasing distance from forest border. We test these hypotheses and describe the species composition and structure of these successional forest stands.

STUDY SITE

Research was conducted at Robert Allerton Park in Piatt County, Illinois (Latitude: N39° 59.9′; Longitude: W88° 38.7′). The park is located along the Sangamon River and was donated to the University of Illinois at Urbana-Champaign in 1946 by Robert Allerton, who had maintained a mixture of forest, agricultural fields, and gardens on his estate. The park is located in the Prairie Peninsula of the oak-hickory forest region (Braun 1950).

Two separate upland forest tracts that were formerly devoted to agriculture and had differing percentages and configurations of forested border were selected. The first stand is located in the southwestern portion of the park and is bisected by a narrow grass corridor. Willow Branch, a tributary of the Sangamon River, runs through the southern portion of this stand, but the associated floodplain forest was not included in this study. The rest of the stand, the portion sampled, is at least 4.5 m above the floodplain of both the Sangamon River and Willow Branch and not subject to periodic flooding. The topography is fairly level with 0 to 7 percent slope. The soils in this stand consist of Miami loams and Xenia and Russell silt loams. They range from moderately well drained (Xenia) to well drained (Miami and Russell). These soils were formed under forest vegetation on till plains in loess, other silty material, and the underlying calcareous loam glacial till (Martin 1991). This stand is approximately 15.4 hectares in size and is referred to as stand 1.

The second stand is located in the eastern part of the park directly south of the Sangamon River, and is approximately 1,200 m northeast of stand 1. Slope ranges from 0 to 7 percent. The soils are in the same series as stand 1 with the addition of minor areas (less than 20 percent of total stand area) of Sunbury silt loam, which is somewhat poorly drained and was formed in loess and the underlying calcareous loam glacial till under forest vegetation (Martin 1991). The stand is at east 6 m above the floodplain of the Sangamon River, and the only areas likely to have standing water are those with the Sunbury silt loam. This second stand is approximately 16.2 hectares in size and is referred to as stand 2.

The critical difference between the stands for the purposes of this study is the amount of original surrounding forest and configuration of the fields. Stand 1 was almost completely surrounded by mature forest and is long and narrow (fig. 1). Stand 2 was bordered by mature forest only along its northern boundary and by sparse tree cover along the eastern side. Its remaining border was adjacent to additional abandoned pasture, and it is wider than stand 1. A previous study determined variability of upland soil properties at Allerton Park, including percent moisture and bulk density, to be low (David and Wang 1989).

While certain portions of Allerton Park were selectively cut for timber between 1847 and 1865 (Johnson and Bell 1975), both study stands have a history of past agricultural use. Local farmers cleared them of their original timber in the late 1800s, and records suggest both stands were used for cattle grazing (Foster 1981). The upper horizons of the soils were examined for signs of past agricultural disturbance. Both stands have signs of past grazing, and in portions there are indications of plowing. Indicators of past agricultural use include an abrupt soil structure change (granular to subangular blockly) at depths of 13 cm to 25 cm, nonpedogenic mixing of the A and B horizons, and evidence of compaction in the lower A horizon.

Aerial photographs from 1936 and maps from 1948 show that both stands were open grassland with a few scattered trees. Dykstra (1999) describes stand 1 as being a secondary forest and stand 2 as being an abandoned field in 1940. Both stands were described as successional forest in 1976 (Jones and Bell 1976). Since the University of Illinois assumed management of the Park in 1946, these stands have been allowed to succeed naturally without direct anthropogenic disturbance. Based on the aerial photographs and observations, it appears both stands began succession to forest in the mid to late 1930s.

