



Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments

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Abstract

Forest edges are known to consist of microenvironments that may provide habitat for a different suite of species than forest interiors. Several abiotic attributes of the microenvironment may contribute to this change across the edge to center gradient (e.g., light, air temperature, soil moisture, humidity). Biotic components, such as seed dispersal, may also give rise to changes in species composition from forest edge to interior. We predicted that abiotic and biotic measures would correlate with distance from forest edge and would differ among aspects. To test these predictions, we measured abiotic and biotic variables on twelve 175 m transects in each of two 24 ha forest fragments in east-central Illinois that have remained in continuous isolation for upwards of 100 years. Both univariate and multivariate techniques were used to best describe the complex relationships among abiotic factors and between abiotic and biotic factors. Results indicate that microclimatic variables differ in the degree to and distance over which they show an edge effect. Relative humidity shows the widest edge, while light and soil moisture have the steepest gradients. Aspect influences are evidenced by the existence of more pronounced edge effects on south and west edges, except when these edges are protected by adjacent habitat. Edges bordered by agricultural fields have more extreme changes in microclimate than those bordered by trees. According to PCA results, species richness correlates well with microclimatic variation, especially light and soil moisture; however, in many cases species richness had a different depth of edge influence than either of these variables. The herbaceous plant community is heavily dominated by three species. Distributions of individual species as well as changes in plant community composition, estimated with a similarity index, indicate that competition may be influencing the response of the vegetation to the edge to interior gradient. This study indicates that edge effects must be considered when the size and potential buffering habitat of forest preserves are planned.

Introduction

Fragmented forest ecosystems change through time as a result of their isolation as well as other human and natural disturbances. A reduction of species may occur in fragments that are too small to support their original flora and fauna (Blake 1983; Blake & Karr 1984; Harris 1984). While the reduction in species may result directly from a decrease in forest area, it is more likely due to the increased perimeter : area ratio that results from fragmentation and the modification

of abiotic and biotic factors at the forest edge (Laurance & Yensen 1991). Edge effects are differences in biotic or abiotic factors that exist along the borders of a habitat fragment relative to the interior environment. Changes in microclimate at forest edges, for example, may favor a plant community different from that found in the forest interior (Noss & Cooperrider 1994; Harris 1984).

In order to understand the dynamics of the forest edge, ideally, we need to know how both the mi-

microclimate and the vegetation vary and co-vary with increasing distance from the forest edge. Microclimate is made up of multiple variables, which can be studied either independently or in unison. Likewise, several variables indicative of changes in vegetation composition, including distributions of individual species, may be integrated through multivariate techniques. The use of multivariate techniques to illuminate interactions between variables may give a more comprehensive view of biotic and abiotic dynamics at the forest edge than analyzing variables individually (Murcia 1995).

The effectiveness of management strategies for forest fragments depends on an understanding of edge width and the changes that occur along habitat edges (Palik & Murphy 1990). Laurance & Yensen (1991) argue that fragment size, shape and edge 'penetration distance' are likely to affect the amount of core area where native flora and fauna are able to persist. They conclude that the penetration distance varies depending upon the variable measured.

Documented changes in microclimate typical of forest edges are: higher light, air and soil temperatures, wind speed, and vapor pressure deficit (VPD); and lower relative humidity and soil or litter moisture (Brothers & Spingarn 1992; Brothers 1993; Matlack 1993; Young & Mitchell 1994; Chen et al. 1995). The extent to which these factors vary with distance from edge may be influenced by aspect, or cardinal direction. Edges facing south and west in the northern hemisphere are typically broader than those facing north and east (Matlack 1993; Fraver 1994).

Typical vegetation responses to the edge environment are: increased presence of exotic species (Laurance 1991; Brothers & Spingarn 1992; Fraver 1994), increased sapling and tree densities (Ranney et al. 1981; Palik & Murphy 1990; Wales 1972; Brothers & Spingarn 1992; Chen et al. 1992; Brothers 1993; Fraver 1994), increased shrub cover (Matlack 1994), and higher species richness (Ranney et al. 1981; Brothers & Spingarn 1992; Fraver 1994). Tree species distributions may also vary with distance from the forest edge (Whitney & Runkle 1981; Brothers 1993; Wales 1972), as may tree mortality from wind throw (Chen et al. 1992; Young & Mitchell 1994; Laurance et al. 1998). Evidence of aspect effects on vegetation include variation in exotic species cover and abundance, species richness, and tree species distribution (Wales 1972; Brothers & Spingarn 1992; Fraver 1994).

Previous studies have been limited by a lack of replication, a lack of continuity in sampling at sev-

eral points from edge to center of the fragment, and a lack of consideration of the potential interactions among variables in the responses of microclimate and vegetation in the edge environment (Murcia 1995). Many studies do not sample far enough into the forest fragment to reach the threshold point at which certain variables no longer vary with distance from the edge. We attempted to avoid these problems by using two forest fragments of similar age and history, sampling at eleven distances on twelve transects from zero to 175 m into the forest at each site, measuring both microclimate and vegetation, and using multivariate statistical methods that look for interactions among variables. Furthermore, because edge effects undoubtedly vary with habitat type, geographical location, and forest structure, it is important to add case studies to the existing body of knowledge. A large sample of studies may allow for broad conclusions to be drawn where there are currently inconsistencies.

This study was designed to: (1) determine how key microclimatic variables change with aspect and increasing distance from forest edge, (2) analyze microclimate as a complex interaction of variables using multivariate techniques, (3) quantify how vegetation changes with aspect and increasing distance from forest edge, and (4) correlate changes in microclimate with changes in vegetation to determine which, if any, microclimatic variables are related to changes in plant distribution.

Methods

Study sites

The study was conducted during March to September, 1994 and March, 1995 in Trelease Woods and Brownfield Woods, located approximately 5 km northeast of Urbana in Champaign County, Illinois. The sites are approximately 2.5 km apart and are separated by agricultural fields. Both woods are 600 m × 400 m (24 ha), and oriented in the cardinal directions, but differ in their immediate adjacent habitats. Brownfield is bordered on the south and southeast by roads flanked by large trees, on the north by a fence lined with grass and small trees, and on the west and northeast by agricultural fields. Trelease is bordered on the north and east by agricultural fields, on the south by a prairie undergoing restoration, and on the west by a road flanked by an old field undergoing succession. Thus, the degree of exposure of each 'edge' varies between sites. Both

have grass roads maintained by mowing immediately adjacent to their perimeter (except the S and E sides of Brownfield which have a fence and a slight gully separating them from the paved road). In addition, Brownfield, with a small stream running through it, has more topographical relief than Trelease.

