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Tree Species Diversity and Composition in Relation to Forest Borders in Two Old-Field Successional Stands at Allerton Park, Piatt County, Illinois USA

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ABSTRACT

Two successional forest stands developed on pastureland abandoned during the 1930's at Allerton Park, Piatt County, Illinois USA were examined for patterns of tree species diversity and composition. After pastures were abandoned the subsequent successional processes were not altered by tree cutting, mowing, or grazing, which usually occur in the region. The most frequent species in both stands were *Quercus imbricaria* Michx., *Ulmus americana* L., *Ulmus rubra* Mühl., and *Juglans nigra* L. The Shannon index of diversity and Simpson index of dominance were calculated for both stands using the jack-knifing procedure. A regression equation using the jack-knifed values quantified a significant decrease in diversity with distance from forest border for the wider old-field stand. The other stand with a higher percentage of forest perimeter and a narrower configuration was more diverse. The R^2 value for the relationships with distance to forest border in the wider stand were 0.30 for diversity, 0.32 for density, 0.34 for basal area, and 0.32 for importance value for species having seed dispersed primarily by animals. These values indicate that factors associated with seed dispersal probably influence the variation of forest composition and structure more than is commonly suggested. Proximity to forest vegetation seems to be important as a determinant of species diversity and composition during old-field succession at this location. The wider tract had more wind and bird dispersed tree species and relatively fewer animal dispersed species. *Quercus imbricaria* was the dominant tree species among oaks and other species in this study, perhaps due to preference of its small acorns by the blue jay, which carries and caches acorns in soil and under litter.

Keywords: Old-field succession; tree species diversity; *Quercus imbricaria*; forest regeneration

INTRODUCTION

In agricultural regions of the Midwest there are few examples of uninterrupted succession from old-field to forest. Mowing, grazing, and tree cutting practices during forest succession are common and alter successional processes in these stands. At Allerton Park in Piatt County Illinois, old agricultural fields set aside as nature reserves in the 1930's have reverted to forest without direct subsequent disturbance. The configurations and proximity to surrounding forest permitted examination and comparison of the composition and diversity of two old-field successional stands.

Adjacent vegetation influences tree invasion during old-field succession (Bazzaz, 1968; Vankat, 1991; Myster, 1993) and species found invading old-fields are often found in proximal forest stands (Ashby and Weaver, 1970; Buell et al., 1971; Crowder and Harmsen, 1998). The ability of tree species to disperse seed might be as important as other factors, such as competition and herbivory, in determining tree species composition in old-fields (De Steven, 1991a; 1991b). Near a forested border, tree density during succession is greater (Myster and Pickett, 1992) and small fields exhibit greater species richness (Crowder and Harmsen, 1998). Differing seed dispersal mechanisms in upland forests (wind, bird, or mammal) are important in determining the ability of trees to invade an old-field. Seed dispersal affects the timing of invasion and distribution of individual species (Bard, 1952; Buell et al., 1971; Connell and Slatyer, 1977; Oliver, 1981; McDonnell and Stiles, 1983; Christensen and Peet, 1984; Burton, 1989; Myster and Pickett, 1992) and can influence species composition by limiting the number of species that successfully establish at greater distances from seed sources.

If proximity to forest border influences the species composition and densities of successional forests on old-fields, then differing amounts of forest border along the perimeter of old-fields and the extent to which the forest surrounds an old-field should also have an effect on tree species composition and diversity of successional forests. At Allerton Park, we studied two forest stands with differing original amounts of forest border that developed on pastureland abandoned in the 1930's. We hypothesized that a forest stand that developed on a narrow field with 92 percent forest border would have greater species diversity than a forest stand that developed on a wider field with only a 50 percent forest border. We further hypothesized that species diversity and the abundance of mammal dispersed tree species would decrease with increasing distance from forest borders. In the present study we test these hypotheses and describe the species composition and structure of the two successional forest stands.

STUDY SITE

The study location was Robert Allerton Park in east-central Illinois (N39° 59.9′; W88° 38.7′), along the Sangamon River in Piatt County, Illinois. Allerton Park was established in 1946 and is owned by the University of Illinois at Urbana-Champaign, which maintains it as a reserve for research and education. Robert Allerton, a wealthy benefactor, had established an estate and gardens at the site, prior to donating it to the University of Illinois. Most of the 600 ha of the park are rolling terrain and floodplain with both old-growth and second growth upland and bottomland forests. Robert Allerton set aside this land as a nature reserve. The park is located in the Prairie Peninsula of the oak-hickory forest region in the central United States (Braun, 1950). Allerton Park is located in the Grand Prairie Natural Division of Illinois (Schwegman, 1973).