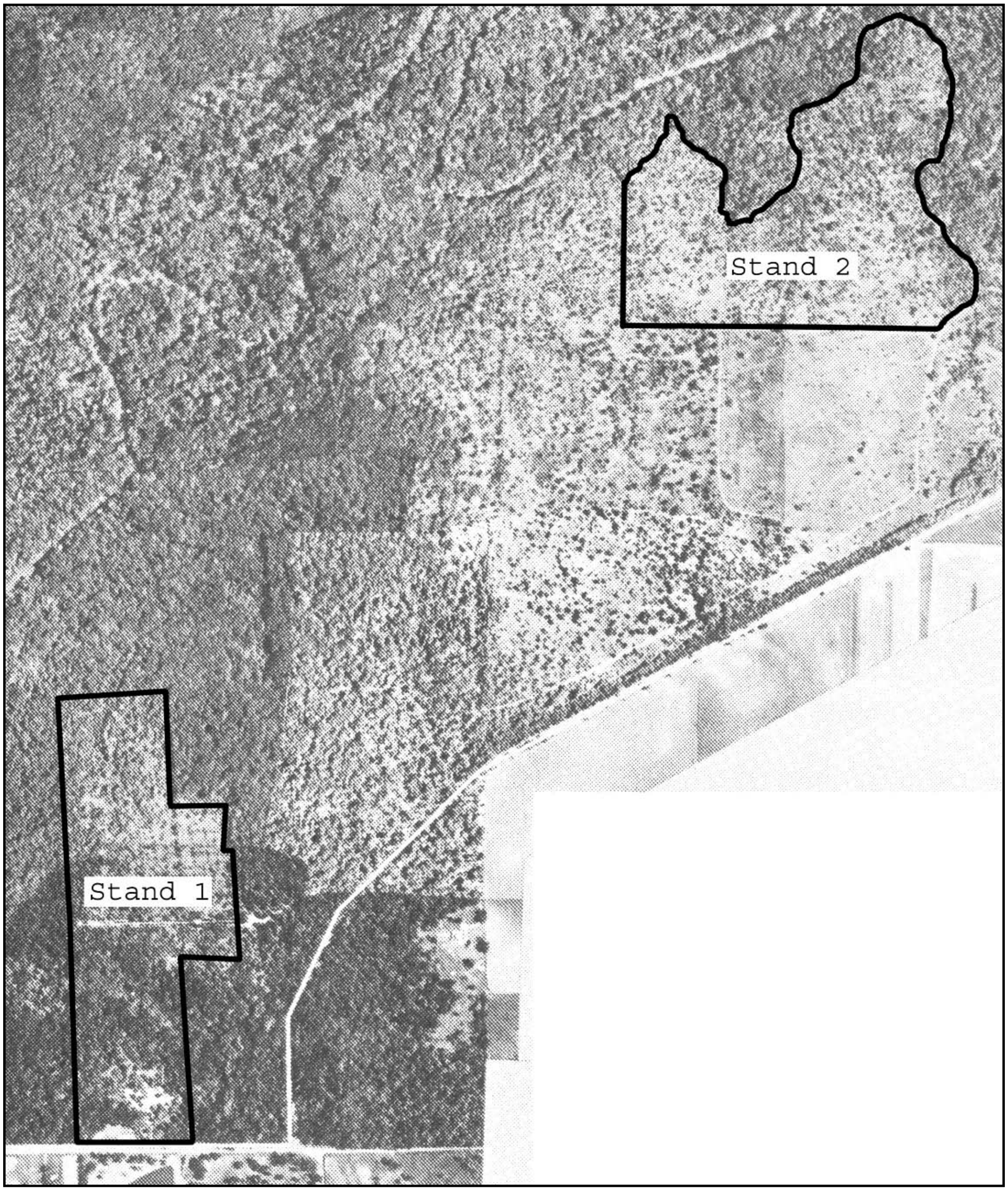

Figure 1.—*Aerial photograph showing stands 1 and 2 in Allerton Park during the 1970s. The Sangamon River can be seen in the upper (north) portion of the photograph (Jones and Bell 1976).*

METHODS

The forest overstory in both stands was sampled using 0.081 ha circular plots systematically located 63.3 m apart at cardinal azimuths, resulting in a 20 percent inventory. There were 38 plots in stand 1 and 40 plots in stand 2. Within each plot, all woody stems greater than 6 cm diameter at breast height (dbh) were recorded. Dbh was measured to the nearest centimeter, and each stem was recorded by species in 1-cm diameter classes. Fieldwork was conducted in late summer and fall of 1998 for stand 1, and late summer and fall of 1999 for stand 2. The number of stems per ha, basal area in m^2 per ha, and frequency were calculated for each species within each stand.

Importance values (IV) were calculated using a sum of relative density, relative basal area, and relative frequency, and were scaled to 100 by dividing by three. Importance values were also calculated for each individual plot using only relative density and relative basal area. Distance to nearest forested border (m) was determined by denoting plot location on the 1936 aerial photographs, and measuring to the nearest forested border that had at least 50 percent canopy closure.

A Shannon index of diversity ($H'=-\Sigma p_i \ln p_i$ where p_i equals the proportion of importance for the ith species) and Simpson index of dominance ($D=\Sigma p_i^2$ where p_i equals the proportion of importance for the ith species) were calculated for each stand using the importance values from individual plots based on relative density and relative basal area. Both the Shannon diversity index (H′) and the Simpson index of dominance (D) were used because of differences between the indices in sensitivity to species richness and dominance. The Shannon index is biased towards species richness, while the Simpson index is biased towards dominance (Magurran 1988). The stands appeared to be different with respect to both of these attributes.

A jack-knifing procedure (Zahl 1977) was used to calculate the indices for each stand. This resampling procedure calculates the index n times, where n is the number of plots. Each time the index is calculated, one plot is removed from the sample. A series of jack-knife estimates (VJ) are created for each plot, and represent the diversity of the stand with an individual plot removed. A series of n pseudovalues (VP) are also created, and are reliable for significance testing (Zahl 1977). The mean of the VP values is the best estimate of the index. Jack-knifing an index of diversity allowed us to examine the influence of individual plots on the overall diversity of a stand without losing this overall diversity. Calculating an individual index value for each plot and then an average would not accurately reflect the true diversity of a stand because diversity is sensitive to sample size (Magurran 1988).

In accordance with our hypothesis, we expected plots close to the forest border to have a positive influence, plots far from the border to have a negative influence, and intermediate plots to have little influence on diversity of a stand. The stands were tested for differences with t-tests using the VP values for both H′ and D. The VJ values from the jack-knifing procedure using H′ were examined for relationships with distance from forest border (m). In addition, a linear regression analysis was used to statistically quantify the relationship of VJ with distance from forest border for the wider stand 2.