Brownfield and Trelease are classified as mixed-mesophytic forests and are fragments of the former 'Big Grove' that, prior to European settlement, occupied a 16 km² area along the Salt Fork of the Vermilion River in Champaign County, Illinois (Telford 1926). Prairie groves, such as the Big Grove, were fragments of forest that were protected from fire by their close proximity to rivers or streams in the midst of the 'Grand Prairie' (Gleason 1913; Boggess 1964; Miceli 1977). The original composition of the Big Grove was undoubtedly different from that of the two remnants today. Conditions present when today's trees established were different, largely due to fire suppression, resulting in succession from an open forest to a closed canopy forest (Gleason 1913; Telford 1926). Thus, the forest canopy is made up of scattered shade-intolerant oak species such as *Quercus macrocarpa* Michx. and *Q. rubra* L., some of which are 200–300 yr old, as well as shade-tolerant *Acer saccharum* Marsh. In contrast, the sub-canopy and sapling communities are heavily dominated by *Acer saccharum*, with very few *Quercus spp.* present. Herbaceous prairie/savanna species continue to exist at forest edges (Gleason 1913).

These forest fragments, isolated since the late 19th century, have been owned and managed by the University of Illinois as research study sites since 1917 (Trelease) and 1939 (Brownfield) (Brandeis 1988). Prior to their acquisition by the University, both had been selectively logged, moderately grazed by cattle, and, in addition, Brownfield had many recreational visitors (Telford 1926; Boggess 1964). Since their acquisition both woods have been fenced and protected as biological research reserves. These fragments, owing to their isolation, artificially maintained edge, and lack of recent human disturbance, provide good sites for determining the effect that the human-imposed edge is having on forest microclimate and on distributions of understory herbaceous species and saplings of tree species.

Study design

In each fragment, three 175 m transects were established perpendicular to the forest edge on each of the four aspects (N, E, S, W). The location of each tran-

sect was chosen randomly under the constraint that it was at least 50 m from a corner. Measurements of vegetation and environmental variables were collected at 0 (edge), 2, 5, 10, 15, 25, 40, 60, 80, 100, and 175 m (interior) along each transect for a total of 12 transects and 132 sampling points in each woods. The edge (0 m) can be defined as by Murcia (1995); it was maintained at the point of creation by a fence or a mowed border so that the line of large tree trunks was considered the edge.

Microclimate

The environmental variables measured are in three categories: components of air mixing (relative humidity, CO₂ concentration, and air temperature), attributes of the soil environment (soil temperature and moisture), and an estimate of the amount of light hitting the forest floor (percent canopy openness). Each variable was measured at each of the 132 sampling points in each site. All environmental variables were measured in mid-summer (July) after the overstory canopy was fully developed, with the exception of percent canopy openness, which was measured in late-summer (August). Soil moisture was measured gravimetrically two weeks after a rainfall.

Relative humidity, CO₂ concentration and air temperature were measured at the forest floor using a LI-6200 portable gas exchange system (LiCor Instruments, Lincoln, NE) between 10:00 and 16:00 h in order to minimize the confounding effects of differences in weather throughout the day. Each site was measured on a single day, and the two sites were measured on consecutive days. Simultaneously with the LiCor measurements, soil temperature was measured 10 cm below the soil surface using a soil probe. Soil samples, collected using a 30 cm soil probe, were weighed, dried, and reweighed until weights ceased to change to determine percent soil moisture. Percent canopy openness was estimated using hemispherical photographs of the forest canopy taken on overcast days between 10:00 and 16:00 hours with a Nikon 8.5 mm fisheye lens born on a 1 m high tripod and oriented vertically upward. Photographs were digitized using Adobe Photoshop, and percent canopy openness was calculated using SOLARCALC (Chazdon 1987). This method was chosen because it uses the latitude and longitude, as well the calendar day of the photograph, to calculate an estimate of the diffuse light coming through a 176° field of view.

Vegetation

Herbaceous vegetation was surveyed once in mid-summer using the same transect points as the environmental variables. A 10 m transect perpendicular to each main transect was placed at each of the 11 sampling points. Five 0.5 m² quadrats were placed at 2 m intervals on each perpendicular transect for a total area of 2.5 m² sampled at each distance. Cover was estimated for all herbaceous species using modified Daubenmire cover classes (<1, 1–5, 5–25, 25–50, 50–75, 75–95, >95%) (Mueller-Dombois & Ellenberg 1974). Tree saplings less than 1 m tall were included in the herbaceous vegetation. The midpoint of each cover class was used to calculate absolute and relative cover for species in each 0.5 m² plot. Variables derived from herbaceous vegetation are species richness (total number of species in the 2.5 m² area) and frequency of exotics (percent of the five 0.5 m² plots at each transect point that contained an exotic). In addition, plants were placed in one of four categories according to their ecological origin: (1) species that are native to the region and characteristic of forest vegetation, (2) species that are native to the region and characteristic of prairie or savanna, (3) species that are native but are characteristic of frequently disturbed woodlands such as floodplain forests, and (4) exotic species (Appendix 1). Exotics are characterized according to Mohlenbrock (1986), while other species are categorized according to J. Taft (pers. commun.); Mohlenbrock (1986), Swink & Wilhelm (1994).

Saplings were also surveyed along each of the 10 m transects perpendicular to the main transect. All saplings >1 m tall and <6 cm DBH were counted in a 2 m × 10 m quadrat (1 m on either side of the 10 m transect). Saplings <6 cm DBH were recorded as either <1 cm or 1–6 cm DBH. Voucher specimens were deposited at the herbarium of the Illinois Natural History Survey (ILLS). Plant taxonomy follows Mohlenbrock (1986).

Statistical analyses

Statistical analyses were done using SAS (SAS Institute 1985) and CANOCO (PCA for vegetation only) (ter Braak 1988). Prior to conducting statistical analyses, each variable was tested for deviations from the normal distribution and for homoscedasticity using Levene's test for equality of variances. All variables, including distance from forest edge, were log-transformed in all analyses to normalize their distributions in order to meet this assumption of param-

etric statistics. In addition, variables that were measured between 10:00 and 16:00 h with the LiCor were further transformed because a systematic bias in collection time resulted from diurnal variation in the air variables. To correct for this, the value of each variable at each distance was converted to the proportion of that value relative to the outer (0 m) initial measurement for that transect. All analyses were done separately on data collected in Brownfield and Trelease Woods.

Microclimate and vegetation response variables were plotted as functions of distance separately for each aspect ($n = 3$ at each distance). The depth of edge influence (DEI) is subjectively estimated as by Chen et al. (1995), and is defined as the distance over which the variables increase or decrease by an unspecified amount before their values cease to change with increasing distance from the forest edge. This threshold point is then considered the distance at which the 'interior' of the forest has been reached for that variable. The DEI was tested statistically for microclimate and vegetation variables in two steps. First, a one-way ANOVA was used to test for significance of the effect of the independent variable, distance from forest edge, on each individual dependent variable, and second, a least significant difference (LSD) test was used to find which distances differed significantly from one another.

Multivariate statistical analyses on microclimate variables were conducted in two steps as suggested by Hatcher & Stepanski (1994). First, a MANOVA using all microclimate variables was conducted to test the overall treatment effect of distance from edge and aspect. Second, one-way ANOVAs were carried out on each variable to test for the effects of distance and aspect. Those variables for which the F-statistic was significant for either distance or aspect, or both, were retained for the principal components analysis.

