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FARMLAND FENCEROWS: FOREST EDGE ANALOGS IN FRAGMENTED LANDSCAPES?

by

Ron Fritz, BES

**A thesis submitted to the
Faculty of Graduate Studies and Research
in partial fulfilment of the requirements
for the degree of
Master of Science**

Department of Biology

Carleton University

Ottawa, Ontario

17 April 1991

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Acceptance Sheet

**The undersigned hereby recommend to the
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in partial fulfilment of the requirements

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Master of Science

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Supervisor

Abstract

Fencerows provide movement corridors for various organisms in fragmented landscapes, and so are important in genetic and demographic processes. The hypothesis that fencerow structure is analogous to the edge structure of forest remnants was tested in farmland south of Ottawa, Ontario to determine whether fencerows effectively extend forest patches in terms of vegetation structure, architecture, and habitat quality.

Fencerows had greater canopy structural diversity and more biotically dispersed species than forest edges. Forest edges had more woodland species and mainly wind dispersed, shade tolerant species. Differences in abundance of canopy species clearly separated the two edge types.

Horizontal foliage density in fencerows was more evenly distributed than in forest edges, and greater at heights below 1 m and above 1.5 m. Vines and grasses were more frequent in fencerows. Fewer sub-canopy gaps occurred in fencerows. Forest edges had greater overall architectural heterogeneity.

Morphometry and biomass of three phytometer species showed fencerow habitat quality to be inadequate to invoke fencerows as effective corridors for movement of woodland plants.

Acknowledgments

I would like to give recognition to all who have contributed to the successful culmination of my research program at Carleton.

To the individual plants used as phytometers, and to their respective populations, I express sincere appreciation for enduring my experiment--now returned to their original sites, may they continue to grow as beautiful as the flowers they are.

To Dr. Roger Suffling, my undergraduate advisor at University of Waterloo--your support for my shift from Geography to Biology and your continued interest in my progress is appreciated. To Dr. Gray Merriam, my thesis supervisor, for giving me unlimited opportunity to explore. To Drs. Hans Damman and David Currie of my advisory committee, for your sensitively constructive criticisms. To the Natural Sciences and Engineering Research Council, for the scholarship support during the first two years of my research. To Dr. Andrew Brook and the students of *Environmental Ethics*, for the delightful opportunity to stretch out intellectually in a vital and fascinating area.

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And to psychedelic Easter bunnies with whom I rediscovered enchantment.

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"Le drapeau va au paysage immonde, et notre patois étouffe le tambour.

"Aux centres nous alimenterons la plus cynique prostitution. Nous massacrerons les révoltes logiques.

"Aux pays poivrés et détrempés!--au service des plus monstrueuses exploitations industrielles ou militaires

"Au revoir ici, n'importe où. Conscrits du bon vouloir, nous aurons la philosophie féroce; ignorants pour la science, roués pour le confort; la crevaisson pour le monde qui va. C'est la vraie marche. En avant, route!"

---Arthur Rimbaud

It is very necessary these days to apologize for being concerned with philosophy in any form whatever....In my opinion, the greatest scandal of philosophy is that, while all around us the world of nature perishes---and not the world of nature alone---philosophers continue to talk, sometimes cleverly and sometimes not, about the question of whether this world exists.

---Karl R. Popper

Girdling the old oak to squeeze one last crop out of the barnyard has the same finality as burning the furniture to keep warm.

---Aldo Leopold

**Sunrise startles magpies from the gate,
And crows perched within hedges scatter.
But the cold river flows, an immaculate
Patience against those who will return.**

---Lao Tzu

General Introduction

Forested areas in farmland are invariably patches of forest remaining after land has been cleared to establish farming. Fencerows, on the other hand, have developed more recently, arising certainly only after the establishment of field boundaries, though one or a few individual trees within a fencerow may possibly remain from previous forest clearing. Erection of various forms of fences (split rail, post- or barbed wire, stacked stone) or deposition of fence-like structures (piled stumps, rocks or other field debris) provide subsequent reinforcement of the field boundaries. Many contemporary fencerows have large canopy trees and dense shrub vegetation at the periphery.

The effects that reduced area and relative isolation of forest patches have on individual organisms and their populations, which formerly inhabited contiguous forest have been the focus of much research. Out of this has emerged the concept that fencerows provide a connecting network between forest patches. Ecological literature now frequently refers to fencerows and their European counterpart, hedgerows, as "corridors" that allow some organisms to persist in otherwise inhospitable anthropogenic landscapes. Such corridors are frequently cited as contributing significantly to connectivity (*sensu* Merriam 1984) in landscapes of heterogeneous habitat patches, otherwise isolated in demographic or genetic terms. But fencerow corridors may also increase the exposure of forest patches to predation, facilitate invasions of opportunist species or extend contagion effects such as fire and disease (Simberloff & Cox 1987) into forest patches. These disadvantages notwithstanding, it is interesting to consider whether fencerows serve the more beneficial corridor function equally for all organisms by contributing importantly to metapopulation structure (Merriam 1984). Is the physical connection fencerows provide in fragmented

landscapes adequate for this corridor function, or must an effective corridor also be of comparable structure to the patches it is purported to connect? If the latter, how similar is sufficient?

At the moment, we lack clear answers to these questions. Surveys of the vegetation structure of fencerows have been carried out in the context of broader research (e.g. Brewer *et al.* 1969, Baudry & Forman 1983, Lutz & Runkle 1985, Somerlot 1982, Whitney & Somerlot 1985). Except for the work of Somerlot (1982) and Baudry (1984), and their collaborations (Whitney & Somerlot 1985, and Forman & Baudry 1984), the particular structural character of North American fencerows, especially in the mid-west agricultural region, has gone largely undescribed. However, species typical of woodland interior flora have been observed within fencerows (Baudry and Forman 1983, Lutz & Runkle 1985; Merriam, personal communication; Fritz, unpublished data). The presence of these species in fencerows, as well their origins and persistence, interested me, and further, may have implications for conservation planning.

A fencerow may typically arise through several phases of development. Once field boundaries are designated, a fencerow begins to develop. First it may just be a conceptual boundary separating fields set to disparate purposes, but as the farm operates, this conceptual structure begins to take on physical dimensions. Landscape context and configuration influence fencerow genesis. Cultural and ecological history, regional vegetation formations, and adjacent patch types will determine what will contribute to fencerow structure--that is, the species composition, architectural form and resulting habitat conditions of fencerows. Distance from source patches (e.g. forest, farmstead), length and direction of long axis, and number and type of intersecting elements will affect the rate of fencerow development, as well as how well the fencerow can act as a corridor, by constraining interactions with other landscape elements (Forman & Baudry 1984).

In strips of untended land at field margins, grasses and weedy vegetation begin to grow unrestrained at the nascent field margin. Ploughing of adjacent fields exposes soil to the desiccating effects of sun and wind, and induces rapid aerobic breakdown of organic matter and mixing with mineral soil. This leads to greater incidence of winds blowing denuded surface soil from fields to be deposited at the first obstacle encountered--invariably the emerging vegetation at the field margin. Because the soil may never have been tilled where older fencerows exist, possibly these fencerows have retained the soil qualities of the forest that once covered the area, as well as a forest seed bank.

The progress of wind-blown seeds will also be impeded by the emerging fencerow vegetation. As seeds accumulate at field margins, species tolerant of open habitat will germinate and amplify the obstacle effect. Movements of animals also contribute to the developing fencerow structure, particularly by introducing the seed-bearing fruits of woody species. Birds, using fenceposts as vantages for territorial displays or rest stops between forest patches, probably poop while perched, thereby depositing seeds suitably conditioned and nutrient enriched for successful germination (McDonnell & Stiles 1983). Small mammals, evading winged predators, opt for the sheltered passage along the field margins given by fencerows rather than risk their skins crossing an open field. Of course, seasonal exceptions occur. Once a crop begins growing well, entering the field may not be so risky to a chipmunk (*Tamias striatus*) or white-footed mouse (*Peromyscus leucopus*), but the direction to one's destination may not be so clear. Perhaps these organisms rely upon familiar pathways to travel through the landscape.

So wind-blown and animal dispersed seeds arrive in plentiful supply to the field margins. These strips between fields get rather little attention from the farmer, other than perhaps a contribution of rocks every spring, empty seed sacks, old tires, pruned wood or sour baies of hay. Unintended contributions may also come in the form of fertilizers,

pesticides, or seeds drifting in from field work by the farm hands. In this neglected state the fencerows can develop structurally. Woody biomass becomes an increasingly important element here. Occasionally, standing wood may be removed from a mature fencerow for fuel, or simply to remove an encroaching obstacle to efficient operation of farm machinery, but generally fencerows are left unmanaged.

Remnant forest patches in farmland provide the sole source of propagules of the woody species found in fencerows, except perhaps for the exceptional fruit tree or ornamental shrub that has escaped from cultivation either at the farmstead or in a local orchard. So, considering just mode of dispersal, the species contributing to the woody biomass of fencerows would be expected to be no different from those in the forest, particularly those inhabiting the edges of forest where agents of dispersal would be most active (Biber 1988). Compositionally, then, fencerows may be "woodland edges without the woods" (Pollard *et al.* 1974). Forman and Baudry (1984) found the predominant species in New Jersey fencerows to all be forest edge species, and typically included thorny shrubs and non-native species.

The similarity in species composition between fencerows and forest edges in particular would also be expected because fencerows are not wide, and so may be thought of as having no appreciable "interior", but rather to be edge across their entire width (*cf.* Wales 1972, Ranney *et al.* 1981). Absence of interior habitat conditions in fencerows may mean that the shade tolerance of woody species would be similar in the two edge types--that is, in the edge of forests, and in fencerows, which are practically all edge. Assuming that species have an equal chance of arriving at fencerows, regardless of mode of dispersal, then the presence of those species will be dependent upon successful germination and growth of arriving propagules.

For fencerows to support a ground flora typical of woodland interiors, fencerow

structure would need to be such that habitat conditions match those of woodlands. Abundance of these species in fencerows may not be as great as in forest edges simply because fencerows are less structurally developed, or the difference could be related more complexly related to spatial (landscape context, fencerow configuration) as well as other temporal factors (historical effects).

For non-woody species, the similarity between fencerows and forest edges may not be as readily apparent, if expected at all. Fencerows, being more exposed to climatic elements, would have different habitat qualities. Sunlight, for instance, is capable of penetrating the forest edge only at low angles. Wind effects on evapotranspiration and temperature reach further into the forest from edges facing into the wind (Ryszkowski & Kedziora 1987, Young 1988), but generally the forest edge preserves interior microclimate (Geiger 1965). These effects would be expected to be greater in fencerows because these corridors have much less canopy breadth and are accessible to elements from both sides simultaneously. In temperate zones this effect may increase if the long axis is east-to-west. This means light and wind could reach the fencerow centre with greater intensity than in the forest edge, and so preclude the presence of an interior habitat. The presence of woodland species in fencerows suggests that either the vegetation structure of fencerows can filter intense light and buffer the effects of wind sufficiently to accommodate woodland herbs, or that these species have evolved adaptations which allow them to persist in these conditions (Middleton & Merriam 1983).