RESULTS

The Appendix lists all tree species encountered in either stand by both the scientific and common name. The best estimate (mean of VP values) of H′ is 2.99 for stand 1 and 2.44 for stand 2, indicating a greater diversity for stand 1. An estimated D value of 0.13 for stand 2 indicates a greater dominance by the common species than observed in stand 1, which had an estimated D value of 0.06. A higher dominance index indicates a lower diversity because fewer species are common. Both indices indicate stand 1 is more diverse. The two stands are significantly different for both indices according to the results of the t-tests (for H′: df=75; $p\text{-value}<0.0001$; for D: df=49; $p\text{-value}<0.0001$).

The plots of VJ values (H′) and distance (m) showed a trend for stand 2, but not stand 1. When plots from stand 2 that were close to the forest border were removed from diversity calculations during the jack-knifing procedure, diversity decreased, and when plots far from the border were removed diversity increased, indicating plots closer to forested border had a positive influence on diversity and plots far from the border had a negative influence on diversity. This can be interpreted to indicate that plots closer to the forest border are more diverse.

The results of the linear regression analysis, where $VJ=2.41+0.00011*\text{Distance (m)}$, shows a significant relationship between the VJ values and distance (df=39; $p\text{-value}<0.001$). The R^2 value is 0.30. Considering the many factors that influence forest succession and community structure, and thus the variation in the VJ values, the significant regression relationship with an R^2 of 0.30 suggest that distance to forest border is an important factor contributing to variance of diversity among the plots.

Table 1 shows the ranking of importance values for stand 1. Shingle oak has the highest IV, followed by slippery elm and American elm. Other oak species include black oak, white oak, northern red oak, and bur oak. Black walnut and white ash also rank high in IV. Four hickories are present, including shagbark hickory, pignut hickory, bitternut hickory, and mockernut hickory. Although no individual hickory species has a high IV, their combined IV is greater than any other individual species except shingle oak and slippery elm.

The number of stems per hectare in five size classes for stand 1 is shown in table 2. The smallest size class (6 to 10 cm) is composed

Table 1.–*Relative density (RD, number of trees for species/total number of trees), relative basal area (RBA, basal area (m*^{2}*) for species/total basal area), relative frequency (frequency of species/total frequencies) (RF), and importance value (IV (RD+RBA+RF)/3) for stands 1 and 2*

	Stand 1					Stand 2			
Species	RD	RBA	RF	IV	Species	RD	RBA	RF	IV
Quercus imbricaria	11.4	15.3	6.5	11.0	*Quercus imbricaria*	22.2	27.8	10.0	20.0
Ulmus rubra	12.2	5.2	7.1	8.2	*Ulmus americana*	22.4	17.7	10.0	16.7
Ulmus americana	10.9	4.3	7.8	7.7	*Juglans nigra*	6.0	8.8	8.2	7.7
Quercus velutina	5.4	11.0	5.1	7.2	*Sassafras albidum*	10.7	5.9	6.0	7.5
Fraxinus americana	7.7	6.5	6.7	7.0	*Prunus serotina*	5.8	6.7	8.0	6.8
Juglans nigra	5.9	9.9	5.1	7.0	*Ulmus rubra*	7.7	4.6	7.5	6.6
Quercus alba	3.1	11.3	3.6	6.0	*Acer saccharinum*	4.5	5.6	4.7	4.9
Sassafras albidum	8.6	3.4	4.9	5.6	*Quercus velutina*	2.4	5.9	6.5	4.9
Gleditsia triacanthos	3.6	7.6	5.1	5.4	*Celtis occidentalis*	3.6	2.6	6.5	4.2
Celtis occidentalis	5.2	3.1	5.1	4.5	*Gleditsia triacanthos*	1.5	5.8	3.5	3.6
Prunus serotina	3.7	2.7	5.8	4.1	*Crataegus spp.*	2.9	0.7	6.5	3.4
Quercus rubra	2.7	3.3	4.9	3.6	*Quercus rubra*	1.7	3.1	2.0	2.3
Quercus macrocarpa	1.5	3.3	3.1	2.6	*Fraxinus americana*	1.5	0.7	3.5	1.9
Cercis canadensis	3.1	0.8	3.3	2.4	*Malus spp.*	1.8	0.4	3.2	1.8
Carya ovata	2.0	1.7	3.3	2.4	*Cercis canadensis*	1.5	0.5	3.0	1.7
Carya glabra	2.0	3.2	1.8	2.3	*Quercus macrocarpa*	0.7	0.9	1.5	1.0
Acer saccharum	1.5	0.5	3.1	1.7	*Acer negundo*	0.7	0.5	1.7	1.0
Tilia americana	1.4	0.9	2.7	1.7	*Carya cordiformis*	0.6	0.3	2.0	1.0
Juniperus virginiana	2.4	0.7	1.8	1.6	*Tilia americana*	0.4	0.4	1.5	0.8
Carya cordiformis	1.2	1.1	2.4	1.6	*Carya ovata*	0.5	0.4	0.7	0.6
Carya tomentosa	0.9	0.9	2.9	1.6	*Quercus alba*	0.3	0.6	0.7	0.6
Acer saccharinum	0.4	0.6	1.6	0.9	*Acer saccharum*	0.2	0.1	1.0	0.4
Viburnum prunifolium	0.4	0.0	1.6	0.7	*Carya tomentosa*	0.1	0.1	0.5	0.2
Platanus occidentalis	0.3	0.9	0.7	0.6	*Viburnum prunifolium*	0.1	0.0	0.5	0.2
Crataegus spp.	0.8	0.2	0.9	0.6	*Carya glabra*	0.1	0.0	0.2	0.1
Morus rubra	0.3	0.3	0.9	0.5	*Maclura pomifera*	0.0	0.0	0.2	0.1
Acer negundo	0.7	0.2	0.4	0.4	*Morus rubra*	0.0	0.0	0.2	0.1
Fraxinus quadrangulata	0.4	0.0	0.4	0.3	*Cornus florida*	0.0	0.0	0.2	0.1
Fraxinus pennsylvanica	0.1	0.2	0.4	0.2					
Robinia psuedoacacia	0.1	0.3	0.2	0.2					
Maclura pomifera	0.2	0.2	0.2	0.2					
Prunus spp.	0.0	0.0	0.2	0.1					
Cornus florida	0.0	0.0	0.2	0.1					
Total	100	100	100	100	Total	100	100	100	100