A principal components analysis (PCA; using a correlation matrix) was done on all microclimatic variables that qualified as described above. Sample points were plotted on the first two principal components (PC I and PC II). Our *a priori* prediction was that plots of similar distances from the edge would show patterns of clumping (i.e. 'edge plots' or 'interior plots') due to similarities in the values of microclimatic variables measured.

Vegetation variables were analyzed for DEI as described above. In addition, Pearson's correlation tests were conducted using the scores from principal components I and II of the microclimate PCA and the vegetation summary variables. We explain pat-

Table 1. Approximate edge width (m) by site and aspect for microclimatic variables and species richness. Values are significant at the $p < 0.05$ level, and were calculated from an LSD test following a one way ANOVA for the effect of distance from forest edge. In some cases, the LSD indicated significant differences between individual distances when the overall ANOVA model was not significant at the $p < 0.05$ level. Variables that show no discernible pattern across the edge-interior gradient are designated as 'np'.

Aspect site	N		E		S		W	
	B	T	B	T	B	T	B	T
Canopy openness	15	15	15	5	np	40	15	10
Soil moisture	15	15	np	15	15	40	60	40
CO ₂	10	np	np	np	np	15	25	np
Relative humidity	10	np	np	np	np	np	80	25
Air temperature	10	np	np	np	np	np	5	np
Species richness	25	60	np	np	40	40	40	15

B = Brownfield and T = Trelease.

terns in vegetation by first interpreting loadings of the microclimate PCA and correlating these PC axes to vegetation data.

Sørensen's qualitative and quantitative indices of similarity (Mueller-Dombois & Ellenberg 1974) were used to analyze similarities in species composition between plots of different distances. The qualitative index compares plots on the basis of species presence/absence. The quantitative index is calculated using the absolute cover of each species. A comparison of the two indices can be informative; the first measures the number of co-occurring species in plots, while the second takes into account the relative abundance of species based on their absolute covers. Indices were calculated for the comparison of each of the 55 possible pairwise combinations of the 11 distances, first separately by aspect ($n = 3$ at each distance) and then for the average of the four aspects ($n = 12$ at each distance). Data are presented for the average of the four aspects, and are a comparison of each distance plot relative to the interior (175 m) plot. Our prediction was that edge plots would be least similar to interior plots and that the similarity to interior plots would increase and stabilize at the point where the edge penetration distance had been reached.

Finally, a PCA was done on the herbaceous vegetation data using a correlation matrix of the relative cover of all species in both woods combined. The goal of this analysis was to determine which plant species were most influential in determining the composition of the plant community.

Results

Microclimate

Most microclimatic variables show some degree of change with increasing distance from the forest edge. Variables differ, however, in both the degree to which they change over the gradient and the distance at which they stabilize according to the one-way ANOVA for distance effect and subsequent LSD test (Figures 1 and 2). Values of depth of edge influence (DEI) for microclimate and vegetation variables by aspect were subjectively estimated using patterns evident in Figures 1 and 2 and results of the LSD tests (Table 1). In some cases, the overall model of the one-way ANOVA was not significant, whereas the LSD test found significant differences at the $p < 0.05$ level between some distances. These results are considered valid because they verify patterns in the data that are apparent but may not have been significant in the one-way ANOVA due to a large amount of variation in the data.

Canopy openness was significantly related to distance from edge on all aspects except for south in Brownfield and west in Trelease (Figures 1 and 2). The DEI for canopy openness ranged from 5–15 m on most aspects, except for south in Trelease where it reached 40 m (Table 1). Soil moisture was significant in Brownfield with a DEI of 15 m on the north and south aspects, and 60 m on the west. In Trelease, soil moisture was significant with DEI values of 15 m on north and east aspects, and 40 m on south and west aspects. CO₂ was significant on the west aspect of Brownfield with a DEI of 25 m, as was relative humidity with a DEI of 80 m. Air temperature varied the least of all variables and was significant only on the north and west aspects of Brownfield, with DEI values of 10 and 5 m, respectively. Soil temperature was uniform across all measurements and is not discussed further.

The MANOVA (treatment effects of distance from edge and aspect on all microclimate variables combined) and the ANOVAs (treatment effects of distance from edge and aspect on all individual microclimate variables) both indicated that all variables were significant contributors to the model and should be retained for the PCA.

The PCA had similar results in both woods, with eigenvalues for the first two components accounting for 71.1 and 66.9% of microclimatic variation in Brownfield and Trelease, respectively (Table 2). Variable loadings are considered meaningful if they are

Table 2. Results of a Principal Components Analysis (PCA) of microclimate variables. Each site was analyzed separately ($n = 132$).

Component	Brownfield		Trelease	
	1	2	1	2
Eigenvalue	2.39	1.17	2.01	1.34
Cumulative % variance explained	47.7	71.1	40.2	66.9
Variable loadings				
Air temperature	-0.79	0.13	-0.84	0.39
CO ₂	0.87	-0.11	0.54	0.23
Relative humidity	0.93	-0.15	0.92	-0.23
Soil moisture	0.12	0.82	0.30	0.73
Canopy openness	-0.37	-0.67	-0.26	-0.74

> 0.45 for this sample size (Stevens 1992). Microclimatic variables that load highly on PC I are air temperature (-), CO₂ (+), and relative humidity (+). Variables that load highly on PC II are soil moisture (+) and canopy openness (-) (Table 2). Sample points are identified by distance and aspect and plotted on PC I and PC II (Figure 3). Both sites show points clustered by distance, with 0–5 m plots being more distinct than other distance classes. Sites in the 0–5 m category cluster on the negative sides of PC I and II indicating low soil moisture, high canopy openness, high relative air temperature, low CO₂, and low relative humidity.

Sample plots also cluster by aspect in Trelease and Brownfield with plots of the south aspect being the most distinct in Trelease, and those of the west aspect being most distinct in Brownfield (Figure 3). South sample plots in Trelease appear on the positive side of PC I and mostly on the negative side of PC II. West sample plots in Brownfield appear on the positive side of PC I while they are evenly distributed over PC II.

Vegetation

Some vegetation summary variables varied with distance from forest edge. Exotic species were rare and almost exclusively limited to the perimeter of both woods so frequency of exotic species was not analyzed for aspect or distance from edge variation. Density of saplings 1–6 cm DBH and <1 cm DBH were combined into a total sapling variable because numbers were low. Species richness was significant in Brownfield on the north and west aspects with DEIs of 25 and

40 m, respectively, in addition to a DEI of 40 m on the south aspect (Figure 1, Table 1). In Trelease, species richness was significant on the north and south aspects with DEIs of 40 and 60 m, respectively, in addition to a DEI of 15 m on the west aspect (Figure 2, Table 1). Total saplings were significant only on the south side of Brownfield, and no patterns were consistent enough to discern a DEI.