Two separate upland forest tracts used as pasture prior to the 1930's were selected as study sites. Stand 1 is located in the southwestern portion of the park and is approximately 15.4 ha in size. The portion sampled is at least 4.5 m above the floodplain of the Sangamon River and not subject to periodic flooding. Slopes range from 0 to 7 percent. The soils consist of Miami (Oxyaquic Hapludalf) loams and Xenia (Aquic Hapludalf) and Russell (Typic Hapludalf) silt loams. They range from moderately well drained (Xenia) to well drained (Miami and Russell). These soils were formed under forest vegetation on till plain in loess, other silty material, and the underlying calcareous loam glacial till (Martin, 1991).

Stand 2 is approximately 16.2 hectares in size and is located in the eastern part of the park directly south of the Sangamon River approximately 1200 m northeast of stand 1. Slopes range from 0 to 7 percent. The soil types are the same as those of stand 1 with additional minor areas (less than 20 percent of total stand area) of Sunbury (Aquollic Hapludalf) silt loam, which is somewhat poorly drained and was formed in loess and underlying calcareous loam glacial till under forest vegetation (Martin, 1991). The stand is at least 6 m above the floodplain of the Sangamon River, but can occasionally have standing water in depressions associated with Sunbury silt loam. Variability of soil properties, including percent moisture and bulk density, for these and other upland forest soils at Allerton Park is low (David and Wang, 1989). A preliminary principal components analysis showed no relationship between tree species composition and soil types (unpublished data).

The critical differences between the stands for the purposes of this study are the amount of surrounding forest at the time of abandonment and the configuration of the fields. Stand 1 has a long and narrow configuration (Figure 1) and was almost completely surrounded by mature forest, having 92 percent of its perimeter contiguous with original forest. Stand 2 had 50 percent of its border forested along its northern boundary. Its remaining border was adjacent to abandoned pasture that was converted to tallgrass prairie. This recreated prairie is burned periodically to favor prairie and eliminate trees. Stand 2 has a wider configuration than stand 1 (Figure 1).

Quercus alba L. and *Quercus velutina* Lam. were the two most important species in an old-growth upland community located immediately west of stand 1 (Boggess and Geis, 1967). In this study *Ulmus rubra* Mühl. and *Ulmus americana* L. were ranked 3 and 6, respectively, due to a high number of stems in small diameter classes. The species composition of the portion of Allerton Park northeast of stand 2 has also been well documented (Bell, 1974; Johnson and Bell, 1975; Bell, 1980). *Quercus alba* dominated the upland forest and the second most dominant oak species was *Q. velutina*. Small *Ulmus* spp. were present in high densities. In the transitional zone between the uplands and floodplains, which is subject to minor flooding, *Quercus imbricaria* Michx. and *Celtis occidentalis* L. were the most important species. The floodplains were dominated by *Acer saccharinum* L. The majority of the forest presently bordering both stands is upland, with small percentages of riparian forest border. However, the north side of Stand 2 is within 30 m of the main floodplain and transitional forests of the Sangamon River (Figure 1).

Although separated by an upland forest similar in composition to the forest surrounding Stand 1, stand 2 has greater proximity to floodplain and transitional forest seed sources than Stand 1.

Records indicate that both study stands were cleared in the late 1800's and subsequently used for cattle grazing (Foster, 1981). Aerial photographs and maps show that both stands were originally grassy pastures with scattered trees (Holmberg Air Mapping Company, 1936; University of Illinois, 1948). Dykstra (1999) indicates that stand 1 was a secondary forest and stand 2 was an abandoned field in 1940. Both stands were described as successional forest in 1976 (Jones and Bell, 1976). These observations indicate that both stands began succession from pasture to forest in the mid to late 1930's. These stands have been allowed to succeed naturally without direct anthropogenic disturbance since 1946.

METHODS

Aerial photographs from 1936 and maps from 1948 were used to describe site history and to delineate stands. Both stands were sampled using 0.081 ha circular plots systematically located 63.3 m apart along cardinal azimuths. There were 38 plots in stand 1 and 40 plots in stand 2. All woody stems greater than 6 cm in diameter at breast height (dbh) (Root et al., 1971; Boggess and Geis, 1967; Johnson et al., 1978; Edgington, 1991) within a plot were recorded by species to the nearest cm dbh, and dead standing trees were also recorded. Field work was conducted in the summer and fall of 1998 and 1999. For each stand the number of stems per ha (density), basal area (m^2) per ha, and frequency were estimated for tree species. Species importance values (IV) were calculated using a sum of relative density, relative basal area, and relative frequency, were scaled to 100 by dividing by 3, and are referred to hereafter as IVa. Importance values were also calculated for each individual plot using only relative density and relative basal area. These were also scaled to 100 and are referred to hereafter as IVb. Species were selected for comparisons based on two criteria: they were either one of the 10 most dominant species in either stand based on IVa or they were a species primarily dispersed by mammals. For the selected species, the mean plot values for density, basal area, and IVb were calculated for each stand. These means were used in t-tests to examine differences between stands in ecological values for the selected species. The distance to nearest forested border in 1936 was determined from aerial photographs, border forests being defined as those contiguous areas having at least 50 percent canopy closure. The upper soil horizons in both stands were examined for indicators of past agricultural use.