My main aim was to compare fencerow vegetation structure with that of forest edges, and relate this to the proposed corridor potential of fencerows for plants. The evidence for animals using fencerows as corridors (Wegner & Merriam 1979, Henderson *et al.* 1985) gives credence to this contention. But to extrapolate this corridor function to plants is perhaps stretching the case (*cf.* Pollard *et al.* 1974, Helliwell 1975, Baudry &

Forman 1983, Baudry 1984, Lutz & Runkle 1985). Birds, small mammals, and some insects transport themselves, actively selecting paths and destinations. Where and when they travel are critical to their immediate survival as well as to the persistence of their populations. It is possible that such organisms are not too selective about the particular condition of a corridor because they are essentially itinerants there.

Other than vegetative reproduction and clonal extension of a population, which demand physical connection between source and potential colonial habitats, terrestrial vascular plants in temperate zones generally rely on external dispersal agents. Because plants are more intimately coupled to their subsistence resources, a potential corridor may need certain qualities comparable to those of the species' typical habitat. The relatively passive dispersal of many plants, requiring external agents to carry propagules from a source location to some other receptive site, and the intimate proximity of plants with habitat, led me to hypothesize that for fencerows to act as corridors for plants, 1) fencerows must be connected physically or functionally (by supplying dispersal agents) to source patches, and 2) fencerows must provide habitat comparable to that of source patches. The first condition permits plants to migrate from the source habitat to some other habitat. This may be expected to occur only if the second condition is fulfilled, that is the path of movement is conducive to the growth and reproduction of the particular species on the move.

The fate of seeds dispersed in fragmented landscapes faces a problem. Even the heavy traffic of dispersal agents along corridors does not guarantee germination sites will be reached, unless either the habitat quality of a corridor is comparable to that of the source patch, or the species being transported has evolved some means of dealing with habitat heterogeneity. Middleton and Merriam (1983) have suggested that woodland species have always been faced with spatial discontinuities in habitat, and point to the

persistence of these species in modern anthropogenic landscapes as evidence for evolution of a mechanism of movement associated with dispersal mode. Natural selection of the kinds of organisms involved in dispersal also selects the direction and setting to which a particular agent will transport seeds.

Wind and animals involved in seed dispersal in farmland may follow fencerow structure, and so carry propagules from the exposed edge of forests to nearby fencerows, potentially extending the forest edge into the surrounding land. Still, a reciprocal movement of seeds from fencerow to forest edge would also be expected, resulting instead in invasion by non-forest species. Not all of these propagules will succeed in developing into mature plants. Many factors may be involved, but the complex of factors that comprise what can be referred to as habitat quality are primary ingredients for the success of arriving propagules. Although a fencerow may support the activity of some animals, it does not necessarily support the species of plants that those animals can deliver.

Recapitulating then, for fencerows to act as corridors for plant movement, two conditions would be expected. First, a fencerow would need to be either physically connected to a source habitat (*e.g.* forest) or it would need to be functionally connected--that is, there would have to be operating some actual means of getting propagules of source habitats to fencerows. Second, fencerow habitat quality would be expected to be similar to that of source patches in order to support similar plant life. Literature previously cited allowed me to assume that the first condition is generally met. The focus of my research then was on whether the habitat quality of fencerows would allow them to be effective movement corridors for plants.

Aims of the Study

The aims of this study are to describe the vegetation structure of fencerows relative to that in forest edges in eastern Ontario farmland, and to test whether structure of the two edge types is the same. From this it may be inferred whether fencerows could provide habitat qualities conducive to the movement of woodland plants in fragmented landscapes.

In Chapter I, I describe the species composition of fencerow vegetation in greater detail than previous North American studies. I also compare the composition of fencerow and forest edge vegetation to determine whether fencerows effectively extend forest patches into fragmented landscapes. In Chapter II, I compare the architectural structure of fencerows to that of forest edges. In Chapter III, results of field experiments testing for habitat affinity between fencerows and forest edges are presented. A final section summarizes my conclusions and briefly discusses the importance of fencerow corridors to plant movement in fragmented landscapes.

General Methods

Fieldwork was conducted in farmland near the town of Manotick, 30 km south of Ottawa, Ontario. This area falls within the Great Lakes-St. Lawrence Forest Region of Canada (Rowe 1977). The landscape consists of remnant forests (1-25 ha) within farmland dissected by fencerows. Forest edge and fencerow samples were selected on the basis of visual assessment of the overall similarity in dominant vegetation and stage of development. Elements with obvious signs of recent disturbance were excluded from the sample.

Sampling employed transects running perpendicular to the width of both edges.

Transects were established at 10 m intervals along edges; distance intervals of sample points and plots along transects varied between the particular data sets, but were consistent within a data set. Sampling of vegetation and architecture took place during June to August 1989. The phytometer experiment was run through the 1989 season and concluded in June 1990. Detailed methodology is presented in each chapter.

For each sample site, data were summarized as transect means to obtain a measure of variation across the width of forest edges and fencerows. These means then were used as independent estimates of each parameter in statistical tests. Except for contingency analyses, univariate (t-tests, ANOVA) and multivariate (MANOVA, discriminant and cluster analyses) tests used standardized, natural log-transformed data.

For MANOVA, Pillai's trace (v) was chosen as the most powerful and robust test criterion among several available in SPSS PC + v.2.0 (1987). For two independent samples (*i.e.* forest edges and fencerows) with multiple dependent variables, the transformed statistics for Pillai's v are distributed exactly as F (Norusis 1985), so only the multivariate F -ratios are presented. When edge type was shown to significantly affect the multiple dependent variables, univariate F -ratios were examined to determine which particular variables were most affected. Overall, significance of test statistics was accepted at $p \leq 0.05$, but significance (p) values were generally estimated to four decimal places to illustrate relative significance among similar tests. For tests that resulted in highly significant differences, p was reported as being less than the smallest appropriate number with four decimal places.

A discriminant function was considered a good descriptor of edge type if it resulted in a large eigenvalue, a small value for Wilk's lambda (λ), and a canonical correlation coefficient with a value significantly greater than 0.5. Eigenvalues were calculated as Between Edge Type Sum of Squares/ Within Edge Type Sum of Squares. Wilk's λ

represents the proportion of variation in the discriminant score not explained by group differences (*i.e.* Within Edge Type SS/ Total SS). The canonical correlation coefficient in this two group situation was equivalent to Pearson's correlation coefficient. Discriminant functions then were tested with a jackknife procedure to assess the precision of the function. The SPSS PC+ (version 2.0) computer software was used for all multivariate analyses.

I

Vegetation Structure in Fencerows

Introduction

One component of my assessment of the corridor potential of fencerows for plants was an examination of the species composition and abundance in fencerows. I compared the vegetation structure of fencerows to that of forest edges in the same farmland context. Forest edges were the most likely source of propagules and structurally were the most similar in vegetation in this landscape. The woody component was expected to have most species in common due to the absence of any significant seed source other than local forest edges. Herbaceous species may be significantly different due to many factors such as diverse sources of propagules other than forest edges, greater sensitivity to habitat quality and relative exposure to disturbance. Still, I had seen several species typical of woodland ground flora in fencerows during reconnaissance.

The working hypotheses were: 1) species richness and diversity observed in fencerows would not differ from those observed in forest edges, and 2) the vegetation abundance in the two edge types would not be different.

Species richness, as the number of species in each edge type, should be similar if the effect of having an exposed edge is the same regardless of what is on the opposite side of that edge. In this case, the forest edge is backed up by the main structure of the forest interior, whereas fencerows are assumed to have no interior as such, but instead to be edge across their entire width. If doubling of edge length or perimeter, as in fencerows, also increases the edge effect on species composition then more species should be expected (Leopold 1933) in fencerows due to double edge effect.

Evenness, the distribution of individuals among the species within each edge type, should show no difference unless the double edge effect is invoked, thus precluding clear dominance in fencerows. In attempting to establish whether fencerows could function as corridors for woodland plants in particular, species typical of woodland interior habitats were considered separately. A difference in overall estimates of abundance (e.g. total of the means of percent cover, total mean basal area, total density) as well as abundance of individual species occurring in the forest would suggest more favorable habitat in woodlands.

Methods

Fencerows and forests in farmland 30 km south of Ottawa were surveyed for this study. Three forest edges and 7 fencerows with north-south axes were selected to give an east-west solar aspect. The forests were all chiefly maple stands 5-15 ha in area. The edge of one stand converged upon a cornfield, while mixed hayfields abutted the edges of the other two stands.

The seven fencerows chosen were of spontaneous (unplanted) origin, at comparable stages of development (mean age *ca.* 60 yr), and had not recently been subject to detectable anthropogenic disturbance. Although ditches commonly occur along field boundaries in the Ottawa region to facilitate drainage, fencerows in this study lacked ditches.

Fences occurred in two of the forest edges (FE), though at different distances from the field margin. The dilapidated rail fence in FE 1 was 7 m from the field margin whereas the stone fence (1.5 m high) of FE 2 was 3 m from the field margin. Not all fencerows had

intact fences, but it could be determined whether a fence had been present. Fences encountered included page-wire, split rail, and a low (1.5 m) stone wall. All occurred at the approximate centre of the fencerows, relative to the field margins on either side. However, due to the different widths of the fencerows in this study, distance from field margin to fence was not constant. The average fencerow width in my sample was 9.5 m (range 6-12 m). So the mean distance from field margin to fence in fencerows was comparable to that in the forest edge sample. Fencerows were not selected for a constant width, as the general nature of fencerows which I was intent on exploring seems to lie in their high variability (Wegner & Merriam 1979, Fritz unpubl. data).

Transects were established across all edges at 10 m intervals, beginning 30 m from the start of a given edge. All sites were sampled from field margin toward interior. Fencerow transects spanned the entire fencerow width, while forest edge transects extended 15 m in from the field margin. This latter distance represents empirically based estimates of forest edge width (Wales 1972, Ranney 1977, Levenson 1981).

Nested quadrats were used to sample vegetation along transects across each edge type (Table 1). Canopy trees were sampled with 10 X 10 m plots in forest edges. To provide equal sample unit area in fencerows, trees were sampled with plots that were 10 m along the edge by the entire fencerow width. Within each tree plot, the shrub layer was sampled with 3 X 3 m plots, and ground vegetation was sampled within these shrub plots with 1 X 1 m plots. To replicate sampling effort in the two edge types, plots were equally spaced along forest edge transects, whereas fencerow plots were contiguous to compensate for the narrow width of fencerows.

Species presence and percent cover (5% increments) were recorded for all strata. The shrub layer was delimited as being above knee height (> 0.5 m) and included stems under 5 cm dbh. Tree stems (≥ 5 cm dbh) were counted by species, stem diameter was

measured at 1.5 m height, and canopy cover was estimated for the quadrat. Tree diameter was later converted to basal area.

Surveys were done after canopy closure, so certain species of ground vegetation were absent or under-represented in the sample. This was not expected to affect the results of the comparison. Cover estimates used in analyses have been standardized with Wisconsin double standardization (Bray & Curtis 1957) prior to transforming to a log-octave scale (Gauch 1982). Species with less than 5% frequency in either sample (fencerow or forest edge), or with less than 5% total cover were excluded from analyses (Gauch 1982, Causton 1988).

Analysis

Comparisons of vegetation structure between the two edge types included species richness, diversity and abundance. The focus was on how individual species and groups of species contribute to the vegetation structure of the two edge communities. A complementary survey (presented in the following chapter) focused upon the contribution to structure of various architectural elements, apart from the context of species.