See Appendix 1 for nomenclature

mostly of slippery elm and American elm, which combined, represent about 30 percent of the stems. Sassafras, shingle oak, white ash, and hackberry also have high numbers of stems in this size class. In the next size class (11 to 20 cm) the elms, shingle oak, and sassafras comprise a major portion of the total stems, along with white ash and black walnut.

In the 21 to 30 cm dbh size class shingle oak is the most dominant tree. Honeylocust also represents a large portion of stems in this size class (table 2). Shingle oak is the most common tree in the 31 to 40 cm diameter class. The elms are rare in this size class, with black oak and northern red oak both having more stems than the elms. In the largest size class, 41 cm and greater, black oak and white oak outnumber shingle oak, the third most common species. The oaks combined make up almost 69 percent of the stems in this size class. Black walnut and honey locust are also common. The total basal area for stand 1 is 24.0 m^2 per hectare, with 782 stems per hectare.

In stand 2, shingle oak and American elm are the two species with the highest IVs (table 1). Black walnut is third, but has less than half the IV of American elm. Black oak, white oak, bur oak, and northern red oak are also present in

Table 2.—*Density (number of trees per hectare), basal area (BA, m² per hectare), and frequency (number of plots in which species occurred/total number of plots) by size classes (dbh in cm), ranked in order of importance value (table 1) for stand 1*

	Density						BA	Freq.
Species	6-10cm	11-20cm	21-30cm	31-40cm	41+cm	>6cm	>6cm	>6cm
Quercus imbricaria	27.6	27.6	14.6	12.7	6.5	89.1	3.67	76.3
Ulmus rubra	54.6	32.5	7.2	1.0	0.0	95.3	1.25	84.2
Ulmus americana	49.7	28.3	5.2	1.6	0.0	84.9	1.03	92.1
Quercus velutina	9.4	12.4	7.2	5.5	7.5	41.9	2.66	60.5
Fraxinus americana	22.8	23.1	8.5	4.9	1.0	60.1	1.57	78.9
Juglans nigra	8.5	20.5	7.8	3.9	5.2	45.8	2.38	60.5
Quercus alba	4.6	6.8	3.6	1.6	7.5	24.1	2.70	42.1
Sassafras albidum	35.8	26.3	4.9	0.0	0.0	67.0	0.82	57.9
Gleditsia triacanthos	1.3	7.8	10.7	5.2	2.9	28.0	1.84	60.5
Celtis occidentalis	22.8	10.4	5.9	1.6	0.3	41.0	0.75	60.5
Prunus serotina	11.4	8.5	7.8	0.7	0.3	28.6	0.66	68.4
Quercus rubra	7.2	6.5	4.2	2.0	1.3	21.1	0.79	57.9
Quercus macrocarpa	4.9	2.6	1.3	0.7	2.3	11.7	0.80	36.8
Cercis canadensis	15.9	8.1	0.0	0.0	0.0	24.1	0.19	39.5
Carya ovata	6.2	4.9	2.9	2.0	0.0	15.9	0.42	39.5
Carya glabra	0.7	6.8	4.2	3.3	0.3	15.3	0.76	21.1
Acer saccharum	7.8	3.6	0.7	0.0	0.0	12.0	0.12	36.8
Tilia americana	5.2	3.9	0.7	1.0	0.0	10.7	0.23	31.6
Juniperus virginiana	10.4	7.8	0.3	0.0	0.0	18.5	0.18	21.1
Carya cordiformis	3.9	2.3	2.6	0.7	0.0	9.4	0.26	28.9
Carya tomentosa	2.9	2.0	1.3	1.0	0.0	7.2	0.21	34.2
Acer saccharinum	1.0	1.3	0.7	0.0	0.3	3.3	0.16	18.4
Viburnum prunifolium	3.3	0.0	0.0	0.0	0.0	3.3	0.01	18.4
Platanus occidentalis	0.0	0.7	0.3	0.7	1.0	2.6	0.22	7.9
Crataegus spp.	3.3	2.9	0.0	0.0	0.0	6.2	0.05	10.5
Morus rubra	0.7	0.7	1.3	0.0	0.0	2.6	0.07	10.5
Acer negundo	2.9	2.3	0.0	0.0	0.0	5.2	0.05	5.3
Fraxinus quadrangulata	2.9	0.0	0.0	0.0	0.0	2.9	0.01	5.3
Fraxinus pennsylvanica	0.0	0.0	0.3	0.3	0.0	0.7	0.05	5.3
Robinia pseudoacacia	0.0	0.0	0.3	0.7	0.0	1.0	0.08	2.6
Maclura pomifera	0.0	1.0	0.7	0.0	0.0	1.6	0.05	2.6
Prunus spp.	0.0	0.3	0.0	0.0	0.0	0.3	0.00	2.6
Cornus florida	0.3	0.0	0.0	0.0	0.0	0.3	0.00	2.6
Total	327.7	261.7	105.0	50.7	36.4	781.6	24.0	1181.6