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 calculated with relative density and relative basal area. The Shannon index of diversity and the Simpson index of dominance are heterogeneity indices that combine information on both species richness and species evenness (Peet, 1974). The Shannon index is biased towards species richness, while the Simpson index is biased towards the abundance of the most common species (Magurran, 1988). Since the stands differed with respect to both of these attributes, both indices were used.

A jack-knifing procedure (Zahl, 1977) was used to calculate the indices for each stand. This re-sampling procedure calculates the index n times, where n is the number of plots. Each time the index is calculated, one plot is systematically 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. The variance of the VP values is better than other estimates of H′ variance (Adams and McCune, 1979), making the VP values 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 the 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 (greatest tree diversity), plots far from the border to have a negative influence (least tree diversity), and plots in between to have little influence (intermediate tree diversity) on the diversity of a stand. The two 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 which afforded sufficient width to do so. The values for tree density, basal area, and IVb for major mammal dispersed species were pooled by plot for stand 2. The values were pooled because many species were absent from a large number of the plots, making an analysis of individual species problematic. Regression analyses were performed with each pooled variable and distance from plots to forest border to examine relationships between the abundance of the mammal dispersed species and the distance to forest border.

RESULTS

The soil examinations from both stands showed evidence of past grazing and in portions there were indications of plowing. Indicators of past agricultural use included an abrupt soil structure change (granular to subangular blocky) at depths of 13 cm to 25 cm, non-pedogenic mixing of the A and B horizons, and evidence of compaction in the lower A horizon.

The two stands had similar species composition (Tables 1 and 2). In stand 1 *Q. imbricaria* had the highest IVa, followed by *U. rubra* and *U. americana* (Table 1). *Ulmus rubra* and *U. americana* comprised about 30 percent of the stems in the smallest size class (6-10 cm). *Sassafras albidum* (Nutt.) Nees, *Q. imbricaria*, *Fraxinus americana* L., and *C. occidentalis* also had high numbers of stems in this size class. In the 11-20 cm size class *Ulmus* spp., *Q. imbricaria*, and *S. albidum* made up a major portion of the total stems, along with *F. americana* and *Juglans nigra* L. In the 21 to 30 cm dbh size class *Q. imbricaria* was the dominant tree. *Gleditsia triacanthos* L. also had values reflecting a high degree of dominance. *Quercus imbricaria* was the most common tree in the 31 to 40 cm diameter class. *Quercus velutina* and *Quercus rubra* L. had more stems than the *Ulmus* spp. in this size class. In the 41 cm and greater size class, *Q. velutina* and *Q. alba* outnumbered *Q. imbricaria*, the third most common species. The *Quercus* spp. combined made up almost 69 percent of the stems in this size class. *Juglans nigra* and *G. triacan-*

thos were also common. The total basal area for stand 1 was 24.0 m^2 per hectare, with 782 stems per hectare.

In stand 2, *Q. imbricaria* and *U. americana* had the highest IVa (Table 2). *Juglans nigra* was third, but had less than half the IVa of *U. americana*. The ranking of seventh in IVa for *A. saccharinum*, a floodplain species, on upland stand 2 is noteworthy. *Quercus imbricaria* and *U. americana* dominated the three smallest size classes in stand 2. *Sassafras albidum* had a large number of stems in the two smallest size classes. *Juglans nigra* represented a significant portion of the 21 to 30 cm size class. *Acer saccharinum* also had a large proportion of its total number of stems per ha in this size class. In the 31 to 40 cm size class, *Q. imbricaria* was the most common species, followed by *U. americana* and *J. nigra*. *Gleditsia triacanthos* had its highest density in this size class. The largest size class (41+ cm) was dominated by *Q. imbricaria*. *Ulmus americana* had a much lower percentage of the total stems per ha in this size class than in smaller size classes. There were 798 stems per ha having a total basal area of 21.1 m^2 per ha for stand 2.