Species richness

Contingency tests were used to determine if species richness (simply, the number of species present) was independent of edge type for each of three strata, herbaceous and woody species, and total richness. To eliminate differences arising due to unequal sample sizes, I took a probability perspective to determine what would be the expected number of species in fencerows and forest edges if sample sizes were equal. The rarefaction method (Hurlbert 1971, Simberloff 1972, Heck et al. 1975, James & Rathbun 1981, Ludwig and Reynolds 1988) calculates the number of species expected from different

communities if all samples are reduced to a standard size (Equation 1). This approach assumes that sample size bias can be overcome with an underlying sampling model that applies to all communities concerned (James & Rathbun 1981). It also assumes that the ratio of numbers of individuals to numbers of species do not differ between communities being compared (Peet 1974). Equation 1 computes $E(S_n)$, the expected number of species in a random sample of size n by considering the sum of probabilities that each species will be included in the sample.

$$E(S_n) = \sum_{i=1}^S 1 - \left[\frac{\binom{N-n_i}{n}}{\binom{N}{n}} \right] \quad (1)$$

where S is the total number of species present in a particular community (forest edge or fencerow), n_i is the number of individuals of species i , and N is the total number of individuals.

The number of woody species found in different lengths of British hedges has been found to be indicative of the age of the hedge (Hooper 1970, Helliwell 1975, Dowdeswell 1987). Most simply, for every one hundred years, one new species arrives per 27.4 m length of hedge sampled. Assuming a similar relationship between richness and age in my Ottawa study area, then forest edges and fencerows would be expected to have the same number of species per unit length only if they were at comparable developmental stages.

I examined the relationship between species richness and length of edge sampled in both shrub and ground vegetation. Even if the British hedgerow model is inappropriate, information about the internal heterogeneity of fencerows and forest edges would be revealed. Linear regression models of richness on edge length for each edge type were examined for goodness of fit with ANOVA, and by calculating a coefficient of determination, R^2 . Slopes for forest edge and fencerow samples were then compared in t-

tests, and 2-way ANOVA was used to determine whether significant interactions occurred between edge type and length to influence richness. Transect means were used in these comparisons, as well as in the following tests.

Two possible effects on number of woodland species present in fencerows (Appendix 1), fencerow width and distance from nearest forest (Baudry 1985), were examined with contingency tests and linear regression. The fencerow sample provided a range of widths (6-12 m). Three distance classes were used: 1) fencerows connected directly to forest edge, 2) fencerows not directly connected, but less than 0.5 km from the nearest forest edge, and 3) fencerows greater than 0.5 km from the nearest forest edge. Random sampling of transect means from fencerows in distance classes 2 and 3 were used to provide equal sample sizes among all the three distance classes.

Community Similarity and Diversity

Several measures of community similarity and species diversity were calculated to compare the distribution of individuals among species present in forest edges and fencerows. Jaccard's community similarity was based on the initial species list before editing. In the remaining equations, summations were made over all species not meeting the previously stated deletion criteria. Jaccard's similarity coefficient, *CS* (Equation 2), gives equal emphasis to species rarely observed in a sample and species more commonly encountered.

$$CS = \frac{\text{Number of species co-occurrences}}{\text{Total number of species}} \quad (2)$$

where the numerator is the number of species common to both forest edge and fencerow samples, and the denominator is the total number of species for both samples. Euclidean distance, *ED* (Equation 3), emphasizes dominant species, while percentage similarity, *PS* (Equation 4), provides an intermediate measure through a linear weighting of species

abundance (Gauch 1982, Pielou 1984).

$$ED = \sqrt{\sum_{i=1}^S (A_{ij} - A_{ik})^2} \quad (3)$$

where A is the abundance (relative frequency or cover) of species i in sample j or k .

$$PS = \sum_{i=1}^S \min(A_{ij}, A_{ik}) \quad (4)$$

where $\min$ calls for the lesser of two values between samples j and k for species i as input.

Shannon's diversity, H' (Equation 5), calculated for estimates of species frequency, cover, dominance and overall importance, was compared between fencerows and forest edges in t-tests for each abundance parameter. This, and the diversity indices following, are independent of sample size as they use relative abundance values.

$$H' = -\sum_{i=1}^S p_i \ln p_i \quad (5)$$

where p_i is the proportion of the total abundance (frequency, cover, importance) of species i . As indicated, I used natural logarithms. Variance of H' was estimated as:

$$s^2 = \frac{\sum f_i \ln^2 f_i - (\sum f_i \ln f_i)^2 / n}{n^2} \quad (6)$$

Evenness, J' , was determined to assess the distribution of total sample abundance among all species in each edge type. Maximum diversity, $H'_{\max}$, occurs when every species has equal abundance, and was estimated as the natural logarithm of the number of species in each sample. J' then was taken as the ratio of H' to $H'_{\max}$.

Cuba (1981:278) has suggested that a change in species composition constitutes

a greater variation than does a change in the distribution of individuals among the species within a given sample. So a community with more species is always more diverse than one with fewer species. Cuba proposed an index of evenness (Equation 7) that measures internal heterogeneity and separates the influences of species richness and their distribution.

$$\text{Cuba's Evenness, } X = 1 - \left(\sum_{i=1}^S \frac{d_i}{2N} \right) \quad (7)$$

where d_i is the deviation of species i from uniform evenness.

Finally, Horn's (1966) information theoretic index of community similarity, R_o (Equation 8), was determined for canopy trees based on relative measures of species frequency, cover, dominance and importance.

$$R_o = \frac{H_{\max} - H_{\text{tot}}}{H_{\max} - H_{\min}} \quad (8)$$

where $H_{\max}$ is H' if each species abundance from fencerows and forest edges was from a different species, $H_{\min}$ is the minimum H' possible with maximum overlap of species abundances between edge types, and H_{tot} is H' considering fencerow and forest edge data as a single sample (Brower & Zar 1984).

Abundance

Within forest edge and fencerow samples, means for abundance measures were computed for each transect. These means then were used as independent estimates of abundance for comparing edge types. Species abundance in the two edge types included frequency and percent cover for shrub and ground vegetation, and cover, density and dominance for canopy trees. Frequency was the number of plots in which a species

occurred. Cover was an estimate of the proportion of plot area covered by a species. Tree density was the number of individual stems within a plot. Dominance was the relative contribution of a tree species to total basal area of all tree species for each edge type. All abundance estimates were based on untransformed data. Subsequent analyses for an effect of edge type on species composition used transformed data.

Relative measures of abundance calculated for all vegetation strata in each edge type were summarized as importance values. An importance value (IV) was calculated as the mean of the summed relative abundance measures for a given species in each stratum.

The vertical distribution of leaf cover in fencerows and forest edges was compared using an index (Foliage Height Distribution, *FHD*; Equation 9) that described the relative heterogeneity in foliage distribution among canopy, shrub and ground layers (Ambuel & Temple 1983).

$$FHD = \sum \frac{1}{p_i^2} \quad (9)$$

where p_i is the proportion of total foliage cover in the i^{th} layer. A similar measure of vegetation patchiness has been useful in predicting bird species diversity in homogenous stands of vegetation (MacArthur 1964); however, as fencerows clearly have highly variable vegetation cover, the main intent here was to obtain an index that would illustrate differences that may be present between edge types in total foliage distribution.

Comparisons of species composition between fencerows and forest edges also considered both modes of seed dispersal and shade tolerance classes. Species were grouped by mode of seed dispersal (Appendix 2) as either abiotically or biotically dispersed (Harper *et al.* 1970, Schopmeyer 1974). The former group includes species that have seeds dispersed primarily by wind (e.g. *Acer*, *Ulmus* and *Fraxinus*) while the latter (e.g. *Asarum canadense*, *Prunus*, *Crataegus*, *Quercus*) relies on other organisms to disperse

seeds. Biotic agents of dispersal include ants (Beattie & Culver 1981, Handel *et al.* 1981), birds (Darley-Hill & Johnson 1981, Johnson & Adkisson, Malmborg & Willson 1988) and small mammals (Janzen 1971, Heithaus 1981, Howe & Smallwood 1982).

Canopy tree species were grouped into three shade tolerance classes (after Baker 1949, Fowells 1965): tolerant to very tolerant, intermediate, and intolerant to very intolerant (Appendix 2a). The distribution of shade tolerance among species in fencerows was compared with that of forest edges. Numbers of species and the frequency of those species in each dispersal and tolerance class were used to test for an effect of edge type.

Discriminant analysis determined whether observed differences between fencerows and forest edges would provide adequate means for predicting the edge type of an unknown sample. Linear combinations of independent variables (the predictors) were formed from species abundance data for each stratum. The analysis showed which vegetation characteristics figured most importantly in the resulting discriminant function.

Cluster analysis using an agglomeration based on squared Euclidean distances provided a graphical means for assessing the multivariate distance between edge types and between their component samples. The fencerow sample was also examined separately to see whether the established discriminant function could distinguish fencerows that were most similar to forest edge. This comparison was used to arrive at a relative index of fencerow habitat quality relative to forest edge.

Results

Species Richness

Species recorded in the vegetation survey of fencerows and forest edges are listed with their common names in Appendix 1. Overall, forest edges and fencerows shared 55% of the 87 species observed, and approximately 20% of the remaining species were unique to each edge type. The overall number of species present was independent of edge type (Fisher's Exact Test, $p = 0.234$). Ground layer vegetation had the most species (75 species or 86% of the total), followed by the shrub layer (37, or 43%), and finally the canopy trees (19, or 22%). Contingency tests found species number in each stratum to be independent of edge type (Table 2).

Overall, and in each stratum, fencerows and forest edges had equivalent numbers of unique species. The 17 species present in forest edges but absent from fencerows were mainly woodland species (e.g. *Carpinus carolinianus*, *Carya cordiformis*, *Viburnum trilobum*, *Circaea quadrisulcata*, *Arisaema triphyllum*, *Caulophyllum thalictroides*). The 21 species unique to fencerows were more typical of species of open or disturbed habitats (e.g. *Quercus alba*, *Acer negundo*, *Clematis* spp., *Rhamnus alnifolia*, *Geum aleppicum*, *Vicia cracca*). Non-native species were not well represented in either edge type.

None of the rarefaction curves (Figures 1a-d) showed an appreciable difference between the two edge types in expected species richness, either by stratum or by vegetation type. For all strata, expected richness compared at the maximum standard sample size showed differences of 2 to 3 species at most. These minor differences were not consistent--the additional species occurred in forest edges in shrub and ground vegetation but in fencerows for trees. Expected richness of woody species in forest edges exceeded that in fencerows by 3 species (Figures 1a,b). Rarefaction curves for fencerows

and forest edges were almost coincident for all herbaceous species (Figure 1c) as well as for just those considered to be woodland interior dwellers (Figure 1d). The latter result is interesting considering that 73% of species unique to forest edge ground flora were woodland species (*cf.* 25% in fencerows). The main difference in overall richness between fencerows and forest edges then was in woody species richness.

The mean number of species found in forest edge shrub and ground layer vegetation with increasing edge length was greater than fencerow mean richness at all lengths, but no difference was found between slopes of the two edge types in species-edge length regressions (Figures 2,3). Regression equations fit shrub (Figures 2a,b) and ground layer (Figures 3a,b) data well in both edge types.