While there was an overall decline in herbaceous species richness with increasing distance from forest edge, species demonstrated distinct patterns with respect to ecological groups (Figure 4). Species richness of native forest species (ecological origin Category 1) was higher relative to the other three categories in both Trelease and Brownfield (Figure 4). Native savanna species (Category 2) penetrate to 15–25 m in Brownfield and to 40–60 m in Trelease. Exotic species (Category 4) exist only in the 0–2 m class and 5–10 m class in Brownfield Woods and to 40–60 m in Trelease, but only in small numbers. The number of disturbance-tolerant forest species (Category 3) is consistent across all distance classes. Comparisons of the relative covers of vegetation categories in Brownfield show an increase in disturbance-tolerant forest species with a corresponding decrease in native forest species from edge to interior (Figure 4). In Trelease, relative cover of native forest species decreases to 15–25 m and then increases toward the forest interior; the opposite trend exists for disturbance-tolerant forest species.

The herbaceous plant community is strongly influenced by three species. Sixty percent of the variation in herb cover is explained by the first two axes of the PCA. Cover of *Laportea canadensis* (L.) Wedd. dominates the first axis, while *Hydrophyllum appendiculatum* Michx. and *Sanicula gregaria* Bickn. dominate opposite ends of the second axis. The relative covers of these three herbaceous species are plotted by distance category in Figure 5. *L. canadensis* greatly increases in cover toward the interior of the forest, while *H. appendiculatum* increases, but less so. *S. gregaria* increases to 15–25 m in Trelease and then decreases toward the interior, while in Brownfield it remains constant to 5–10 m and thereafter decreases toward the interior.

The results of the Pearson Correlation tests on the principal component scores and derived vegetation variables indicate significant negative correlations between microclimate and two variables. In Brownfield, total saplings were negatively correlated with PC II ($r = -0.17$, $p < 0.05$); whereas species richness was negatively correlated with PC I ($r = -0.19$,

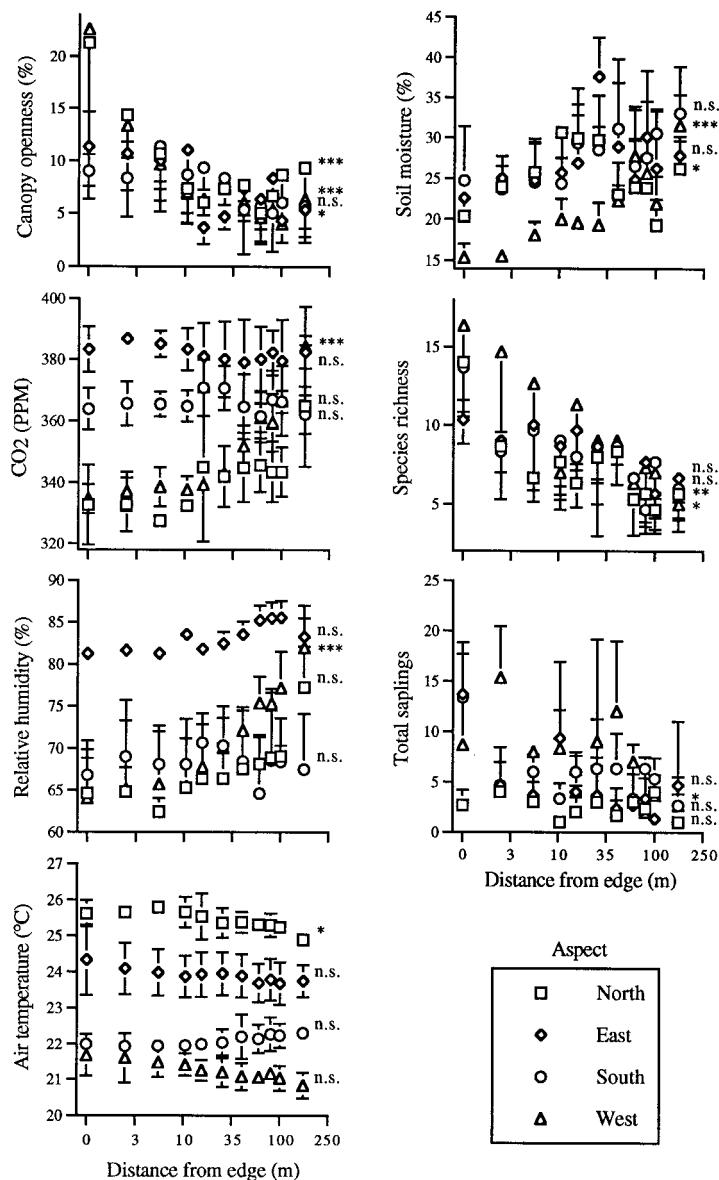


Figure 1. Mean values (± 1 SE) for microclimate and vegetation variables in Brownfield Woods as a function of distance from edge and separated by aspect ($n = 3$ at each of eleven distances). Species richness and total saplings are defined in the text. Actual values of variables transformed for analyses are given. Distance is plotted on a log scale with actual corresponding distances given. Significance values are given to the right of the 175 m point for the results of a one-way ANOVA for the effect of distance from forest edge on each variable (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

$p < 0.05$) and PC II ($r = -0.45$, $p < 0.001$). In Trelease, species richness was negatively correlated with PC II ($r = -0.50$, $p < 0.001$).

In both woods, Sørensen's quantitative and qualitative indices of floristic similarity have similar overall trends: edge plots are least similar to interior plots, and plots become more similar to interior plots as they get closer to them (Figure 6). In Brownfield, the two

indices are similar in value, with the qualitative index stabilizing at about 15 m and the quantitative index stabilizing at about 10 m. In Trelease, qualitative index values are consistently higher than those of the quantitative index until 40 m where the latter index stabilizes (Figure 6). Qualitative values level off sooner at 15 m. Thus, in Trelease, plots are more similar in