The t-tests revealed significant differences between stands in density, basal area, and IVb for some of the selected tree species (Table 3). *Quercus imbricaria, U. americana, Prunus serotina* Ehrh., and *A. saccharinum* from stand 2 had significantly higher values for the three variables than in stand 1. *Quercus velutina, F. americana, Q. alba, Carya glabra (Mill.) Sweet, Quercus macrocarpa Michx., Carya ovata (Mill.) K. Koch,* and *Carya tomentosa (Poir.) Nutt.* from stand 2 had significantly lower values for all three variables. Also in stand 2 *Gleditsia triacanthos* had significantly lower density and *Carya cordiformis (Wangenh.) K. Koch*. had significantly lower IVb and basal area relative to stand 1. *Quercus rubra* was the only oak species that was not significantly different for any of the three variables. *Juglans nigra* also did not differ significantly in mean values for any of the variables between stands. *Quercus imbricaria* was the only oak species that had a significantly higher density, basal area, and IVb in stand 2.

The estimate of H′, which is the mean of the VP values, is 2.99 for stand 1, the narrow stand with 92 percent original forest border. The estimate of H′ for stand 2, the wide stand with only 50 percent original forest border, is 2.44. The H′ values are significantly different (df=75; p-value<0.0001) indicating that stand 1 is more diverse than stand 2. The estimate of D for stand 1 is 0.06; the estimate of D for stand 2 is 0.13. The D values are also significantly different (df=49; p-value<0.0001). This indicates that the most common species are more dominant in stand 2 than in stand 1.

There was an apparent relationship between the VJ values of H′ and distance from original forest border (m) in stand 2. When stand 2 plots that were close to the forest border were removed from diversity calculations during the jack-knifing procedure, diversity decreased. When plots far from the border were removed, diversity increased. This indicates plots closer to forested border positively influenced the H′ value for stand 2 and plots far from the border negatively influenced the H′ value. In stand 2 diversity was highest close to the forest border and decreased as distance from the forest border increased. The results of the linear regression analysis, where VJ=2.41+0.00011*Distance (m), showed a significant relationship with distance from the forest border (df=39; p-value<0.001). The R^2 value was 0.30, suggesting that distance to original forest border was an important factor contributing to the variance in diversity among the plots.

The species with seeds primarily dispersed by mammals from stand 2, for which the density, basal area, and IVb values were pooled, were *J. nigra*, *Q. velutina*, *Q. rubra*, *Q. macrocarpa*, *C. cordiformis*, *C. ovata*, *C. tomentosa*, and *C. glabra*. The regression analyses between pooled values of density, basal area, and IVb and the distance to forest border were all significant (df=39; p-value<0.001). For density, the relationship was Density=16.59-0.0831*Distance (m), with an R^2 value of 0.32. The relationship for basal area was Basal Area=0.76-0.0040*Distance (m), with an R^2 value of 0.34. For IVb, it was IVb=32.06-0.1564*Distance (m), with and R^2 value of 0.32.

DISCUSSION

The greater percentage of border perimeter shared with forest during succession and a narrower configuration of stand 1 with respect to stand 2, most likely contributed to the greater diversity of stand 1 by providing a proximal seed source during colonization and old-field succession.

Small fields have been shown to have higher species richness closer to a forest border (Crowder and Harmsen, 1998). A significant increase in diversity with proximity to original forest border was evident only for stand 2. This relationship was likely not seen in stand 1 because of its narrow configuration and higher percentage of forested border. No plots in the narrow stand were far enough from the forest border to decrease seed dispersal of any tree species in a way that significantly influenced stand diversity. The average and maximum distance from a plot to forest border for stand 1 were 47 m and 99 m, respectively, as opposed to average distance of 103 m and maximum distance of 204 m for stand 2.

During early succession to forest, tree density is usually highest near forest borders. As succession progresses, tree density begins to increase further from the forest border until eventually the entire field is stocked (Myster and Pickett, 1992). At greater distances from the nearby forest, tree species with longer seed dispersal ranges could establish earlier during succession, affording them a competitive advantage. Close to the forest border, where a greater number of species could successfully disperse their seeds, greater diversity would be expected. Wind-dispersed species, followed closely by bird-dispersed species, often invade old fields in advance of mammal-dispersed species (Bard, 1952; Buell et al., 1971; Smith, 1975; Christensen and Peet, 1984; Myster and Pickett, 1992; Myster, 1993).

The reduced abundance in stand 2 for most of the *Quercus* and *Carya* spp. (Table 3) suggests their ability to invade the stand was reduced with increasing distance from a forest border. The notable exception was the greater abundance of *Q. imbricaria* in stand 2. Considering that the seeds of oak and hickory species are commonly distributed by mammals and gravity, more surrounding forest cover with seed and associated dispersal agents seemed to increase the chances for these species to successfully disperse into the site. In stand 2, the significant reduction in the IVb, density, and basal area with greater distance from forest border for species primarily dispersed by mammals is consistent with this idea. Similarly, *Quercus and Carya* spp. were absent in southern Illinois old-fields less than 25 years old (Bazzaz, 1968; 1975).