stand 2, but have lower IVs than in stand 1. The same four hickory species from stand 1 are present in stand 2, but also have lower IVs. Other common species in stand 2 include sassafras, black cherry, and slippery elm. The ranking of seventh in IV for silver maple, a floodplain species, on the upland stand 2 is noteworthy. Species present on stand 2 are for the most part identical to stand 1, but with differences in IVs.

In terms of stems per hectare, shingle oak and American elm dominate the two smallest size classes in stand 2 (table 3); sassafras also has a large number of stems. Black walnut has few stems in the 6 to 10 cm size class, but represents a significant portion of the 11 to 20 cm size class. Silver maple has a large proportion of its total number of stems per hectare in this size class as well. Shingle oak and American elm dominate the 21 to 30 cm size class, and along with black walnut and silver maple make up almost 65 percent of the stems.

In the 31 to 40 cm size class, shingle oak is the most common species, followed by American elm (table 3). Black walnut is also common, and honey locust has its highest density in this size class. The largest size class (41+ cm) is dominated by shingle oak, and American elm has a much lower percentage of the total stems per hectare in this size class than in the lower size

Table 3.—*Density (number of trees per hectare), basal area (BA, m*^{2} *per hectare), and frequency (number of plots in which species occurred/total number of plots) by size classes (dbh in cm), ranked in order of importance value (table 1) for stand 2*

	Density						BA	Freq.
Species	6-10cm	11-20cm	21-30cm	31-40cm	41+cm	>6cm	>6cm	>6cm
Quercus imbricaria	65.2	68.3	22.2	9.9	11.4	177.0	5.86	100.0
Ulmus americana	79.1	66.7	24.7	5.9	2.2	178.5	3.73	100.0
Juglans nigra	7.4	19.8	14.5	5.3	1.2	48.2	1.85	82.5
Sassafras albidum	38.9	39.5	5.3	1.2	0.3	85.2	1.24	60.0
Prunus serotina	12.0	20.1	8.6	3.7	1.5	46.0	1.40	80.0
Ulmus rubra	31.8	22.9	5.6	0.9	0.3	61.5	0.96	75.0
Acer saccharinum	7.1	15.4	10.5	1.9	0.9	35.8	1.18	47.5
Quercus velutina	3.1	6.2	4.9	1.5	3.1	18.8	1.24	65.0
Celtis occidentalis	13.6	9.9	4.0	0.6	0.3	28.4	0.54	65.0
Gleditsia triacanthos	0.3	3.1	1.9	4.0	3.1	12.4	1.22	35.0
Crataegus spp.	18.2	5.3	0.0	0.0	0.0	23.5	0.15	65.0
Quercus rubra	3.1	4.6	3.4	1.9	0.9	13.9	0.65	20.0
Fraxinus americana	6.2	5.3	0.6	0.0	0.0	12.0	0.15	35.0
Malus spp.	12.7	1.5	0.0	0.0	0.0	14.2	0.08	32.5
Cercis canadensis	8.0	3.1	0.6	0.0	0.0	11.7	0.11	30.0
Quercus macrocarpa	1.2	1.9	1.5	0.6	0.0	5.3	0.19	15.0
Acer negundo	3.4	1.9	0.0	0.6	0.0	5.9	0.10	17.5
Carya cordiformis	3.1	1.2	0.6	0.0	0.0	4.9	0.06	20.0
Tilia americana	1.2	1.5	0.6	0.0	0.0	3.4	0.08	15.0
Carya ovata	2.2	1.2	0.6	0.3	0.0	4.3	0.09	7.5
Quercus alba	0.6	0.6	0.3	0.6	0.3	2.5	0.13	7.5
Acer saccharum	0.9	0.0	0.3	0.0	0.0	1.2	0.01	10.0
Carya tomentosa	0.3	0.6	0.0	0.0	0.0	0.9	0.02	5.0
Viburnum prunifolium	0.6	0.0	0.0	0.0	0.0	0.6	0.00	5.0
Carya glabra	0.0	0.6	0.0	0.0	0.0	0.6	0.01	2.5
Maclura pomifera	0.3	0.0	0.0	0.0	0.0	0.3	0.00	2.5
Morus rubra	0.3	0.0	0.0	0.0	0.0	0.3	0.00	2.5
Cornus florida	0.3	0.0	0.0	0.0	0.0	0.3	0.00	2.5
Total	321.2	301.1	110.9	38.9	25.6	797.8	21.1	1005.0

classes. The total basal area is less than stand 1 at 21.1 m^2 per hectare and at 798 stems per hectare there are more trees per hectare than in stand 1.