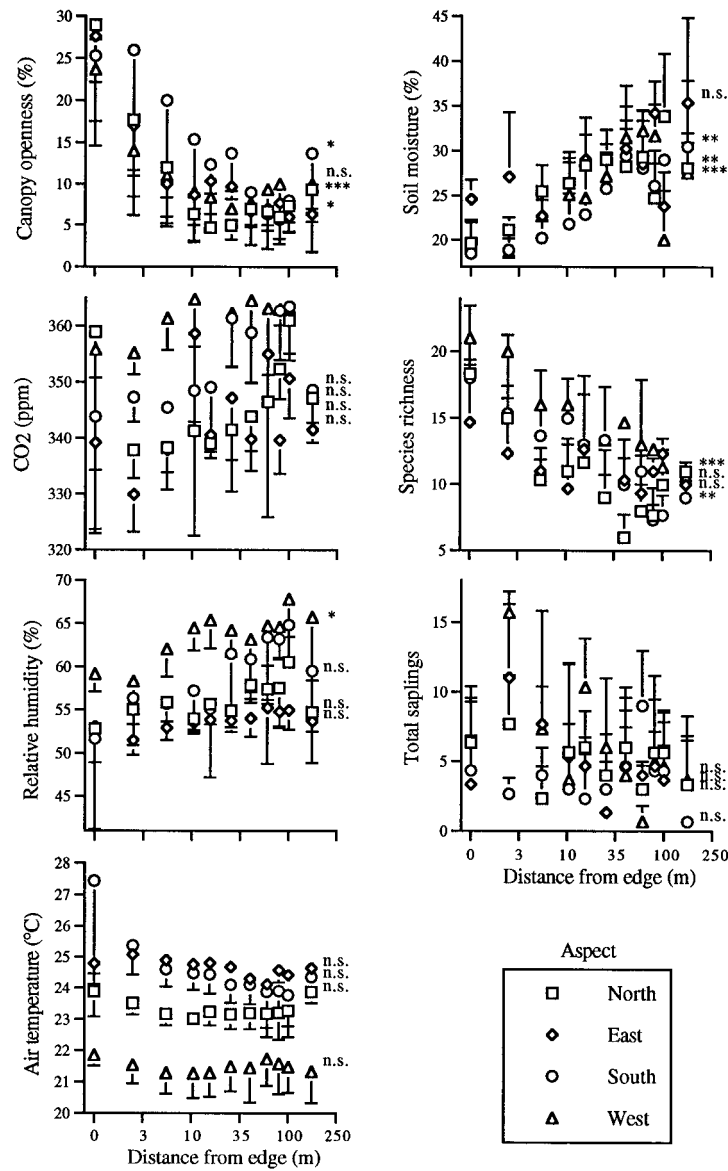


Figure 2. Mean values (± 1 SE) for microclimate and vegetation variables in Trelease Woods as a function of distance from edge and separated by aspect ($n = 3$ at each of eleven distances). See Figure 1 for description.

terms of relative covers than species presence/absence until 40 m where the two indices coincide.

Some differences are apparent when indices are plotted separately for the four aspects. In Brownfield, the quantitative index values of the south aspect increase to 60 m where they level off, while those of the west aspect continue to increase across the entire transect; the qualitative values fluctuate but do not show a net increase or decrease across the transect. In Trelease, the south quantitative index values are

lower than all other aspects and they increase to 80 m where they stabilize. In contrast, the south qualitative index values are relatively stable. In general, plots lose unique species in ecological origin categories 1, 2, and 4 as they become further from the forest edge, while covers of disturbance-tolerant species remain relatively stable across the entire transect.

Seven distributional patterns are apparent for the herbaceous plants in Trelease and Brownfield that may help describe the changes in similarity indices across

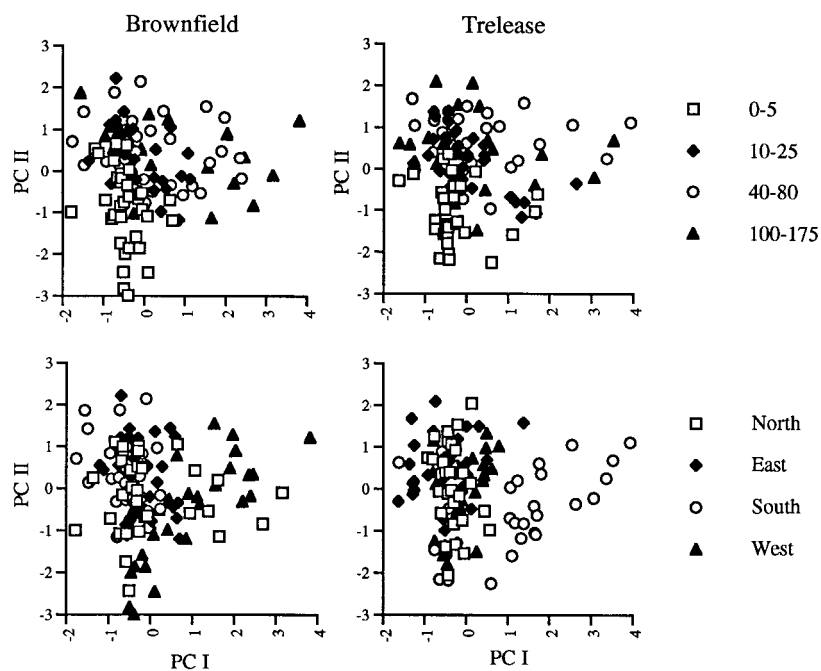


Figure 3. PCA-derived loadings for each woods plotted on the first two principal component axes. Figures are given for Brownfield and Trelease Woods separately ($n = 132$ in each woods). Points are plotted with symbols for distance from edge (top) and aspect (bottom).

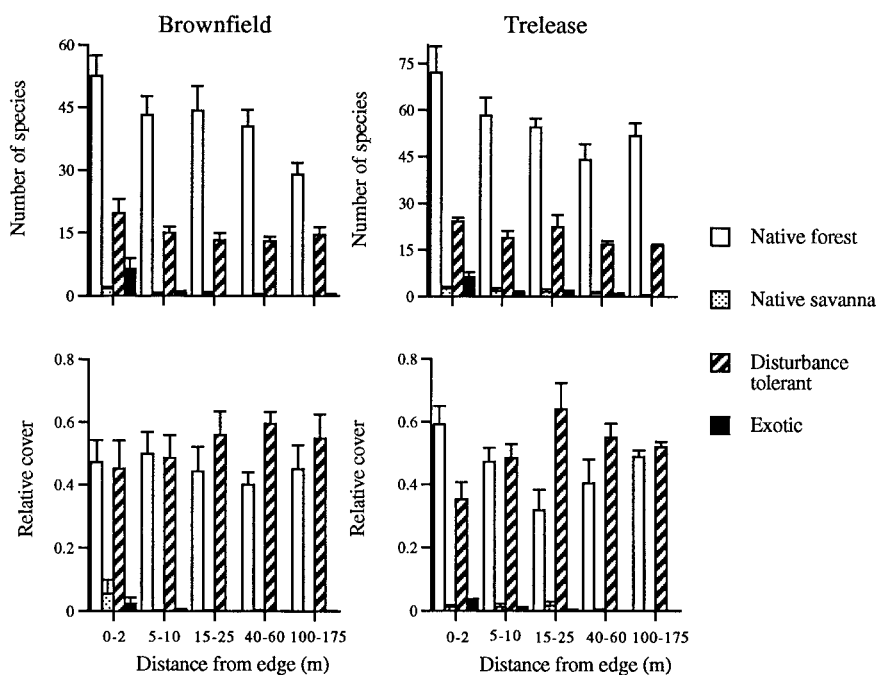


Figure 4. Differences among distances in mean number (+ 1 SE) of species (top) and relative cover (bottom) for each of four plant groups of contrasting ecological origin (defined in text). Distances are grouped into five categories ($n = 6$ in each of five categories).