Less forest border and the greater width of stand 2 probably favored wind-dispersed species compared to mammal-dispersed species. For example, *A. saccharinum* and *U. americana* had greater abundance in this stand (Table 3). *Acer saccharinum*, a floodplain species able to tolerate wet soils, was most common on, but not restricted to, the Sunbury silt loam, a somewhat poorly drained soil found in upland depressions. Its lower abundance in stand 1 might have been due to the absence of this poorly drained soil type, which would favor the flood tolerant species noted above. *Ulmus* spp. were distributed throughout the stand, not solely on the poorly drained Sunbury silt loam, indicating a greater ecological amplitude for this species with respect to soil moisture conditions. Elsewhere at Allerton Park and along the Sangamon River, small diameter *Ulmus* spp. were common across the entire hydrological gradient while *A. saccharinum* dominated the floodplain forests and poorly drained soils (Boggess and Geis, 1967; Root et al., 1971; Bell, 1974; Johnson and Bell, 1975; Johnson et al., 1978).

Quercus imbricaria's natural habitat is wooded floodplains, especially the margins of floodplains, but it occurs more frequently as a pioneer species in the disturbed or agricultural landscape (Wagner and Schoen, 1976). Besides the successional stands, at Allerton Park and other forests along the Sangamon River in central Illinois *Q. imbricaria* had its greatest importance in transition zones between floodplain and upland forests; it was not as common as other *Quercus* spp. in undisturbed upland forests (Boggess and Geis, 1967; Root et al., 1971; Bell, 1974; 1980). *Quercus imbricaria* is an important *Quercus* sp. in other old-field stands in Illinois (Bazzaz, 1968; Jokela and Sawtelle, 1985). *Quercus imbricaria* is also drought tolerant (McCarthy and Dawson, 1990), an attribute of early successional species (Bazzaz, 1979). The greater mass of *Q. imbricaria* and other *Quercus* spp. acorns relative to the seed mass of wind dispersed species may afford the *Quercus* spp. seeds an advantage in penetrating through grassland plant communities (Jokela and Sawtelle, 1985; Fowler, 1986; Hamrick and Lee, 1987). In addition, *Quercus imbricaria* may be primarily dispersed by the blue jay (*Cyanocitta cristata* L.) (Darley-Hill and Johnson, 1981; Harrison and Werner, 1984; Johnson and Webb, 1989; Johnson et al., 1993; Johnson et al., 1997) which prefers small acorns (Scarlett and Smith, 1991) and is known to take the small *Q. imbricaria* acorns (Hermes, 1991). Seed dispersal by the blue jay, which, unlike most birds, caches acorns in the soil and under litter, could explain *Q. imbricaria's* dominance in both stands and its greater abundance in stand 2 than in stand 1. Most other *Quercus* spp. were less abundant in stand 2 than in narrow stand 1. *Prunus serotina*, the seed of which is also commonly dispersed by birds, was more abundant in stand 2 (Table 3).

Mature pasture trees could have provided a seed source within the field. Observations on the ground reveal that two of the seven large pasture trees identified in the 1936 photograph of stand 2 could have been *Q. imbricaria*. These two trees were less than 40 m from the forest border and by themselves could not likely have contributed to the differences observed between stands in this study through seed or sprouts. *Quercus imbricaria* sprouts (Dolan, 1994), and sprouting from root systems of seedlings that developed during the pasture phase might explain *Q. imbricaria's* dominance. It is unlikely, however, that there were many residual sprouts from root systems of pasture trees at the time of agricultural abandonment because cattle browsing usually eliminates sprouts and clearing the forest for crops typically entailed the removal of large tree roots and stumps.

The large number of *U. americana* stems in the smaller size classes (Tables 1 and 2) and its intermediate shade tolerance (Bey, 1990) suggest that existing elm trees may not have been initial colonizers. *Ulmus americana*, however, comprised 9 percent of the stems in the 41 cm and greater size class in stand 2. Recruitment into larger size classes is likely limited due to Dutch elm disease mortality, which Bell (1997) found to be highest in trees with a dbh greater than 26 cm. *Ulmus* spp. currently represent 18.4 percent of the density and 30.2 percent of the basal area of dead standing trees in stand 1, and 28.3 percent of the density and 53.7 percent of the basal area of dead standing trees in stand 2. *Ulmus americana* has been found to be an initial invader (Briggs and Gibson, 1992; Crow et al., 1994; Crowder and Harmsen, 1998) and a dominant early to mid-successional species in northern Illinois (Bell and del Moral, 1977; Bell, 1997). *Ulmus rubra* was codominant in 90 year old successional stands in Ohio (Vankat and Snyder, 1991), and an early to mid-successional species in other parts of central Illinois (McClain and Ebinger, 1968).