DISCUSSION

The two successional stands are different with respect to diversity and dominance. Stand 1 is more diverse and is less dominated by the most common species. It had a greater percentage of border shared with existing forest during succession and a narrower configuration than stand 2, and this apparently contributed to the increased diversity of the succeeding forest by providing a proximal seed source.

In stand 2, diversity is highest close to the forest border and decreases as distance from the forest border increases. Small fields have increased species richness closer to a forest border (Crowder and Harmsen 1998). The increase in diversity with proximity to border is evident only for stand 2. This relationship is not seen in stand 1, probably due to its narrow configuration and high percentage of forested border. No one plot was far enough from a surrounding forest border for a decrease in diversity to occur. The greatest distance from a plot to forest border for stand 1 is 99 m, as opposed to 204 m for stand 2.

Tree stem density is highest near forest borders early in succession, but as succession progresses through time, tree density at distances further from the forest border increases, eventually stocking the entire field with trees (Myster and Pickett 1992). Tree species which could disperse seeds on the portions of an old-field further from the forest border could establish themselves early and have a competitive advantage over species whose seed arrives later. Close to the forest border, a greater number of species can successfully disperse seed, thus increasing diversity.

De Steven (1991a, 1991b) postulated that differential seed rain may be as important a factor as competition and herbivory in determining the species composition of successional forests. De Steven tested the effects of existing vegetation cover and herbivory on the germination (De Steven 1991a), growth, and survival (De Steven 1991b) of five hardwood species on upland old-fields of the piedmont. Using the results, a prediction was made as to which three species should be most commonly found naturally invading old-fields. Of the three predicted species, only one was found as frequently as expected.

The influence of nearby seed sources was put forward as a possible explanation of the actual frequency of species, which differed from what was predicted. In southern Illinois, approximately 300 km south of Allerton Park, tree species dominant in old-fields apparently are derived from trees common in adjacent forests, but competition may also be an important determinant of success or failure in the establishment of certain species (Ashby and Weaver 1970). Even if a species has the life history traits necessary to survive and compete in a successional environment, a lack of seed dispersal onto an old-field will obviously prevent its occupation of the site.

Few species in our study occur in only one of the stands, and all these have low IVs (table 1). The majority of species are present on both stands, but have different IVs. With the exception of shingle oak, the oaks have a greater total IV, density, and dominance (BA) in stand 1. The same is true for the hickories. Black walnut is relatively equal in IV and density between stands (tables 1, 2, and 3). Considering that these species, with the possible exception of bitternut hickory, produce seeds commonly distributed by mammals (Graney 1990; Johnson 1990; Rogers 1990; Sander 1990a, 1990b; Smalley 1990; Smith 1990a, 1990b; Williams 1990), more surrounding forest cover with seed and associated dispersal agents would seem to increase the chances of these species successfully dispersing into the old-field.

Wind dispersed species are often the first to invade old-fields (Harper and others 1970, Buell and others 1971, Smith 1975, Christensen and Peet 1984, Myster and Pickett 1992, Crowder and Harmsen 1998). The reduced forest border conditions and wider configuration of stand 2 would have provided an advantage for the wind-dispersed species over mammal-dispersed species. Silver maple has a higher IV in stand 2, where it was most dominant on, but not restricted to, the Sunbury silt loam, a somewhat poorly drained soil. Its lower IV in stand 1 is likely due to a lack of such poorly drained soils, which would favor such floodplain species.

The combined elms increase in IV in stand 2 (table 1), and are distributed throughout the stand irrespective of the Sunbury silt loam. American elm has a higher IV and slippery elm had a lower IV than in stand 1. The forest adjacent to stand 2 transitions, within 30 m of its border, to floodplain forests of the Sangamon River, where American elm is the more common elm species (Bell 1974, 1980), and this might account for predominance of American elm over slippery elm in stand 2.

The composition of old growth and other forested areas not converted to agricultural use at Allerton Park has been well documented (Boggess and Geis 1967; Bell 1974, 1980), and these forest stands represent the predominant forest composition for Allerton Park and the seed source for both stands. The composition of an old growth forest stand immediately west of stand 1 was dominated by oaks and hickories in 1963, with white and black oak being the two most important species. Slippery elm had the third highest IV, with American elm sixth. Both elms had high densities in smaller diameter classes that strongly contributed to their IVs. Shingle oak was present, but not very common (Boggess and Geis 1967).

On a portion of Allerton Park northeast of stand 2, and other nearby forests, Bell (1974, 1980) found American elm and hackberry most dominant in transition zones between floodplains and uplands that receive limited flooding. Shingle oak was present and also had its highest IV in these transition zones. The most dominant upland oak species was white oak, followed by black oak.