Taken independently, shrub and ground layer richness were more greatly influenced by edge type than by edge length, and no edge type-edge length interaction was found in 2-way ANOVA in either the shrub layer ($F = 0.920$, $DF = 1,4$, $p = 0.454$) or ground vegetation ($F = 0.512$, $DF = 1,4$, $p = 0.727$). For the combined species richness of shrub and ground vegetation, the effect of length on species richness was found to interact significantly with edge type in MANOVA ($F = 15.41$, $DF = 8,264$, $p < 0.0001$).

Among fencerows, width affected richness and frequency of herbaceous woodland species alone, and with woody species included (Table 3). The weak correlation between width and both richness and frequency of woodland species make it difficult to interpret the significance of fencerow width. The greatest woodland species richness and frequency coincided with the middle of the range of fencerow widths (9 m).

Distance from the nearest woodland also had a significant effect on woodland species richness and frequency in fencerows (Table 4). Neither richness nor frequency, however, showed a linear relationship to distance. Woodland species richness in fencerows attached to forests was closer to that of fencerows in the furthest distance class, while

fencerows at intermediate distances from forest had appreciably fewer woodland species, and lower frequencies of these species, than fencerows in both of these other distance classes.

So overall, species richness appeared to be not significantly different between forest edges and fencerows. A marginally greater number of woody species were present in forest edges. Edge type did affect the number of species found with increasing edge length. Within fencerows, richness and frequency of woodland species showed differences associated with fencerow width and fencerow distance from the nearest forest; however, these results are ambiguous as none of the associations were linear.

Community Similarity and Diversity

Several indices of community similarity showed that forest edge and fencerow samples had similar diversity in species frequency, density, percent cover, dominance and importance values. Percentage similarity (PS) between fencerows and forest edges was lowest for species importance values in canopies (PS = 0.26), and higher in shrub (PS = 0.45) and ground (PS = 0.36) layers. Although the edge types were not similar (all PS < 0.5), the indices indicated that contributions of individual species to total importance differed more in the canopy than in the lower two strata.

Euclidean distances (ED) between edge types were smaller for species importance values in shrub and ground layers (ED = 0.32 for both) than in canopies (ED = 0.64). In the lower two strata, the main difference between edge types was in relative cover ($0.40 < ED < 0.50$); frequency was least different here ($ED < 0.25$). The influence of dominant canopy tree species was brought out in the greater differences between fencerows and forest edges, especially in relative cover (ED = 0.68) and dominance (ED = 0.80).

Horn's community similarity, R_h , again showed species composition and relative

abundance to be most similar between edge types in shrub and ground layers ($R_s = 0.65$). Canopies were the least similar ($R_s = 0.39$) between edge types.

The diversity of species relative abundance in fencerows and forest edges was not significantly different in any stratum (Table 5b). In both edge types, diversity (H') was greatest in the ground layer, least in the canopy. Maximum diversity (H_{max}) showed this same distribution among strata in both edge types (Table 5c).

Even considering J' to be an overestimate of evenness (Brower & Zar 1984), importance values of canopy trees were more evenly distributed among species in fencerows than in forest edges. Evenness in lower strata was more similar between edge types (Table 5c). Cuba's (1981) evenness index corroborated the biased distribution of importance values in forest edge canopies previously described by similarity indices. The combined evidence above shows that the canopy layer contributes most to the differences between forest edges and fencerows observed in vegetation diversity.

Abundance

Stand summaries for species abundance in fencerows and forest edges are given in Appendix 2. Total mean percent cover and density in forest edges and fencerows canopies were not appreciably different, although the total basal area in forest edges exceeded that in fencerows by 14%. All individual abundance parameters achieved their highest values in forest edges solely due to the distinct dominance of *Acer saccharum* in the forest edge canopy (Table 6). Fencerows had a more equitable distribution of importance value (IV) among several species.

Of 12 canopy species, *Acer saccharum* was clearly the most important in forest edges, providing more than 50% of the total mean cover and basal area (relative dominance), and contributing 30% of the stem density (Table 6).² *Ostrya virginiana* and

Fraxinus americana had density similar to *Acer saccharum* in forest edges, but substantially less cover and basal area. Together, these three dominant species accounted for approximately 90% of the total canopy cover, 80% of the stem density, and 95% of the basal area in forest edges. A subdominant group consisted of *Tilia americana*, *Carpinus carolinianus* and *Ulmus* spp., each accounting for greater than 1% of the total importance value, and together making up nearly all remaining cover.

Among the 16 tree species in fencerows, *Fraxinus americana* dominated the canopy in all respects and contributed greater cover, basal area and density than found in forest edges for this species (Table 6). *Crataegus* sp. had density in fencerows comparable to *Fraxinus americana* though less cover and basal area. In a second pair of species, *Viburnum lentago* and *Quercus alba*, each accounted for greater than 10% of the total fencerow canopy importance values. This dominant foursome together accounted for greater than 75% of the total canopy cover, 80% stem frequency and 90% of the basal area in fencerow. A subdominant group consisted of 7 species: *Ulmus* spp., *Tilia americana*, *Prunus serotina*, *Acer negundo*, *Acer saccharum*, *Prunus virginiana* and *Populus tremuloides*. This group accounted for a further 16% of the total canopy cover.

Only *Fraxinus americana* was a dominant canopy species in both edge types. This species had its highest importance value in fencerows, though this was not significantly different from forest edges ($F = 0.320$, $DF = 1,46$, $p = 0.574$). *Ulmus* spp. and *Tilia americana* occurred as subdominant species in both forest edges and fencerows; their importance values in fencerows were not significantly different from those in forest edges (Table 6). Of the seven remaining tree species in common to both edge types, two had significantly greater importance in forest edges (*Acer saccharum*: $F = 64.97$, $p < 0.0001$; and *Ostrya virginiana*: $F = 52.54$, $p < 0.0001$; both with $DF = 1,46$), and one (*Crataegus* sp.) had significantly greater importance in fencerows ($F = 5.81$, $DF = 1,46$, $p = 0.02$).

In the shrub layer, both edge types had similar total mean percent cover, but forest edges accounted for 40% greater total frequency. Each edge type had a clearly dominant group of species.

Two of 27 species in forest edges appeared to dominate the shrub layer. Both *Acer saccharum* and *Fraxinus americana* had IV > 15%, and together accounted for 50% of the total cover and 25% of species frequency in the forest edge shrub layer (Table 7). Three species (*Viburnum lentago*, *Tilia americana*, *Prunus virginiana*), each with IV > 5%, comprised a subdominant group which together accounted for an additional 25% of the total cover and 25% of the total frequency. Eleven other species, each with IV > 1%, made up a further 20% of the total mean cover and nearly all of the remaining total frequency (ca. 50%).

Crataegus sp., *Prunus virginiana* and *Viburnum lentago*, each with IV > 15%, comprised the dominant group of the 22 species in the fencerow shrub layer and accounted for 56% of the total cover and 35% of the total frequency (Table 7). A subdominant quintet of species consisting of *Rubus idaeus*, *Vitis riparia*, *Cornus stolonifera*, *Parthenocissus vitacea* and *Ribes americanum* contributed an additional 27% to the total cover and 30% to total frequency. Each of these 5 species had IV > 5%. Eight other species with individual IV > 1% accounted for a further 14% of the total cover and 30% of the total frequency.

Half of the 16 species found in the shrub layer of both edge types showed statistically significant differences in cover between fencerows and forest edges (Table 7). Only *Prunus virginiana* and *Viburnum lentago* were dominant in both edge types, though both species had significantly greater cover in fencerows ($F = 11.59$, $p < 0.001$ and $F = 10.13$, $p < 0.002$ respectively; both with $DF = 1,80$). The remaining differences were accounted for by the greater cover of *Acer saccharum*, *Fraxinus americana* and *Tilia*

americana in the forest edge shrub layer, and greater cover of *Crataegus* sp. and *Rubus idaeus* in fencerows (Table 7).

Importance values for ranked species present in the ground vegetation (Table 8) follow similar trends in both edge types. As found in the shrub layer, total frequency was greatest in ground vegetation of forest edges, but total cover in fencerows exceeded that of forest edges by nearly 10%. Considering just herbaceous species increased the difference in total cover in favor of fencerows; however, forest edges retained the greater share of total frequency.

Acer saccharum seedlings dominated the 37 species present in forest edge ground vegetation (Table 8) with 34% of total cover and 15% total frequency ($IV = 25\%$). A subdominant group ($IV > 5\%$) consisting of *Fraxinus americana*, *Prunus virginiana*, *Viola* spp., and grasses (Gramineae) accounted for an additional 25% of both cover and frequency. Sixteen other species had $IV > 1\%$, providing further 40% cover. Herbaceous species alone accounted for over 30% of both total cover and frequency.

Grasses overwhelmed 37 other species in fencerows in terms of total cover (41%), though grasses had under 5% total frequency (Table 8). A subdominant group, including *Parthenocissus vitacea*, *Rubus idaeus* and *Prunus virginiana* accounted for 26% of the total ground cover and 10% of the total frequency. A second group of species provided an additional 25% cover and 12% total frequency. These species each had $IV > 2\%$ and included *Cornus stolonifera*, *Viola* spp., *Solidago* sp. and *Fragaria vesca*. Herbaceous species alone accounted for 14.5% of the total ground cover in fencerows, and more than 10% of the total frequency. *Viola* spp. were the most abundant herbaceous species ($IV = 2.31$).

Of nine species showing significant differences in cover between edge types, only

3 (grasses, *Rubus idaeus* and *Prunus virginiana*) were present as either dominant or subdominant species in both edge types (Table 8). This group all had significantly higher cover in fencerows ($F = 33.16$, $p < 0.0001$; $F = 10.99$, $p = 0.001$; and $F = 6.02$, $p = 0.02$ respectively, all with $DF = 1,80$). Of the remaining species, 4 had greater cover in forest edges (*Acer saccharum*, *Tilia americana*, *Fraxinus americana* and *Ulmus* spp.), while 2 had greater cover in fencerows (*Parthenocissus vitacea* and *Viburnum lentago*). Except for *Parthenocissus vitacea* and the grasses, all species showing significant differences in cover between edge types had greater frequency in forest edges (Table 8).

Grasses and woodland species were important components of ground vegetation. The contribution of grasses (Gramineae) to total cover was 58%, but grasses accounted for only 15% of the total frequency. Removing grasses from the totals equalized the contributions of both edge types to total cover to approximately 50%, yet the total frequency associated with each edge type remained essentially unchanged. Although total relative cover for typically woodland species was equivalent between edge types, these species occurred in forest edges with 50% greater frequency. Typically woodland species made up 55% of the total importance in forest edge ground flora, compared to fencerows where woodland species accounted for less than 7% importance.

Considering species continuity among all three strata, *Acer saccharum* maintained the highest importance values in forest edge canopies through to the ground vegetation. *Fraxinus americana* importance changed little among the forest edge strata, but the other canopy subdominants lost considerable importance in lower strata where *Tilia americana*, *Prunus virginiana* and *Viburnum lentago* gained importance. In fencerows, however, dominant canopy species were poorly represented in the ground vegetation. Importance of both *Fraxinus americana* and *Quercus alba* diminished in the fencerow shrub layer, though *Crataegus* sp. and *Viburnum lentago* retained importance in this layer. Here *Prunus*

virginiana, *Cornus stolonifera* and two woody vines, *Parthenocissus vitacea* and *Vitis riparia*, gained a prominence which persisted into the ground vegetation. With grasses removed from calculations of importance values, these last species accounted for 45% of total importance in fencerow ground vegetation. Neither value nor ranking of species importance in forest edges showed appreciable changes when grasses were excluded. So, grasses appear to have a much greater influence on ground vegetation abundance in fencerows than in forest edges.