This study is unique for several reasons. While the jack-knifing procedure has been used previously to estimate and test the Shannon and Simpson indices, and has been shown to provide superior accuracy, to our knowledge the technique has not previously been applied to assess the influence of individual plots in studies of forest succession. The procedure allowed us to examine the influence of individual plots on overall stand level diversity, making it possible to quantify the diversity of a single plot while still permitting a comparison of diversity between stands. Calculating the diversity of each plot separately and using the mean to quantify stand diversity is problematic because it is possible for two plots to have identical values for diversity yet be composed of completely different species. Also the study site is unique in that areas of undisturbed succession in central Illinois are rare because of the typical history of both timber harvesting and grazing in secondary forests.

In the old-field successional forest stands examined in this study, proximity to forest border was significantly associated with increased tree species diversity and differences in species composition. The R^2 values of 0.30 for the relationship between distance to forest and diversity and 0.32, 0.34, and 0.32 for the relationships between distance to forest and density, basal area, and IVb, respectively, for species whose seed is dispersed primarily by mammals indicate that seed dispersal mechanisms influence the variation of stand composition, diversity and structure more than is commonly suggested. Many studies focus exclusively on site characteristics, resource availability, and competition as important determinants of forest successional patterns (Kimmins, 1997). The importance of seed dispersal is often noted, but with no quantification of the variability associated with seed sources. Proximity to surrounding forest vegetation has been shown in the present study to be important as a determinant of species diversity and composition during old-field succession. Reduced forest border and increased distance from forest stands increases establishment of wind and bird dispersed tree species over mammal dispersed species. *Quercus imbricaria* was the most dominant tree species in the successional forests of this study, and preference of its small acorns by the blue jay, which caches acorns in soil and under litter, might be a primary factor in its ability to more successfully invade old-field successional stands than other oaks and mammal-dispersed tree species.

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Table 1. Density (number of trees per hectare), basal area (BA, m^2 per hectare), frequency (number of plots in which species occurred / total number of plots), and importance value (IV, (relative density + relative BA + relative frequency) / 3) by size classes (dbh in cm) for stand 1.