Bell (1980) also sampled Hart Woods, another forest along the Sangamon River, located about 35 km northeast of Allerton Park. An inventory of Hart Woods (Johnson and others 1978) found white, black, and red oak to be the three most dominant species with respect to BA. American elm and slippery elm both had high densities, and had shown a substantial increase in smaller stems since the previous inventory in 1965

(Root and others 1971, Johnson and others 1978). The increase in smaller elms was from regeneration following the mortality of mature elms from Dutch elm disease and phloem necrosis (Root and others 1971, Johnson and Bell 1975). Results from the latest inventory of Hart Woods in 1995 (Shaffer and Edgington 2003) show both elm species to continue to be common in the smaller diameter classes, but absent from the larger ones. Shingle oak is present but not a dominant species.

In successional forests in northern Illinois (approximately 180 km northeast of Allerton Park), an early stand that was dominated by hawthorns (*Crataegus* spp.) changed to one in which the hawthorns shared dominance with American elm, and then succeeded to a stand composed of sugar maple, northern red oak, American elm, black cherry, and hawthorns (Bell and del Moral 1977). Eighteen years later, hawthorns were greatly reduced in importance due to heavy mortality, and sugar maple was the most dominant species, followed by American elm. These two species are replacing the northern red oak and black cherry (Bell 1997).

A small woodlot developed on a clearing in Edgar County, Illinois, approximately 80 km southeast of our study site, was composed primarily of large numbers of small white ash, elm, maple, and black walnut (McClain and Ebinger 1968). Oaks comprised the majority of stocking on small sawtimber and pole-sized timber stands originating from abandoned pasture on the Springfield plain of south central Illinois (Jokela and Sawtelle 1985).

In the Shawnee Hills of southern Illinois, persimmon and sassafras dominated an early shrub community, with winged elm (*Ulmus alata*), eastern redcedar, and *Rhus* spp. (Sumac) also present in 3 to 15 year fields. At 25 years, persimmon and sassafras dominated in dense thickets, with winged elm, eastern redcedar, black gum (*Nyssa sylvatica*), and hawthorns also present. The same general composition was found in 40-year fields, but three hickory species (pignut, shagbark, and mockernut), sugarberry (*Celtis laevigata*), shingle oak, and tulip tree were also present in the tree layer.

The length of time necessary for oak invasion to begin may have been dependent on the time necessary for conditions to develop that favor squirrels, the primary dispersal agents for oaks, and the amount of nearby mature oak-hickory forest, which serves as a seed source as well as attractive habitat for dispersal animals (Bazzaz 1968). This general pattern is similar to that of this study. However, the higher dominance of shingle oak in stand 2 does not fit this pattern. If shingle oak relies on forest border for seed dispersion, then a lower IV would be expected in stand 2 because of its lower percentage of forest border and wide configuration.

The high water use efficiency of shingle oak seedlings under drought conditions (McCarthy and Dawson 1990) relative to other oak species is an attribute of early successional species (Bazzaz 1979), and may be a factor in its dominance, allowing it to assert itself early in the initial woody colonization period. The natural habitat of shingle oak is wooded floodplains, but it occurs more frequently as a pioneer species along dry disturbed roadsides and hedgerows (Wagner and Schoen 1976). At Allerton Park, shingle oak is a common species in undisturbed forest transition zones between floodplains and uplands (Bell 1974, 1980), but it is more dominant in the disturbed, upland successional forests of this study. The weight of shingle oak acorns may offer it an advantage over wind dispersed seeds in penetrating plant litter, which can prevent seeds from reaching the soil surface (Jokela and Sawtelle 1985, Fowler 1986, Hamrick and Lee 1987).

Dispersal mechanisms may be the major key to shingle oak's dominance on both stands, especially stand 2. The blue jay (*Cyanocitta cristata* L.), an important long distance disperser for oak acorns, is known to cache acorns along forest boundaries and in open early successional habitat, and facilitates germination by burying acorns in the ground and under litter (Darley-Hill and Johnson 1981; Johnson and Webb 1989; Johnson and others 1993, 1997). Blue jays prefer smaller acorns (Darley-Hill and Johnson 1981, Johnson and Webb 1989, Scarlett and Smith 1991, Johnson and others 1997), and are know to take shingle oak acorns (Hermes 1991). This could explain the greater abundance of shingle oak in both stands compared to the other oaks present on the study sites, which all have larger acorns (Harlow and others 1996). Harrison and Werner (1984) suggested the blue jay as a possible agent for oak invasion on the successional habitat of their study.

The high densities of shingle oak relative to other species in the upper size classes and its high percent frequency (tables 2 and 3) suggest that it was one of the initial invaders in both stands. Oaks and other mammal-dispersed species do not invade old-fields until later in forest succession, preceded by wind and bird dispersed species (Bazzaz 1968, Buell and others 1971, McDonnell and Stiles 1983, Christensen and Peet 1984, Myster and Pickett 1992, Myster 1993, Crowder and Harmsen 1998). Thus, it is likely that shingle oak seeds were dispersed onto the old-fields at Allerton primarily by the blue jay, rather than by mammals. This would explain the higher IV of shingle oak in stand 2, where all other oaks had a lower IV.

Another possible explanation for high shingle oak IV is mature pasture trees which could have provided a seed source within the field. Field observations reveal that two of the seven large trees identifiable in the 1936 photograph of stand 2 could have been shingle oak, based on the presence of two large shingle oaks in a plot located where two pasture trees can be seen in the photograph. These two trees, however, are less than 40 m from the forest border. A few additional pasture trees can be seen in the photograph to the west and south of stand 2, and it is possible that these are shingle oaks, but field observations could not confirm this. Large black oaks were found near the center of stand 2 in plots located where other pasture trees can be seen in the 1936 photograph, but this species did not exhibit a higher IV for stand 2.