The vertical distribution of foliage was considerably different in the two edge types. Ground vegetation contributed proportionally more to total mean cover in forest edges than in fencerows (Table 9), and this alone resulted in the greater difference in foliage height distribution (FHD) in fencerows ($FHD_{FE} = 10.12$; $FHD_{FR} = 17.60$). Foliage height distribution indices calculated with ground vegetation removed showed no appreciable difference between edge types for foliage distribution in these two strata.

Seed Dispersal

In all strata, the number of species with a given mode of seed dispersal was independent of edge type, but frequency of dispersal modes showed a highly significant association with edge type (Fisher's Exact Test, $p = 0.0001$). Considering just tree species ($dbh \geq 5$ cm), 83% of the dominant tree species in forest edges had abiotic seed dispersal, whereas 45% of dominant fencerow tree species had primarily biotically dispersed seeds (Figure 4a).

In the shrub layer of both edge types, biotic seed dispersal characterized more than 70% of all species with $IV > 1\%$. In considering all species present in each of shrub and ground vegetation, forest edge species had equal relative frequencies of abiotic and biotic seed dispersal, while fencerows retained a distinctly higher frequency of biotically

dispersed species (Figures 4b,c). Mode of seed dispersal mode was significantly correlated with edge type. In the two sub-canopy strata of fencerows particularly, biotically dispersed species had higher frequency and importance values in the shrub layer ($r = 0.340$, $p = 0.003$ and $r = 0.388$, $p = 0.001$ respectively) and higher frequency in ground vegetation ($r = 0.265$, $p = 0.004$).

Shade Tolerance

For all strata, the number of species in a given tolerance class was independent of edge type, but the frequency of these species was highly dependent upon edge type (Figure 5). Over 50% of trees in forest edges were tolerant species, and fewer than 20% were intolerant (Figure 5a). Although class differences were not as consistently pronounced in fencerows, this edge type had proportionately greater numbers of intolerant species in all strata. The relative frequency of tolerant species increased in lower strata to a high of 47% in the ground vegetation (Figures 5b,c).

Dominant forest edge canopy species were all either shade tolerant or moderately so. Fencerows had equal proportions of the three tolerance classes, including 6 intolerant species that either did not contribute appreciably to forest edge canopies (*Prunus serotina*, *Crataegus* sp. and *Betula papyrifera*, each with IV < 1%), or did not occur in forest edges at all (*Quercus alba*, *Pyrus malus* and *Populus tremuloides*). Shade tolerance characterized 67% of the dominant group of forest edge shrub layer species. Only 17% of the forest edge shrub layer species were intolerant of shade, while 40% of the dominant fencerow species in this stratum were shade intolerant.

Classification of Edge Types

Discriminant analyses of species abundance estimates distinguished between

fencerows and forest edges. The best discriminant function for canopy trees, illustrated by cluster analysis of discriminant scores (Figure 6), resulted when all measures of relative abundance were combined. This discriminant function consisted of 10 significant components, including 7 species. Only *Acer saccharum* contributed to the function for all three abundance parameters, *Carpinus carolinianus* for cover and basal area, and *Cornus stolonifera* for frequency and cover. *A. saccharum* and *C. carolinianus* were shown earlier to have canopy dominance in forest edges significantly greater than in fencerows, and the latter of these two species was not represented in fencerows at all. *C. stolonifera*, while occurring in both edge types, contributed little to either canopy (IV < 1%). The remaining species and abundance parameters contributing to the discriminant function included *Ostrya virginiana* (basal area), *Betula papyrifera* and *Tilia americana* (cover). Of these species, only *O. virginiana* had shown a significant difference in abundance between edge types.

Ranked discriminant scores for canopy trees showed the uppermost 20% to contain forest edge cases exclusively, so the small forest edge sample apparently had not affected the determination of a reliable function. The discriminant function performed well in jackknife tests, with each case left out of the analysis being correctly classified.

Discriminant functions for the lower two strata were generated using species cover data. One function clearly distinguished between shrub layer cover of the two edge types (Figure 7), and correctly classified any case left out of the analysis. The function for ground vegetation showed this layer to be nearly indistinguishable between fencerows and forest edges as depicted in the agglomeration dendrogram (Figure 8).

To determine whether some fencerows were more similar to forest edges than others, the discriminant function found for canopies (above) was used to examine the fencerow canopy vegetation separately. Cluster analysis isolated FR 1 and FR 2 from other

fencerows (figure 9a). A separate function was computed for the fencerow sample alone to clarify the basis for the distinction. Results from cluster analyses of discriminant scores for fencerow canopies suggested that FR 1 and FR 2 are most similar in canopy structure to forest edges, though the previous analysis of canopies by edge type provided only tenuous support for this. On the basis of the second discriminant function for canopies, FR 1 and FR 2 were indistinguishable from several others.

The best discriminant function generated from canopy abundance data for fencerows accounted for 50% of the variation among fencerows (eigenvalue = 9.276) and the proportion of discriminant scores not explained by group differences was low (Wilk's $\lambda = 0.012$). Between-group differences accounted for most of the total variance (Canonical correlation coefficient = 0.950).

Cluster analysis of fencerows with the new discriminant function revealed two main groups: one group composed of FR 4, the other of the remaining six fencerows (Figure 9b). Multiple comparisons between pairs of fencerows showed FR 4 to be significantly different from all other fencerows in the sample (Table 10). Of comparisons that did not include FR 4, several showed no significant differences. So not only was FR 4 the most different from the rest, the remaining fencerows were similar to at least one other of that group. The main group difference appeared to be the disproportionately high importance of *Tilia americana* in FR 4 ($F = 25.40$, $DF = 6,27$, $p < 0.0001$), plus the unique presence of *Populus tremuloides* and absence of *Acer* spp. there.

Summary

The evidence presented has shown that fencerow vegetation structure is distinct from that of forest edges. This difference comprised several components. Fencerows had greater diversity and evenness in canopy species abundance, greater diversity in the

vertical distribution of foliage, proportionally more grasses and fruit-bearing woody species, more frequent biotic seed dispersal and an even distribution of shade tolerance classes among fencerow species. Forest edges were dominated by a single canopy species, had lower strata had greater frequency of woodland species particularly, and all species generally. Also, forest edges were typified by abiotic seed dispersal and shade tolerant species in all strata.

Discussion

If fencerows effectively extend forest edges into the surrounding farmland, then the two edge types would be expected to have similar species composition. This study has examined species richness, diversity and similarity, as well as several measures of species abundance to determine whether fencerows are structural extensions of forest edges vegetation.

Species richness in tree, shrub and ground strata varied greatly within the sample of seven fencerows, but no difference in richness was found between these fencerows and forest edges occurring in the same agricultural landscape. Rarefaction curves showed that the expected richness remained similar between edge types when sample size was standardized. The fencerow sample then appears to be a representative one in that comparisons of actual species richness and expected richness from the rarefaction probability model yield the same results.

The absence of association between richness and edge type in all cases suggests that the structure and processes influencing richness operate similarly in fencerows and forest edges. But this would be remarkable considering the substantial differences in the spatial configuration of the two edge types which presumably affects accessibility of propagules (Kellman 1981). Fencerows are more susceptible and exposed to colonization from itinerant seed sources such as the adjacent fields, orchards and gardens, and fencerows may be subject to concentrated activity or processes due to reduced physical dimensions relative to forest edges.

The interaction among landscape elements, however, constrains species composition (Forman & Baudry 1984, Baudry 1988) such that a fencerow would be expected to have no more species than its nearest neighbor, and thus ultimately no more

than the nearest forest patch. Because no species are fencerow specialists, a reciprocal movement of plant species from fencerow to forest edges may be expected which would tend to increase differences in richness between the two edge types.

The total number of woodland species in each edge type was similar, but the greater proportion of woodland species unique to forest edges indicates a difference between fencerows and forest edges. A difference in habitat quality may be responsible, or the difference may arise from inaccessibility of fencerows for some biotic dispersal agents (e.g. ants) of woodland plant species. The ant-dispersed species (e.g. *Asarum canadense*, *Sanguinaria canadensis*) in fencerows that were spatially distant and disconnected from forest edges are likely relict populations from before extensive landscape fragmentation occurred.

In even small woodlots (≤ 5 ha), the forest edge profile intergrades with an adjacent field margin on one side to an interior area distinguished by transition to greater woody biomass on the other. This edge alone, and certainly the width of edge plus half the width of the forest interior, would be wider than the widest fencerow. In contrast, the opposite margins of a fencerow may coalesce at the fenceline without any appreciable change in vegetation at this centre point. In such a case, for any unit length there will be twice the effective edge in fencerows compared to forest edges. Assuming that the perimeter-to-area ratio of a given stand provides a relative measure of potential edge effect, fencerows would be expected to exhibit more pronounced differences in total species composition than were actually found.

Although fencerow configuration may induce a double edge effect, this would likely also mean that the influence of microclimate and anthropogenic activity would be doubled, that is if both sides of a fencerow experience similar disturbances from work in adjacent fields, such as drift from crop spray, fertilizers and soil-turning machinery operating close

to the outer limits of the fencerow. By limiting lateral spread of fencerow vegetation, secure habitat exists only at the point where woody vegetation has developed.

The increase in species richness found with increases in edge length was not different between edge types when shrub and ground layers were considered separately, yet pooled richness of both strata within each edge type was significantly affected by an interaction between edge length and edge type. The average number of species in forest edges was greater than in fencerows. If these results can be interpreted as an indication of structural development or age, as shown for European hedgerows, then fencerow structural development clearly lags behind that of forest edges. Such a conclusion is reasonable in that the sampled forest edges were of remnant forests, whereas the fencerows are relatively recent landscape elements.

It becomes difficult to extend the analogy of European hedgerows to North American fencerows when the high variance in richness of fencerows is acknowledged. The greater age and relatively more stable landscape context of hedgerows contrasts with the younger fencerows present in landscapes that continue to change, often rapidly, at local and regional scales. This context would likely preclude attainment by fencerows of a stable structure as hedgerows have done, and so the corridor value of fencerows to plants would not be generally supported.

Diversity indices all point to differences in the distribution of relative abundance among canopy species of the two edge types. Specific abundance differences arose primarily due to dominance of a single species, *Acer saccharum*, in forest edges relative to a more equitable sharing of dominance among several species in fencerows. Diversity measures showed edge types to be virtually indistinct for all relative abundance parameters. On the other hand, considerable differences occurred in the role of woody vegetation, mainly in the canopy.

Several species figured prominently in fencerow canopies, whereas forest edges were dominated by a single species. Although the major canopy trees of fencerows also contributed importantly to forest edges canopies, *Acer saccharum* did not even achieve a subdominant role in any of the fencerows studied. In fencerows, the dominance of *Fraxinus americana* and *Quercus alba* can be related to a successional shift associated with the decline of *Ulmus* spp. through disease. *Ulmus* spp. contributed relatively little to fencerow canopies, but many standing dead trees of this species were encountered in fencerows. The opening of the canopy through the death of *Ulmus* spp. provided opportunities for *Fraxinus americana* and *Quercus alba* to gain dominance.