	Density						BA	Freq	IVa
Species	6-10 cm	11-20cm	21-30 cm	31-40 cm	41+ cm	>6 cm	>6 cm	>6 cm	>6 cm
Quercus imbricaria Michx.	27.6	27.6	14.6	12.7	6.5	89.1	3.67	76.3	11.0
Ulmus rubra Mühl.	54.6	32.5	7.2	1.0	0.0	95.3	1.25	84.2	8.2
Ulmus americana L.	49.7	28.3	5.2	1.6	0.0	84.9	1.03	92.1	7.7
Quercus velutina Lam.	9.4	12.4	7.2	5.5	7.5	41.9	2.66	60.5	7.2
Fraxinus americana L.	22.8	23.1	8.5	4.9	1.0	60.1	1.57	78.9	7.0
Juglans nigra L.	8.5	20.5	7.8	3.9	5.2	45.8	2.38	60.5	7.0
Quercus alba L.	4.6	6.8	3.6	1.6	7.5	24.1	2.70	42.1	6.0
Sassafras albidum (Nutt.) Nees	35.8	26.3	4.9	0.0	0.0	67.0	0.82	57.9	5.6
Gleditsia triacanthos L.	1.3	7.8	10.7	5.2	2.9	28.0	1.84	60.5	5.4
Celtis occidentalis L.	22.8	10.4	5.9	1.6	0.3	41.0	0.75	60.5	4.5
Prunus serotina Ehrh.	11.4	8.5	7.8	0.7	0.3	28.6	0.66	68.4	4.1
Quercus rubra L.	7.2	6.5	4.2	2.0	1.3	21.1	0.79	57.9	3.6
Quercus macrocarpa Michx.	4.9	2.6	1.3	0.7	2.3	11.7	0.80	36.8	2.6
Cercis canadensis L.	15.9	8.1	0.0	0.0	0.0	24.1	0.19	39.5	2.4
Carya ovata (Mill.) K. Koch	6.2	4.9	2.9	2.0	0.0	15.9	0.42	39.5	2.4
Carya glabra (Mill.) Sweet	0.7	6.8	4.2	3.3	0.3	15.3	0.76	21.1	2.3
Acer saccharum Marsh	7.8	3.6	0.7	0.0	0.0	12.0	0.12	36.8	1.7
Tilia americana L.	5.2	3.9	0.7	1.0	0.0	10.7	0.23	31.6	1.7
Juniperus virginiana L.	10.4	7.8	0.3	0.0	0.0	18.5	0.18	21.1	1.6
Carya cordiformis (Wangenh.) K. Koch.	3.9	2.3	2.6	0.7	0.0	9.4	0.26	28.9	1.6
Carya tomentosa (Poir.) Nutt.	2.9	2.0	1.3	1.0	0.0	7.2	0.21	34.2	1.6
Acer saccharinum L.	1.0	1.3	0.7	0.0	0.3	3.3	0.16	18.4	0.9
Viburnum prunifolium L.	3.3	0.0	0.0	0.0	0.0	3.3	0.01	18.4	0.7
Platanus occidentalis L.	0.0	0.7	0.3	0.7	1.0	2.6	0.22	7.9	0.6
Crataegus spp. L.	3.3	2.9	0.0	0.0	0.0	6.2	0.05	10.5	0.6
Morus rubra L.	0.7	0.7	1.3	0.0	0.0	2.6	0.07	10.5	0.5
Acer negundo L.	2.9	2.3	0.0	0.0	0.0	5.2	0.05	5.3	0.4
Fraxinus quadrangulata Michx.	2.9	0.0	0.0	0.0	0.0	2.9	0.01	5.3	0.3
Fraxinus pennsylvanica Marsh.	0.0	0.0	0.3	0.3	0.0	0.7	0.05	5.3	0.2
Robinia pseudoacacia L.	0.0	0.0	0.3	0.7	0.0	1.0	0.08	2.6	0.2
Maclura pomifera (Raf.) C. K. Schneid.	0.0	1.0	0.7	0.0	0.0	1.6	0.05	2.6	0.2
Prunus spp. L.	0.0	0.3	0.0	0.0	0.0	0.3	0.00	2.6	0.1
Cornus spp. L.	0.3	0.0	0.0	0.0	0.0	0.3	0.00	2.6	0.1
Total	327.7	261.7	105.0	50.7	36.4	781.6	24.0	1181.6	100

Table 2. Density (number of trees per hectare), basal area (BA, m^2 per hectare), frequency (number of plots in which species occurred / total number of plots), and importance value (IV, (relative density + relative BA + relative frequency) / 3) by size classes (dbh in cm) for stand 2.