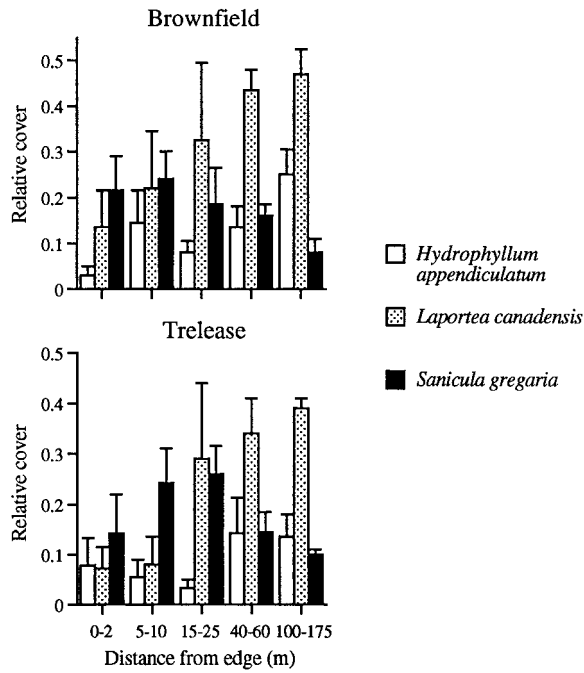


Figure 5. Mean relative covers (± 1 SE) of the three most dominant herb species in Brownfield and Trelease Woods (as indicated by a PCA of all herbaceous plant species) in five distance categories as described in Figure 4 ($n = 6$ in each of five categories).

the edge-center gradient (Appendix 1). The seven patterns of herbaceous species distribution are as follows: (1) species found only at 0, 2, 5 and 10 m (e.g., *Ambrosia trifida* L., *Rosa multiflora* Thunb., and *Taraxacum officinale* Weber.); (2) species found at 0, 2, 5, 10, 15, and 25 m (e.g., *Plantago rugelii* Dcne. and *Lonicera maakii* (Rupr.) Maxim. in Trelease); (3) species found on the edge and as far as 40 and 60 m, but consistently do not exist in 80–175 m plots (e.g., *Anemone virginiana* L., *Carex blanda* Dewey, and *Prunus serotina* Ehrh.); (4) species never found at 0, 2 and 5 m, but exist in low numbers throughout the remainder of the plots (e.g., *Actaea pachypoda* Ell. and *Lindera benzoin* (L.) Blume); (5) species found at almost all distances, but show a net decrease in cover from edge to interior (e.g., *Acer saccharum*, *Celtis occidentalis* L., and *Phlox divaricata* L. ssp. *laphamii* (Wood) Wherry); (6) species found at almost all distances, but show a net increase in cover from edge to interior (e.g., *H. appendiculatum* and *L. canadensis*); and (7) species found consistently in most plots, but do not respond to the distance gradient with a change in relative cover (e.g., *Allium tricoccum* Ait., *Asimina triloba* (L.) Dunal., *Osmorhiza claytonii* (Michx.) Clarke, and *Smilacina racemosa* (L.) Desf.).

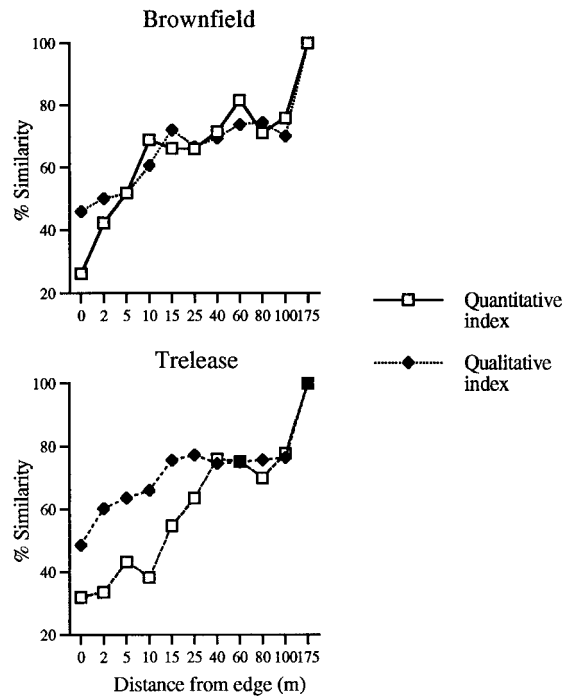


Figure 6. Sørensen's quantitative (open square) and qualitative (solid diamond) indices of similarity for the herbaceous plant species surveyed in Brownfield Woods and Trelease Woods. Values are for the percent similarity of each distance relative to the 175 m plot, and are an average of the four aspects ($n = 12$ at each distance).

Discussion

This study indicates that aspect plays an important role in determining how forest microclimate and vegetation are influenced by the external environment. However, adjacent community type is also important in determining the extent of microclimatic edge effects as is shown by the buffering of the south and west sides of Brownfield and Trelease, respectively. The south aspect of Brownfield is bordered by a residential area, which has large trees, and the west aspect of Trelease is bordered, in part, by an old field which has approximately 25 year old trees. The vegetation responds to microclimate to a large extent, but variation in the plant community is evident beyond the point where microclimate appears to have stabilized. A complex interaction of both microclimate and biotic factors seems to be driving changes in the plant community across the edge to interior gradient.

The univariate analyses indicate that relative humidity has the largest depth of edge influence (DEI) of all the variables, with a DEI of 80 m on the west as-

pect of Brownfield. Results are consistent with Young and Mitchell (1994) who found that vapor pressure deficit (calculated from relative humidity and air temperature) had a wider edge of 50–100 m on the north side and a narrower edge of 20–40 m on the south side (in the southern hemisphere). Previous studies of light penetration into the forest using photosynthetically active radiation (PAR) (Brothers and Spingarn 1992) and photosensitive blueprint paper (Matlack 1993) indicated an edge width of eight to 35 m on north and south aspects, respectively. This study, using percent canopy openness, has similar results on north and east edges, but shows a wider edge of 40 m on south and west aspects of Brownfield and Trelease.

Light availability has been suggested as the driving force behind the responses of other microclimate variables, namely air temperature, relative humidity, and soil moisture (Matlack 1993). However, in this study soil moisture consistently shows a greater DEI than canopy openness. Wind may continue to influence other variables beyond the point where light has reached a consistent low in the forest. The prevailing wind comes from the west at these sites, and, although wind was not measured in this study, it is assumed that it has a strong effect. The DEIs of both soil moisture and relative humidity are largest on the west aspects of both woods, even though Trelease is partially protected on that side.

The multivariate analyses summarize the interactions among microclimatic variables and their effects on aspect and distances from forest edge. The PCA of microclimatic variables shows that the 0–5 m points in both woods are clustered on the negative ends of both PC I and II which correspond to air temperature and light, respectively. The 10–25 m points, in contrast, are on the positive end of PC II, which correspond to soil moisture. Finally, the 40–80 and 100–175 m points, still on the positive end of PC II, are on the positive end of PC I, where relative humidity and CO₂ are associated. These data give us a far more complete picture of the microclimatic DEI by allowing us to detect which microclimatic variables are most influential at each distance from forest edge.

Aspect variation is also apparent in the PCA. The west and south aspects of Brownfield and Trelease, respectively, show stronger patterns of separation than other aspects. Both of these aspects have 0–5 m points on the negative side of PC I and PC II (determined by overlapping distance and aspect plots). A large proportion of the 10–25, 40–80, and 100–175 m points for these aspects remain on the negative side of PC II,

while they are further to the positive end of PC I than points of other aspects. These data indicate that canopy openness may influence points at greater distances on south and west aspects than others, and that CO₂ and relative humidity may influence these aspects more than others. The fact that the south and west aspects of Brownfield and Trelease, respectively, do not show similar patterns is evidence that these edges are being buffered by adjacent habitats.