In fencerows, the frequency of occurrences of woodland plants was affected by both fencerow width and distance from the nearest forest, but the relationship between richness and either width or distance was not clear. This differs from previous studies (Helliwell 1975, Baudry 1985, Baudry 1988) which have found increases in woodland species richness with increases in corridor width. Although the number and frequency of woodland species in fencerows south of Ottawa were affected by fencerow width, the expected linear relationship between species number and width was not found. The lack of association in the case of richness may simply reflect that few woodland species inhabit these fencerows anyway, as borne out by the species survey. One possible factor then is a difference in fencerow structure relative to forest edges, the most likely source of propagules.

If frequency of woodland species is an adequate index of habitat suitability, my results suggest that width can significantly influence habitat quality, but as fencerows of intermediate width had the greatest richness and frequency, width alone cannot determine habitat quality for woodland species. Fencerow width is determined by factors such as presence of a fence, fence type and age, farming practices in adjacent fields, and solar

aspect of fencerow axis. Although fencerow vegetation may arise and develop at field margins through years of neglect, activities such as field cultivation, ploughing, crop spraying, seeding and harvesting, especially with large machinery, impose outer limits upon fencerows, at least at ground level. Field rotation would alleviate such constraining disturbance, temporarily allowing vegetation to begin to merge with the fallowing field, thereby adding to fencerow width. Vertical growth remains unrestricted by farming, though saplings and shrubs emerging at fencerow margins would have limited opportunity for horizontal extension of roots and branches. Canopy trees can extend their upper limbs without constraint, though close ploughing could damage roots extending beyond the field margin. The factors limiting width and the structural development of fencerows influence the habitat quality and corridor potential there.

Associated with width are conditions related to light, water and nutrient resources. Relative to forest edges, wider fencerows would be expected to have more closely matching micro- and macro-environmental conditions than narrower fencerows. Generally, the tallest fencerow trees occurred in the widest fencerows. Assuming for illustration a constant solar angle, then the distance light may penetrate into a stand would be determined by tree height. Theoretically, taller trees would allow light to reach in greater distances. But the shrub layer was shown to provide dense cover and thus would block much of this light, though sunflecks may compensate for this somewhat. The resulting conditions may approach the mesic habitat qualities of woodland. Assuming a means exists to reach such habitats, woodland plants could be expected to be present. These presences would be influenced as well by factors such as distance from source patches to fencerows and seed dispersal mode.

The significant effect that distance from nearest woodland had on the richness and frequency of woodland species in fencerows was not the expected linear relationship.

Again, from Baudry's (1985, 1988) work, more species were expected in attached fencerows, fewer in fencerows more distant from forest. Forests connected directly to fencerows would be expected to act more effectively as potential seed sources than those lacking such connection. These fencerows would then be expected to contain more species or greater populations of woodland species than fencerows further from forest. Attached fencerows here did have the greatest richness and frequency of woodland species, but fencerows in the most distant class had appreciably greater richness and frequency than fencerows at intermediate distances from forest. A sample of more fencerows, and several distance classes, may resolve the apparent inconsistency with previous findings.

Earlier studies of farmland corridors had geographical, cultural and historical contexts that differed from my study, except for Baudry's (1988) work in New Jersey farmland. British hedgerows and *bocages* in France have existed several hundred years longer than the oldest North American fencerow, so there has been more time for woodland species to colonize farmland corridors in Europe. Also, European hedgerows are generally human contrivances built of single species and subsequently managed intensively to optimize their farmland functions. As such, species composition and overall vegetation structure would be expected to be more homogeneous among hedgerows than found among the spontaneously generated and relatively unmanaged fencerows south of Ottawa.

Species abundances describe the particular contribution of dominant species to the structure of each type. Here, *Acer saccharum* dominated all three strata in forest edges, whereas fencerow dominants varied among strata and generally included a group of species rather than a single species. An exception occurred in fencerow ground vegetation where grasses dominated, and likely precluded other species. This was reflected in diversity measures, particularly the greater diversity in the vertical distribution of foliage in fencerows, but not to the extent that forest edges exhibited in canopy diversity.

Whitney and Somerlot (1985) also found that the species dominant in Ohio forest canopies occurred rarely or only sporadically in fencerows. Five tree species reported in the Ohio study (Whitney & Somerlot 1985) were also present in the Ottawa region study. Stem frequencies (by size class) were significantly different between fencerows and forest in one or both of the Ohio studies for each species. A similar comparison using my own data showed stem frequencies of *Prunus serotina* and *Ulmus* spp. to not be different in the two edge types (Table 11).

Comparison of the Ohio fencerows with Ottawa fencerows showed significant differences for stem frequencies of *Prunus serotina*, *Fraxinus americana* and *Quercus alba*. The first was considerably more abundant in Ohio fencerows, whereas the latter two were more abundant in Ottawa fencerows, reflecting regional differences in climate and soils. When all *Quercus* spp. enumerated in Ohio fencerows were included in the comparison with *Q. alba* in Ottawa fencerows, no significant difference in stem frequency was found.

Seed Dispersal and Shade Tolerance

The greater frequency of biotically dispersed species associated with fencerows compares favorably with the findings of both Brewer *et al.* (1969) for fencerow woody vegetation in Kalamazoo, Michigan, and results reported by Somerlot (1982) and Whitney and Somerlot (1985) for fencerows and forests in Wayne County, Ohio. Somerlot (1982) also found significantly greater frequency of wind-dispersed species occurring in forest sites compared to fencerows. However, the distribution of dispersal modes differed significantly between our fencerow samples (G-test 9.34, DF = 1, $p = 0.003$). Both the Mid-west U.S. studies reported *Prunus serotina* as the dominant fencerow species, whereas this species occurred infrequently in the fencerows south of Ottawa where canopy dominance was shared among *Fraxinus americana*, *Crataegus* sp., *Viburnum*

lentago and *Quercus alba*.

The greater frequency of shade tolerant species in forest edges and the greater frequency of intolerant species in fencerows shown here is also comparable to that reported by Somerlot (1982), with the exception of lower relative frequency of intolerant species found in the Ottawa region fencerows. The frequency of shade tolerance classes in the Ohio fencerow study was significantly different from my own (G-test 168.8, DF = 2, $p = 0.0001$). Fencerow species listed by Brewer *et al.* (1969) were also predominantly shade intolerant. The characterization of species found most abundant in Ohio fencerows by Whitney and Somerlot (1985) as species noted for their "mobility and aggressive nature" applies similarly to the Ottawa fencerows.

The discriminant functions computed for vegetation abundance provide a first approximation toward structural classification of fencerows. That a function discriminates clearly between forest edges and fencerows shows that the two edge types have significant differences in vegetation composition and structure. Beyond this, the same function distinguished between two groups of fencerows. FR 1 and FR 2, separated from other fencerows, had greater affinity to forest edges in terms of canopy species abundance.

The distinguishing features revealed in a separate analysis of fencerows were comparable to those suggested by the previous analysis of both edge types--disproportionate abundance of one or more particular species. Although the key species were different for the two functions, basal area was the common discriminating abundance parameter. Within the fencerow sample, isolation of FR 4 from all other fencerows indicates significant differences in the canopy structure of this site. As canopy structure in fencerows has arisen within a context of generally similar disturbance, namely agricultural activity, the difference noted above is inferred to be a result of initial conditions

and the context particular to FR 4, such as previous effects of livestock grazing which now manifest themselves in altered fencerow structure.

In conclusion, the vegetation structure of farmland fencerows has been shown to be substantially different from that of forest edges. At the landscape scale, both of these edge types occurred within the same agricultural context and have been subject to generally similar influences, yet the differences brought out indicate that fencerow structure arises with, or responds to, influences at the scale of individual sites. Comparisons with published data on North American fencerows do allow some generalizations about fencerow structure, particularly that species composition is predominated by biotically dispersed species with a range of shade tolerances, and that fencerow width and distance from source patches have some influence on the presence of woodland species in fencerows.

Species richness varied more among fencerows than between fencerows and a small sample of forest edges, except for the greater number of woodland species present in forest edges. The greater structural diversity in fencerow canopies, and the dominance of fruit-bearing shrubs are important in maintaining faunal diversity and abundance in fragmented landscapes, but these attributes appear not to confer any advantages to the movement of plants, particularly woodland species, in the same landscape. Fencerow vegetation, then, does not effectively extend forest patches into the surrounding landscape.

Architecture of Fencerows and Forest Edges

Introduction

Some fencerow functions have had more interest than others from the economic view of how they may benefit crop production. It is common knowledge among farmers that fencerows influence microclimate, evapotranspiration, water and nutrient retention, and ultimately productivity in adjacent crop fields. On the other hand, fencerows may harbor crop pests or weedy species that can invade crops from field margins. Large scale farming that requires fencerow removal to achieve mechanized efficiency may compensate for the loss of some fencerow benefits simply through the increased scale of operations.

Contemporary ecologists are beginning to take a broader, more biocentric view of corridors such as fencerows, particularly their potential to act as connecting elements for organisms trying to move through otherwise perilous landscape. What structural form a fencerow must have to be an effective corridor remains a mystery, though key factors identified in research of European hedges, such as width, density, vegetation cover, profile, age, and connectedness, are likely also important here. Supplemental to this is a wealth of information on the form and function of forest edges to which fencerows have at least an apparent structural affinity.

Speculations on the ecological function of farmland fencerows in North America (e.g. Forman & Godron 1981, Forman & Baudry 1984) rest on little direct structural information. Generally, the ecological importance ascribed to fencerows has been extrapolated from general studies of the character and effects of European hedgerows (Moore *et al.* 1967, Hooper 1970, Pollard *et al.* 1974, Dowdeswell 1987) and *bocages*

(Baudry & Burel 1983, Baudry 1985), patchwork agricultural landscapes with networks of hedges ramifying throughout. More detailed research from Europe has shown that hedgerow structure influences the distribution and abundance of woodland plants (Helliwell 1975, Peterken & Game 1981), birds (Arnold 1983), snails (Cameron *et al.* 1980), and arthropods (Nazzi *et al.* 1989). Recent studies in North America, with the notable exception of Somerlot (1982) and Somerlot & Whitney (1985), have focused on relatively more contrived structures such as shelterbelts (Yahner 1982a,b; Johnson & Beck 1988) and their influence on animal movements.

A fundamental problem is that European hedgerows are invariably anthropogenic and heavily managed (planted, pruned, coppiced) structures, whereas North American fencerows, particularly in the industrial mid-west, have arisen spontaneously at untended field margins. Differences in origin and management give rise to differences in the architectural form of individual elements, such as branching pattern in trees and shrubs, as well as to the composite structure, such as foliage density.