It is unlikely sprouting from pre-disturbance forest stumps occurred in these stands because indications and records of disturbance suggest both stands were plowed and cropped after initial clearing, necessitating removal of stumps from the previous forest. Shingle oak does sprout (Dolan 1994), and through repeated mowing, grazing, or burning, shingle oaks that could have become established early in the subsequent pasture phase may have developed advanced root systems, leading to seedling sprouts after the pasture was abandoned. However, it is not known how long the stands were pastured before they were left to forest succession, or how other oaks may have similarly persisted as seedling sprouts from root systems established after clearing. White oak and black oak both sprout vigorously (Rogers 1990, Sander 1990b). Thus, we cannot ascertain for certain the proportion of the trees in the successional stands derived from seedling sprouts of root systems developed during the pasture phase relative to trees developed from seedlings established after pasture abandonment.

In other parts of central Illinois, shingle oak accounted for 17 percent of the trees on a previously grazed, poletimber-sized post oak flat, and 14 percent of the trees on a recently abandoned pasture (Jokela and Sawtelle 1985). On the recently abandoned pasture there were scattered mature oak pasture trees, but none were shingle oak. It was estimated that acorns for shingle oak and other oak species found invading the old-field but not represented among the pasture trees had to have traveled up to 500 m to reach the site, further supporting the hypothesis that blue jay dispersal is important for shingle oak.

The high IV of American and slippery elm in both stands fits the general trend of these two species in other forests along the Sangamon River, being most dominant in the smaller size classes (tables 2 and 3). A sampling of the understory in both stands (Bretthauer, unpublished data) shows a high number of seedling and sapling elms. This, combined with the intermediate shade tolerance of American elm (Bey 1990), suggests American elm may not have been one of the initial invaders but a later successional tree. Crowder and Harmsen (1998), however, found American elm to be one of the first tree species to invade old-fields in Canada.

On abandoned agricultural fields in southern Iowa, elms and oaks dominated the seedling- and sapling-size class (Crow and others 1994). American elm also invades tallgrass prairies in Kansas (Briggs and Gibson 1992). At Allerton Park, American elm represents 9 percent of the stems 41 cm and greater in stand 2 (table 3), suggesting it was one of the initial trees present on this site. The recruitment of American elm into larger size classes in these stands is probably limited due to Dutch elm disease. Bell (1997) found mortality to be the highest in American elm when tree diameter reached 26 cm, and found the growth rates of American and slippery elm to be greater in northern Illinois than at Allerton Park.

Proximity to forest border is associated with increased tree species diversity, decreased dominance of the most common species, and differences in species composition of successional forest stands developed on abandoned agricultural lands. Surrounding vegetation seems to be a key variable for explaining the occurrence of tree species that invade old-fields, and should be considered as such together with competition and each individual species' ecological amplitude when attempting to identify mechanisms underlying successional processes. Shingle oak is a dominant tree on both stands, and is more dominant in stand 2 than other oak species bearing larger seeds. A plausible explanation for shingle oaks ability to invade old fields more independently of near proximity to seed source is the documented preferential dispersal of its acorns by blue jays. Our results are indicative of the complexities and interactions inherent in old-field succession in Central Hardwood forests.

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APPENDIX 1: SCIENTIFIC AND COMMON NAMES OF TREE SPECIES

Scientific name	**Common name**
Acer negundo L.	box elder
Acer saccharinum L.	silver maple
Acer saccharum Marsh	sugar maple
Carya cordiformis (Wangenh.) K. Koch.	bitternut hickory
Carya glabra (Mill.) Sweet	pignut hickory
Carya ovata (Mill.) K. Koch	shagbark hickory
Carya tomentosa (Poir.) Nutt.	mockernut hickory
Celtis occidentalis L.	hackberry
Cercis canadensis L.	eastern redbud
Cornus florida L.	flowering dogwood
Crataegus spp. L.	hawthorn species
Fraxinus americana L.	white ash
Fraxinus pennsylvanica Marsh.	green ash
Fraxinus quadrangulata Michx.	blue ash
Gleditsia triacanthos L.	honeylocust
Juglans nigra L.	black walnut
Juniperus virginiana L.	eastern redcedar
Maclura pomifera (Raf.) C. K. Schneid.	osage-orange
Malus spp. Mill.	apple species
Morus rubra L.	red mulberry
Platanus occidentalis L.	sycamore
Prunus serotina Ehrh.	black cherry
Prunus spp. L.	cherry, plum species
Quercus alba L.	white oak
Quercus imbricaria Michx.	shingle oak
Quercus macrocarpa Michx.	bur oak
Quercus rubra L.	northern red oak
Quercus velutina Lam.	black oak
Robinia pseudoacacia L.	black locust
Sassafras albidum (Nutt.) Nees	sassafras
Tilia americana L.	American basswood
Ulmus americana L.	American elm
Ulmus rubra Mühl.	slippery elm
Viburnum prunifolium L.	black haw