The herbaceous plant community is correlated with changes in microclimate across the edge to interior gradient, but the relationship is not a simple one. The significant correlation of species richness to PC II in both woods indicates that canopy openness and soil moisture are important predictors of plant community responses. However, DEIs for species richness are consistently higher than those of canopy openness and soil moisture in both Brownfield and Trelease.

As suggested by Palik and Murphy (1990), plant competition and disturbance history may play a role in determining herb response to the edge to interior gradient. *L. canadensis* is clearly highly influential in this plant community. *L. canadensis* is adapted to periodic flooding in floodplain forests (Swink & Wilhelm 1994), and Grove (1923) found it to be a highly competitive species in Trelease Woods where it grows without co-mingling with other species. It is unclear why *L. canadensis* is so successful in these forest fragments since the periodic flooding regime to which it is adapted is no longer present. Although it was present in all plots, it is not a good competitor in areas of high light, where plants are smaller; it thrives in areas where soil moisture is high and evaporation potential is low (Grove 1923). *L. canadensis* and other disturbance-tolerant species may be partly responsible for trends apparent in the vegetation data. Relative covers of disturbance-tolerant (Category 3) species increase as relative covers of plants in the other three ecological origin categories decrease.

While many studies have found a decline in sapling density with increasing distance from forest edge (Ranney et al. 1981; Palik & Murphy 1990; Wales 1972; Brothers & Spingarn 1992; Brothers 1993; Fraver 1994), this study shows a large amount of fluctuation in sapling numbers, but with evident distributional patterns for certain species. Higher sapling numbers of *Quercus spp.*, *Carya Nutt. spp.*, *Fraxinus (Tourn.) L. spp.*, and *Prunus L. spp.* occur along the forest edge up to 25–40 m, a result that is consistent with prior studies (Ranney et al. 1981; Whitney & Runkle 1981; Palik & Murphy 1990; Wales 1972;

Brothers 1993). This study indicates, as Brothers (1993) suggested, that the forest edge is a refuge for shade-intolerant *Quercus spp.* and *Carya spp.* saplings unable to compete with shade-tolerant *A. saccharum* in the forest interior. As such, the edge may play an important role in maintaining biological diversity, especially in a forest that is undergoing a transition in its canopy species.

This study shows several patterns of distribution with respect to the forest edge for different plant groups. These patterns include species that increase, and those that decrease in number with increasing distance from the edge, as well as species that are only found on the edge or in the interior. Patterns of distribution of the different plant categories suggest that there may be a dynamic whereby shade-intolerant native (ecological origin Category 2) and exotic (Category 4) species outcompete others in 0–25 m plots where light is highest. Highly competitive shade-tolerant species (Category 3) such as *L. canadensis* are present but have low cover values there. With more canopy cover, these species increase and outcompete shade-tolerant native forest species (Category 1) that would otherwise replace edge species (Categories 2 and 4) under low light conditions in the 40–80 m plots. Shade-tolerant native forest species (Category 1) remain in low numbers in the interior and may be able to outcompete disturbance-tolerant species (Category 3) under certain conditions. Relative cover values in Figure 4 for Trelease suggest this; at 40–60 m the cover of disturbance tolerant species (Category 3) begins to decrease as cover of native forest species (Category 1) increases.

These patterns in the distribution of the vegetation may be evidence for the presence of indirect biological effects, as described by Murcia (1995). For example, direct biological effects are obviously present if shade-intolerant species are able to thrive on a human-induced edge with high light. However, an indirect effect exists if, as in this example, the edge conditions of high light and low relative humidity are reducing the ability of an otherwise highly aggressive species,

L. canadensis, to compete with other species (Grove 1923). It may be possible, since relative humidity is indicated to have a wider DEI than canopy openness, that shade-tolerant native forest species could have an advantage over *L. canadensis* at distances where the forest canopy is closed but relative humidity is still low.

The univariate analyses in this study indicate that most microclimatic edge effects disappear within 40–80 m. However, the multivariate analyses indicate that edge effects may penetrate as far as 100–175 m, a wider edge than has generally been found. The results of this study also indicate that edge effects are reduced by the presence of a protective border. As pointed out by Murcia (1995), it is important to consider interactions among variables when analyzing edge effects. The PCA used here gives us an indication of which microclimatic variables are most influential at which distances and on which aspects. Using this information, we may be able to infer how the microclimate affects biotic factors differently throughout the forest fragment. However, more studies are needed that sample microclimate and vegetation beyond 175 m and that analyze species interactions as driving forces behind changes in community composition over the edge to interior gradient.

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Appendix 1

Plant species in Brownfield (B) and Trelease (T) Woods listed with their ecological origin (1 = Native Forest; 2 = Native Savanna; 3 = Disturbance-tolerant; and 4 = Exotic Species) and distribution categories (Categories 1–7 are described in the text). Species that are distributed differently in different sites are defined by site (B or T).