	Density						BA	Freq	IVa
Species	6-10 cm	11-20cm	21-30 cm	31-40 cm	41+ cm	>6 cm	>6 cm	>6 cm	>6 cm
Quercus imbricaria Michx.	65.2	68.3	22.2	9.9	11.4	177.0	5.86	100.0	20.0
Ulmus americana L.	79.1	66.7	24.7	5.9	2.2	178.5	3.73	100.0	16.7
Juglans nigra L.	7.4	19.8	14.5	5.3	1.2	48.2	1.85	82.5	7.7
Sassafras albidum (Nutt.) Nees	38.9	39.5	5.3	1.2	0.3	85.2	1.24	60.0	7.5
Prunus serotina Ehrh.	12.0	20.1	8.6	3.7	1.5	46.0	1.40	80.0	6.8
Ulmus rubra Mühl.	31.8	22.9	5.6	0.9	0.3	61.5	0.96	75.0	6.6
Acer saccharinum L.	7.1	15.4	10.5	1.9	0.9	35.8	1.18	47.5	4.9
Quercus velutina Lam.	3.1	6.2	4.9	1.5	3.1	18.8	1.24	65.0	4.9
Celtis occidentalis L.	13.6	9.9	4.0	0.6	0.3	28.4	0.54	65.0	4.2
Gleditsia triacanthos L.	0.3	3.1	1.9	4.0	3.1	12.4	1.22	35.0	3.6
Crataegus spp. L.	18.2	5.3	0.0	0.0	0.0	23.5	0.15	65.0	3.4
Quercus rubra L.	3.1	4.6	3.4	1.9	0.9	13.9	0.65	20.0	2.3
Fraxinus americana L.	6.2	5.3	0.6	0.0	0.0	12.0	0.15	35.0	1.9
Malus spp. Mill.	12.7	1.5	0.0	0.0	0.0	14.2	0.08	32.5	1.8
Cercis canadensis L.	8.0	3.1	0.6	0.0	0.0	11.7	0.11	30.0	1.7
Quercus macrocarpa Michx.	1.2	1.9	1.5	0.6	0.0	5.3	0.19	15.0	1.0
Acer negundo L.	3.4	1.9	0.0	0.6	0.0	5.9	0.10	17.5	1.0
Carya cordiformis (Wangenh.) K. Koch.	3.1	1.2	0.6	0.0	0.0	4.9	0.06	20.0	1.0
Tilia americana L.	1.2	1.5	0.6	0.0	0.0	3.4	0.08	15.0	0.8
Carya ovata (Mill.) K. Koch	2.2	1.2	0.6	0.3	0.0	4.3	0.09	7.5	0.6
Quercus alba L.	0.6	0.6	0.3	0.6	0.3	2.5	0.13	7.5	0.6
Acer saccharum Marsh	0.9	0.0	0.3	0.0	0.0	1.2	0.01	10.0	0.4
Carya tomentosa (Poir.) Nutt.	0.3	0.6	0.0	0.0	0.0	0.9	0.02	5.0	0.2
Viburnum prunifolium L.	0.6	0.0	0.0	0.0	0.0	0.6	0.00	5.0	0.2
Carya glabra (Mill.) Sweet	0.0	0.6	0.0	0.0	0.0	0.6	0.01	2.5	0.1
Maclura pomifera (Raf.) C. K. Schneid.	0.3	0.0	0.0	0.0	0.0	0.3	0.00	2.5	0.1
Morus rubra L.	0.3	0.0	0.0	0.0	0.0	0.3	0.00	2.5	0.1
Cornus spp. L.	0.3	0.0	0.0	0.0	0.0	0.3	0.00	2.5	0.1
Quercus imbricaria Michx.	65.2	68.3	22.2	9.9	11.4	177.0	5.86	100.0	20.0
Ulmus americana L.	79.1	66.7	24.7	5.9	2.2	178.5	3.73	100.0	16.7
Juglans nigra L.	7.4	19.8	14.5	5.3	1.2	48.2	1.85	82.5	7.7
Sassafras albidum (Nutt.) Nees	38.9	39.5	5.3	1.2	0.3	85.2	1.24	60.0	7.5
Prunus serotina Ehrh.	12.0	20.1	8.6	3.7	1.5	46.0	1.40	80.0	6.8
Total	321.2	301.1	110.9	38.9	25.6	797.8	21.1	1005.0	100

Table 3. Plot means for importance value b (IVb), density, and basal area (BA) in m^2, for selected species. Stand 1 was narrower and had a greater percentage of its perimeter bordered by forest at the time of agricultural abandonment.

	IVb			Density			BA		
Species	Stand 1		Stand 2	Stand 1		Stand 2	Stand 1		Stand 2
Quercus imbricaria Michx.	12.60	*	24.91	7.21	*	14.33	0.30	*	0.47
Juglans nigra L.	8.88		7.61	3.71		3.90	0.19		0.15
Ulmus rubra Mühl.	8.35		5.86	7.71		4.98	0.10		0.08
Quercus velutina Lam.	8.05	*	3.92	3.39	*	1.53	0.21	*	0.10
Ulmus americana L.	7.72	*	20.41	6.87	*	14.45	0.08	*	0.30
Fraxinus americana L.	7.22	*	1.04	4.87	*	0.98	0.13	*	0.01
Quercus alba L.	6.28	*	0.42	1.95	*	0.20	0.22	*	0.01
Sassafras albidum (Nutt.) Nees	5.66		7.75	5.42		6.90	0.07		0.10
Gleditsia triacanthos L.	5.54		3.35	2.26	*	1.00	0.15		0.10
Celtis occidentalis L.	4.42		3.51	3.32		2.30	0.06		0.04
Prunus serotina Ehrh.	3.31	*	6.39	2.32	*	3.73	0.05	*	0.11
Quercus rubra L.	2.96		2.21	1.71		1.13	0.06		0.05
Carya glabra (Mill.) Sweet	2.81	*	0.05	1.24	*	0.05	0.06	*	0.00
Quercus macrocarpa Michx.	2.54	*	0.71	0.95		0.43	0.06	*	0.02
Carya ovata (Mill.) K. Koch	2.07	*	0.52	1.29	*	0.35	0.03	*	0.01
Carya cordiformis (Wangenh.) K. Koch.	1.08	*	0.43	0.76		0.40	0.02	*	0.00
Carya tomentosa (Poir.) Nutt.	0.96	*	0.09	0.58	*	0.08	0.02	*	0.00
Acer saccharinum L.	0.73	*	5.48	0.26	*	2.90	0.01	*	0.10

* Significantly different (probability <0.05)

Figure 1. Allerton Park circa 1936 showing stands 1 and 2. Shaded areas indicated forest cover; non-shaded areas indicate pasture. Adapted from: Jones and Bell (1976)