That fencerows resemble forest edges in agricultural landscapes is more than just a comment on appearance, for woody species most often seen in fencerows are also present in forest edges (Baudry & Forman 1984). And because both elements have edges exposed to farming activities at field margins, fencerows and forest edges may endure similar influences and constraints on structural development. If the flux of organisms across fragmented farmland is channelled through fencerows, it may be because fencerows have a structural affinity to forest edges which have been recognized as zones of movement for many organisms (Yahner 1988), including predators (Andren & Angelstam 1988), or it may simply be because there are no other paths between target patches. For organisms of limited mobility, particularly plants, it is interesting to consider whether fencerow structure provides habitat capable of supporting viable populations. Comparison

of fencerow structure to that of forest edges within the same landscape context would allow some inference about fencerow habitat quality.

This chapter presents research on the architecture of fencerows present in farmland south of Ottawa, Ontario. My aim was to determine whether fencerow architecture was the same as that of forest edges. If no significant difference was found, it could be inferred that fencerows extend forest edges structurally into the surrounding fields and thus could act as effective movement corridors between isolated patches. No difference in architecture would also suggest the potential for comparable habitat quality in fencerows and forest edges, important for organisms of limited mobility such as plants.

Methods

This investigation was carried out in farmland 30 km south of Ottawa, Ontario during the summer of 1989. Fencerow architecture was characterized using a sample of 8 fencerows. As well, comparison between these fencerows and a sample of 3 forest edges provided the basis for determining whether fencerows have structure similar enough to forest edges to be considered extensions of forest edges, and thus effective corridors for woodland species. Transects, initiated at 10 m intervals along the field margin, were sampled every meter across the edge. Transects spanned the entire width of fencerows, whereas forest edge transects terminated at 15 m toward forest interiors.

Three components of architecture were considered: 1) horizontal foliage density, 2) presence of elements contributing to structure, and 3) the relative contribution to structure of selected elements. Each component was used in testing the main hypothesis that fencerow architecture was not significantly different from that of forest edges. The

fencerow sample was also examined independently to assess the degree of structural variation occurring among fencerows.

Horizontal foliage density, measured at 0.5 m height intervals (from 0-2 m), was taken as the percent of an extendable graduated rod obscured by foliage when viewed from 3 m distance, parallel to the field margin. The rod (or "Nudstik", as it was an adaptation of Nudd's (1977) foliage density board) was marked along its length with alternating red and white bands, 10 cm long, corresponding to 20 percent of each 0.5 m segment. Half-meter intervals were delineated by a 1 cm black stripe. Percent foliage density for a given 0.5 m height interval was estimated by sighting the rod perpendicular to the central band of that interval. This protocol precluded standardized estimates above 2 m, but presence of foliage density > 20% in the 2-2.5 m height interval was noted.

Mean foliage density was estimated from transect means computed from raw data. Data transformed to a log scale, to stabilize variance, were used in statistical tests of the hypothesis that foliage density in the two edge types was not significantly different. One-way ANOVA (foliage density at height h by edge type) explored foliage density profiles incrementally. As horizontal foliage density was not expected to be independent of height, multivariate analyses examined foliage profiles as coherent units. MANOVA tested the hypothesis, and discriminant analysis determined the basis of any significant difference that was evident.

The effect of edge type on foliage profile diversity (Ambuel & Temple 1983) was tested using frequencies for each of 32 possible foliage profiles (*i.e.* all unique permutations of foliage presence/absence at the 5 height intervals). Horizontal foliage densities $\geq 20\%$ were taken to indicate foliage presence in each of the five height intervals. The diversity (H' : Equation 5, Chapter I) of foliage profiles was calculated using the proportion which a single profile i contributed to the total number of profiles present

within each edge type. The diversity measures were then compared in t-tests (using variance estimates calculated as given in Equation 6, Chapter I).

The architectural elements censused included trees, shrubs, vines, coarse woody debris, grasses, forbs, moss, rock and litter. Presence or absence was noted at 5 height intervals: 0-0.5 m, 0.5-1.5, 1.5-3.5, 3.5-7, and greater than 7 m. In both fencerows and forest edges, presence and type of fences were also noted. Frequency of each element was taken as the number of sample units in which a given element was present. Mean frequencies were then calculated for each transect and used to test the hypothesis that no difference in the relative frequency of architectural elements occurs between fencerows and forest edges. Due to the large number of independent tests on variables that were not clearly independent of each other, the accepted significance level was adjusted to $p \leq 0.002$ (i.e. $0.05/24$ tests).

Parametric tests for significant effects of edge type used log-transformed mean frequencies for each architectural element. MANOVA tested the effect of edge type on the combined presence of all architectural elements at all heights simultaneously. Discriminant analysis provided a multivariate means of identifying key variables contributing significantly to differences between edge types. The univariate test results helped in interpreting the results of multivariate tests.

The relative contribution of a given architectural element was estimated with an ordinal classification for size and density. The elements included tree stem diameter (0, 5- <10, 10-30, >30 cm dbh), shrub density (0, <5, 5-10, >10), gap size (0, <0.5, 0.5-1, >1 m dia.), rock size (0, <20, 20-50, >50 cm max. dimension), and the size (0, 2.5- <5 cm, 5-20, >20 cm dia.), position (<30°, 30-60°, >60° from vertical), and condition (punky = 1, soft = 2, sound = 3, based on depth of penetration of a 5 mm dia. steel rod) of coarse woody debris.

For testing the effect of edge type on the relative contribution of architectural elements, data for each element were summarized as mean class frequencies, calculated as:

$$\text{Mean Class Frequency} = \sum \frac{x_i f_i}{n} \quad (10)$$

where x is the ordinal class value, f_i is the frequency of element i , and n is the total frequency of i in all classes.

For each of the three architectural components described above, a measure of habitat heterogeneity (HH) was calculated (after Freemark 1983). HH is an information-theoretic index derived from Shannon's diversity index:

$$HH = - \sum_{i=1}^r \sum_{j=1}^c x_{ij} \ln (x_{ij} / \bar{x}_i) \quad (11)$$

where r is the total number of variables used to characterize c samples, x_{ij} is an observation on the i^{th} variable of the j^{th} sample, $\bar{x}_i$ is the mean for variable i , and $\ln$ specifies the natural logarithm. Data were standardized by proportioning each variable by its total in each edge type. Separate calculations of HH were made for each element. These HH indices were then summed to obtain a measure of overall habitat heterogeneity.

Results

Horizontal Foliage Density

Fencerows had significantly greater horizontal foliage density than forest edges at each height sampled, except the 1-1.5 m interval (Table 12a). Foliage density profiles were similar, but edge type significantly affected foliage density ($F = 383.42$, $DF (5,49)$, $p < 0.0001$), particularly above 2 m and below 0.5 m (Table 12b).

The discriminant function for edge types generated from foliage density values (eigenvalue = 0.828 for 100% of variance; Wilk's $\lambda = 0.547$; canonical correlation between discriminant scores and edge type, coefficient = 0.673) performed moderately well, wrongly classifying about 10% of the cases, all from FE 2. This function correlated mainly with foliage density above 2 m and below 0.5 m ($r^2 > 0.440$ for each).

Among fencerows, mean foliage density above 0.5 m was appreciably lower in FR 4 than all other fencerows, but FR 2 and FR 3 had the highest values above 1.0 m (Appendix 3a). The foliage density in any of the 5 height intervals was significantly affected by the fencerow site within which it occurred (Appendix 3b). Foliage density profiles (Figure 10) varied considerably, and foliage density was greatly affected by site ($F = 5.074$, $DF = 35,160$, $p = 0.0001$). The primary discriminant function (eigenvalue = 7.573 accounting for 67% of variance; Wilk's $\lambda = 0.013$, canonical correlation coefficient = 0.9399) generated was correlated with foliage density above 2 m ($r^2 = -0.622$) and reliably classified cases into two main fencerow groups with 2.5% error. A second function, correlated with foliage density at 0-0.5 m ($r^2 = 0.319$), provided only marginal improvement.

As the discriminant function relied heavily on qualitative foliage differences above 2 m, fencerows grouped by discriminant scores did not match the density profiles in

Figure 10. So the same analyses were performed using only quantitative data of foliage density from 0-2 m. Results from MANOVA were essentially the same as before ($F = 4.301$, $DF = 28,128$, $p = 0.001$), but the discriminant function accounted for less of the variation among fencerows (eigenvalue = 2.585). The variable most closely associated with the discriminant function became foliage density at the 0-0.5 m interval ($r^2 = 0.459$), followed by foliage density at 1.5-2 m ($r^2 = 0.422$). This time fencerows grouped by discriminant scores more closely matched the differences illustrated in the foliage profiles.

The presence and absence of foliage ($\geq 20\%$ horizontal density) in 5 height intervals was significantly affected by edge type (foliage profile diversity, $t = 2.299$, $DF = 388$, $p = 0.022$), although the number of different profiles was similarly high in fencerows (22) and forest edges (25). Fifty percent of the fencerow sample had a single foliage profile--foliage in all five height intervals. Thirty percent of the forest edge sample also had this profile, but the remaining 70% was relatively evenly spread among 24 other profiles.

Habitat heterogeneity indices (HH) for horizontal foliage density by height interval were not appreciably different between the two edge types except above 2 m (Table 13), but total HH showed forest edges to have greater heterogeneity in the horizontal distribution of foliage than fencerows ($HH_{fe} = 0.1151$; $HH_{fr} = 0.0752$).

Presence of Architectural Elements

After log-transformation, transect mean frequencies for all variables had approximately normal distributions. The mean frequency of vines (< 0.5 m) and grasses (0.5-1.5 m) were significantly higher in fencerows (Table 14). Other differences between fencerows and forest edges in the mean frequencies of the nine architectural elements

sampled, although not significant, may be important in contribution to composite structure. These differences included higher vine frequency in fencerows at all heights and higher tree stem and branch frequency in forest edges above 7 m.

Mean frequencies of architectural elements were independent of each other (as shown in a linear half-normal plot), so it was appropriate to look for an multivariate effect of edge type. MANOVA results showed that edge type controlled the combination of frequencies of architectural elements at all heights ($F = 648.68$, $DF = 24,31$, $p = 0.0001$). This effect of edge type was most evident in the significantly greater frequency of vines (≤ 0.5 m) and grasses (0.5-1.5 m) in fencerows (Table 14).

Architectural diversity ($H'_{FE} = 1.93$; $H'_{FR} = 2.15$) was not different between edge types ($t = 0.677$, $DF = 347$, $p = 0.499$), though the descriptive index for habitat heterogeneity (HH) showed notable differences between fencerows and forest edges (Tables 15a,b). For individual architectural elements (Table 15a), the largest differences between edge types were the more heterogeneous vertical distribution of vines and grasses in forest edges and the greater heterogeneity of coarse woody debris and mosses in forest edges. Considering the combination of elements present within each height interval (Table 15b), HH was greater in forest edges only below 1.5 m. Above 3.5 m, fencerow HH was greater than that of forest edges. Total HH showed no appreciable difference between edge types, either in combinations of heights or in combinations of elements.

Differences among fencerow architecture were brought out in the high variation in mean frequencies of most architectural elements (Appendix 4a). Only ground litter, mosses, trees (< 3.5 m) and shrubs (> 7 m) had relatively equivalent frequencies among the eight fencerows. Fencerow site had a significant effect on the combination of architectural elements (MANOVA $F = 3.301$, $DF = 168,112$, $p < 0.0001$). The elements most affected by differences among fencerows were the frequency of trees above 7 m,

shrubs (1.5-7 m), vines (0.5-7 m), grasses (< 1.5 m), coarse woody debris, mosses and rock (< 0.5 m; Appendix 4b).