Plant name	Location	Ecological origin	Distribution category
<i>Acer saccharum</i> Marsh.	B, T	1	5
<i>Actaea pachypoda</i> Ell.	B	1	4
<i>Aesculus glabra</i> Willd.	B, T	1	4(B), 7(T)
<i>Agastache nepetoides</i> (L.) Ktze.	T	3	1
<i>Allium tricoccum</i> Ait.	B, T	1	7
<i>Ambrosia artemisiifolia</i> L.	T	3	1
<i>Ambrosia trifida</i> L.	B, T	3	1
<i>Anemone virginiana</i> L.	B	2	3
<i>Arisaema dracontium</i> (L.) Schott.	T	1	4
<i>Arisaema triphyllum</i> (L.) Schott.	B, T	1	4
<i>Asarum canadense</i> L.	B, T	1	6
<i>Asimina triloba</i> (L.) Dunal.	B, T	1	7
<i>Aster ontarionis</i> Wieg.	B, T	1	1(B), 2(T)
<i>Aster pilosus</i> Willd.	T	3	1
<i>Aster shortii</i> Lindl.	B, T	1	3(B), 5(T)
<i>Bidens aristosa</i> (Michx.) Britt.	B, T	3	1(B), 2(T)
<i>Campsis radicans</i> (L.) Seem.	T	3	2
<i>Carex albursina</i> Sheldon	B, T	1	4(B), 7(T)
<i>Carex blanda</i> Dewey	B, T	1	3
<i>Carex brevior</i> (Dewey) Mack.	T	1	1
<i>Carex davisii</i> Schwein. & Torr.	T	1	3
<i>Carex grisea</i> Wahlenb.	T	1	3
<i>Carex hirtifolia</i> Mack.	T	1	1
<i>Carex jamesii</i> Schwein.	B, T	1	7
<i>Carex muskingumensis</i> Schwein.	T	1	1
<i>Carex sparganioides</i> Willd.	B, T	1	1
<i>Carex tribuloides</i> Wahlenb.	T	1	1
<i>Carya cordiformis</i> (Wang.) K. Koch	B, T	1	3
<i>Carya ovata</i> (Mill.) K. Koch	T	1	4
<i>Caulophyllum thalictroides</i> (L.) Michx.	T	1	1
<i>Celtis occidentalis</i> L.	B, T	1	5
<i>Chenopodium album</i> L.	B	4	1
<i>Circaea lutetiana</i> Aschers. & Magnus ssp. <i>canadensis</i> (L.) Aschers. & Magnus	T	3	4
<i>Crataegus mollis</i> (Torr. & Gray) Scheele	B	3	1
<i>Cryptotaenia canadensis</i> (L.) DC.	B, T	1	7
<i>Cystopteris protrusa</i> (Weatherby) Blasd.	B, T	1	4(B), 7(T)
<i>Daucus carota</i> L.	B	4	1
<i>Dioscorea villosa</i> L.	T	1	7
<i>Elymus hystrix</i> L.	B, T	2	2(B), 5(T)
<i>Elymus villosus</i> Muhl.	B, T	1	1
<i>Elymus virginicus</i> L.	B, T	1	1(B), 5(T)
<i>Euonymus atropurpurea</i> Jacq.	B	1	1
<i>Euonymus europaea</i> L.	B	4	1
<i>Eupatorium purpureum</i> L.	B, T	1	1(B), 3(T)
<i>Eupatorium rugosum</i> Houtt.	B, T	3	1
<i>Festuca obtusa</i> Biehler	B, T	1	2(B), 3(T)
<i>Fraxinus americana</i> L.	B, T	1	1(B), 5(T)
<i>Fraxinus pennsylvanica</i> Marsh.	T	1	1
<i>Fraxinus quadrangulata</i> Michx.	B, T	1	4(B), 1(T)
<i>Galium aparine</i> L.	T	3	4
<i>Geranium maculatum</i> L.	T	1	4
<i>Geum canadense</i> Jacq.	B, T	3	7
<i>Gleditsia tricanthos</i> L.	B, T	3	1
<i>Hackelia virginiana</i> (L.) I.M. Johnston	B, T	3	1
<i>Hemerocallis fulva</i> (L.) L.	B	4	1
<i>Hydrophyllum appendiculatum</i> Michx.	B, T	1	6
<i>Hydrophyllum virginianum</i> L.	T	1	7
<i>Impatiens pallida</i> Nutt.	T	1	7
<i>Juncus tenuis</i> Willd.	T	3	1
<i>Laportea canadensis</i> (L.) Wedd.	B, T	3	6
<i>Leersia virginica</i> Willd.	B, T	1	1
<i>Lindera benzoin</i> (L.) Blume	B, T	1	4
<i>Lonicera maackii</i> (Rupr.) Maxim.	B, T	4	1(B), 2(T)
<i>Menispermum canadense</i> L.	B, T	1	3(B), 7(T)

Appendix 1 (continued)

Plant name	Location	Ecological origin	Distribution category
<i>Osmorhiza claytonii</i> (Michx.) Clarke	B, T	1	7
<i>Oxalis stricta</i> L.	B, T	3	1
<i>Panax quinquefolius</i> L.	B	1	4
<i>Parthenocissus quinquefolia</i> (L.) Planch.	B, T	1	1(B), 7(T)
<i>Penstemon digitalis</i> Nutt.	T	2	1
<i>Phlox divaricata</i> L. ssp. <i>laphamii</i> (Wood) Wherry	B, T	1	5
<i>Phytolacca americana</i> L.	B	3	7
<i>Pilea pumila</i> (L.) Gray	B, T	1	4(B), 7(T)
<i>Plantago rugelii</i> Dcne.	T	4	1
<i>Poa pratensis</i> L.	B, T	4	1(B), 2(T)
<i>Poa sylvestris</i> Gray	T	1	7
<i>Podophyllum peltatum</i> L.	T	1	4
<i>Polygonatum commutatum</i> (Schult.) A. Dietr.	B, T	1	5(B), 7(T)
<i>Polygonum cespitosum</i> Blum var. <i>longisetum</i> (DeBruyn) Stewart	B	4	1
<i>Polygonum scandens</i> L.	T	3	7
<i>Polygonum virginianum</i> L.	B, T	1	4(B), 7(T)
<i>Prunus americana</i> Marsh.	B	3	3
<i>Prunus serotina</i> Ehrh.	B, T	3	3
<i>Quercus macrocarpa</i> Michx.	T	2	1
<i>Quercus rubra</i> L.	B, T	1	2(B), 5(T)
<i>Ranunculus septentrionales</i> Poir.	T	1	4
<i>Ribes missouriense</i> Nutt.	T	3	4
<i>Rosa multiflora</i> Thunb.	B, T	4	1
<i>Rubus allegheniensis</i> Porter	B	3	1
<i>Rubus occidentalis</i> L.	B, T	3	1
<i>Rudbeckia laciniata</i> L.	T	1	4
<i>Rudbeckia triloba</i> L.	B	1	3
<i>Rumex crispus</i> L.	T	4	1
<i>Sanguinaria canadensis</i> L.	B	1	7
<i>Sanicula gregaria</i> Bickn.	B, T	3	5(B), 7(T)
<i>Setaria glauca</i> (L.) Beauv.	B	4	1
<i>Silene stellata</i> (L.) Ait. f.	T	2	1
<i>Smilacina racemosa</i> (L.) Desf.	B, T	1	7
<i>Smilacina stellata</i> (L.) Desf.	T	2	1
<i>Smilax ecirrhata</i> Kunth.	B, T	1	3(B), 4(T)
<i>Smilax hispida</i> Muhl.	B, T	3	3
<i>Solidago canadensis</i> L.	B, T	3	1(B), 2(T)
<i>Stellaria media</i> (L.) Vill.	T	4	4
<i>Symphoricarpos orbiculatus</i> Moench.	B	3	1
<i>Taraxacum officinale</i> Weber	B, T	4	1
<i>Teucrium canadense</i> L. var. <i>virginicum</i> (L.) Eat.	B, T	1	1
<i>Tilia americana</i> L.	B, T	1	3(B), 1(T)
<i>Toxicodendron radicans</i> (L.) Kuntze.	B, T	1	1(B), 5(T)
<i>Tradescantia subaspera</i> Ker.	B, T	1	3(B), 4(T)
<i>Ulmus americana</i> L.	B, T	1	7(B), 2(T)
<i>Uvularia grandiflora</i> Sm.	T	1	7
<i>Verbesina alternifolia</i> (L.) Britt.	B, T	1	1
<i>Viola affinis</i> LeConte	B, T	1	7(B), 3(T)
<i>Viola pubescens</i> Ait. var. <i>eriocarpa</i> (Schwein.) Russel	B, T	1	7
<i>Viola sororia</i> Willd.	B, T	1	7
<i>Vitis riparia</i> Michx.	T	1	7
<i>Zanthoxylum americanum</i> Mill.	T	1	1
Total species			117

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