The best discriminant function for the fencerow sample (eigenvalue = 9.168 accounting for 53.6% of variance, canonical correlation coefficient = 0.950, Wilk's λ = 0.0016) was correlated with the amount of ground covered by rock (r^2 = 0.728, p < 0.01). With rock removed from the analysis, vines (0.5-1.5 m) became the element most correlated (r^2 = 0.894, p < 0.01) with the discriminant function (eigenvalue = 3.975 accounting for 47.3% of the variance, canonical correlation coefficient = 0.894, Wilk's λ = 0.016).

Relative Contribution to Structure by Selected Elements

Untransformed data for all variables of this architectural component conformed to normal distributions. Mean frequencies of elements in each class described differences between edge types. Larger size rocks occurred more frequently in fencerows; smaller rocks were more frequent in forest edges. Shrub density greater than 10 stems per m^2 was more frequent in fencerows; shrub density between 5-10 stems per m^2 was more frequent in forest edges. Sub-canopy gaps greater than 1 m dia. occurred nearly twice as frequently in forest edges as in fencerows, whereas frequency of gaps under 0.5 m in fencerows was twice that in forest edges. Coarse woody debris on or near the ground occurred more frequently in fencerows.

Tests for an effect of edge type used estimates of mean class frequency (Table 16). The contribution of individual architectural elements to the structure of forest edges and fencerows showed no differences except for smaller sub-canopy gap size in fencerows (F = 8.708, DF = 1,55, p = 0.005).

Independence among mean class frequencies (shown by a linear half-normal plot

of the variables) allowed multivariate tests for an effect of edge type. Edge type determined the combination of mean class frequencies for all elements ($F = 71.78$, $DF = 7,49$, $p = 0.0001$). Differences were accounted for mainly by greater sub-canopy gap size and shrub density in the forest edge sample. However, the discriminant function did not clearly distinguish between edge types (eigenvalue = 0.327, Wilk's $\lambda = 0.754$).

Differences among fencerow sites affected the overall contribution of architectural elements (MANOVA $F = 4.429$, $DF = 49,238$, $p < 0.0001$). Only shrub stem density and sub-canopy gap size, the two variables shown above to be most affected by edge type, were unaffected by fencerow site (Appendix 5a,b). The best discriminant function (eigenvalue = 8.843, accounting for 60.05% of total variance, canonical correlation coefficient = 0.948, Wilk's $\lambda = 0.0052$) generated from the combination of mean class frequencies for all elements was correlated most strongly with rock size. Discriminant scores for this function showed two main groups of fencerows--one with larger rocks, the other with smaller or no rocks.

Habitat heterogeneity (HH) for the contribution of each individual element was greater in fencerows, except for tree diameter which produced a greater HH in forest edges (Table 17). Total HH in fencerows and forest edges ($HH_{FE} = 0.995$; $HH_{FR} = 1.092$) were not appreciably different, and no difference between edge types was evident in the diversity of this architectural component ($t = 0.687$, $DF = 17$, $p = 0.501$).

Finally, the sum of the three habitat heterogeneity indices (Total HH) for each class of data showed forest edges to have a more heterogeneous composite structure than fencerows (Total $HH_{FE} = 9.121$; Total $HH_{FR} = 7.877$).

Summary

Horizontal foliage density was greater in fencerows below 1 m and above 1.5 m from ground level; foliage profile diversity was equal in the two edge types, though foliage density distribution was less even in forest edges. Tree frequency was greater in forest edges above 3.5 m, but in fencerows at 0.5-1.5 m. Shrubs, coarse woody debris, and mosses were more frequent in forest edges below 1.5 m, while grasses and forbs were more frequent in fencerows within this height range. Rock and litter cover was also greater in forest edges. Frequency of vines at all heights was greater in fencerows. Fewer sub-canopy gaps occurred in fencerows, while tree stem diameter; shrub density; size, position and condition of coarse woody debris, and rock size were not different between the two edge types. Multivariate comparisons showed fencerow structure to be significantly different from that of forest edges which overall had greater total habitat heterogeneity than fencerows.

Discussion

At least some of the architectural elements were sufficiently different between edge types to suggest that the overall structure of fencerows and forest edges to which they contribute are not the same. Many individual elements of the three architectural components were not statistically different between edge types, but the significant difference in composite structure found in multivariate tests have led to rejection of the hypothesis that fencerow architecture is not different from that of forest edges.

Differences found between edge types in horizontal foliage density were the same as those found within the fencerow sample--foliage density was least different at intermediate heights (0.5-2 m) among fencerows, as well as between edge types. The high variability in foliage density within the fencerow sample above 2 m and below 0.5 m did not mask the significant differences between edge types at these heights. Edge types were consistently separated on discriminant scores, but individual fencerows were not. On this basis, the difference noted in foliage density between forest edges and fencerows was accepted as an effect of edge type.

The architectural components contribution to the differences between edge types varied with height. Dense grasses at field margins gave the greater foliage density in fencerows below 0.5 m, while vines, present from ground level to 7 m, contributed greatly to total foliage density in fencerows. Both of these forms of vegetation occurred with considerably less frequency in forest edges. Greater tree presence above 7 m and larger understory gaps in forest edges complemented the differences in foliage density. Shrub density was considered not different between edge types.

Site topography and canopy height are factors likely responsible for the observed differences. A cultural influence was evident in that the remnant forest patches studied all

marked an upland shift in elevation relative to farm fields, whereas all fencerows were level with adjacent fields. Differences in local drainage therefore would be expected, with more lateral drainage occurring at forest edges. This, coupled with water uptake by canopy tree roots extending beyond the field margin and the longer (temporal and spatial) shadow thrown by the taller and broader forest canopy (Bates 1937, Steavenson *et al.* 1943, Harmon 1948), would make the outer margin of the forest edge a difficult place for many grasses.

Fencerow canopies, generally less than 20 m high and only one or two tree crowns in width, would not shade the field margin to the same extent as a forest edge. The lower grade would lessen lateral drainage, thus roots would tend to be directed down, not out. Farming activity adjacent to fencerows would be expected to occur more frequently, and possibly with greater intensity, than at edges of farm woodlots. The spatial configuration of farmland mosaics generally consists of fencerows coincident with linear flows of farm traffic important to the economic viability of the farm, whereas forest patches more likely occur at the terminus or periphery of such traffic.

The greater diversity in foliage profiles of forest edges may equate to more distinct habitats for certain bird species (MacArthur & MacArthur 1961, Arnold 1983), small mammals (Yahner 1983), or invertebrates such as spiders (Hatley & MacMahon 1980, Robinson 1981). Composite structural complexity may also invoke habitat heterogeneity, as well as influence foraging behavior in birds and small mammals (Wegner & Merriam 1979, Landres & MacMahon 1983, Yahner 1983), and in their predators (Andren & Angelstam 1988). The index of total habitat heterogeneity (Freemark 1983, Freemark & Merriam 1986) for forest edges was greater than that for fencerows, though neither of these edge types could be considered structurally homogeneous.

For plants, the greater foliage density of grasses at ground level in field margins

would prevent many species from colonizing the outer fencerow. However, interior herbs such as *Asarum canadense*, *Erythronium americanum* or *Sanguinaria canadensis*, growing closer to the centre of the fencerow would be protected from external climatic (strong winds, heavy precipitation) or anthropogenic (drift from crop spraying, livestock grazing, trampling) disturbances. The greater foliage density above 1.5 m in fencerows, due to shrubs and vines, may approximate forest edge canopy cover and thereby create quasi-mesic conditions within the fencerow interior.

The larger gaps in the forest edge understory occurred away from the field margin towards the forest interior where shrub and sapling growth is suppressed by the shady conditions. Such gaps would allow sunlight penetrating the canopy to reach the forest floor. The narrowness of fencerows, as well as the growth form of trees in such open situations (Brunig 1976, Pickett & Kempf 1980), do not shade the mid-section of the structure adequately to suppress shrub growth entirely, thus gaps were generally smaller and closer to the ground. This would tend to reduce habitat availability for low-growing plants (Howe 1990) near the fencerow centre.

Organic substrate for decomposers and soil development was present equally in both edge types, but not of the same quality. Large diameter snags and fallen logs occurring in fencerows appeared to impose upon structure spatially, yet no aspect of coarse woody debris differed between edge types. Epiphytes and a wide range of heterotrophs would be expected to get by quite nicely in fencerows if all else is assumed equal. Woody matter and leaf litter covered nearly equal surface area in each edge type, but litter was noticeably deeper in the forest edge, as well as more compacted and wetter at the soil surface.

Things happen differently in these two edge types apparently due to differences in structural scale. The absence of a difference between edge types in the condition of coarse

woody debris showed that the organisms and processes required for decomposition of woody material are present in both fencerows and forest edges. However, it was not determined whether the rate of decomposition in both edge types was the same.

Many studies have examined the effect that composite habitat structure has on the kinds and abundance of organisms. The fencerows sampled have been shown to have an architectural form different from that of forest edges within the same farmland. These fencerows, although chosen for their apparent structural similarity, have been shown to have among them distinctly different architectural compositions.

Before concluding that it makes no difference what structure a corridor requires to be effective for plant movement, complementary investigations of fencerow habitat quality were undertaken. Assuming all fencerows have structure different from forest edges, then it remains to be determined if some other aspect of fencerow structure, such as vegetation composition, is similar enough to the forest edge to support woodland species.

III

Measuring Corridor Effectiveness with Phytometers

Introduction

Previous vegetation surveys of agricultural landscapes (Baudry 1988, Baudry & Forman 1983, Middleton & Merriam 1983, Wegner & Merriam 1979) and personal reconnaissance of farmland fencerows in 1988 have found herbaceous species typical of mesic woodland ground flora growing in fencerows. Species observed include *Trillium canadense*, *Asarum canadense*, *Sanguinaria canadensis* and *Erythronium americanum*. These species primarily reproduce vegetatively by clonal growth of underground storage organs so, as may be expected, the observed populations had relatively contagious distributions. That woodland plants can grow in such relatively exposed "edge" habitats suggests that fencerows may be acting as vital demographic and genetic links among populations occurring in the remnant wooded patches of fragmented landscapes.

These observations led to an investigation of the habitat potential of fencerows for woodland herbs existing in forest patches. An experiment was designed to determine whether plants in fencerows would respond similarly to those in forest edges. Plant response was used as an indicator of habitat quality in the two edge types. My rationale was that if fencerow habitat quality, measured by the response of phytometers, showed no significant differences from that of forest edges, then fencerows could be inferred to be effective corridors for plant movement in fragmented landscapes.

Clements (1920, 1928, Clements & Goldsmith 1924) called such experimental plantings "phytometers" as they were meant to act as instruments which would measure the environmental conditions of interest at a given site with their responses. More recently,

Gaudet and Keddy (1988) have incorporated this experimental approach in studies of plant competition for above and below ground resources.

My experiment allowed comparison of the overall growth response of transplants in fencerows and forest edges, as well as response along a hypothetical environmental gradient extending from field margin towards interior. Such comparisons were expected to provide insight into the critical factors influencing the distribution of plants in fencerows. The main questions relevant to this approach are:

1) Does growth response in fencerows suggest suitable habitat conditions for supporting continued populations, or facilitating establishment of new ones? Assuming that woodland plants are capable of reaching fencerows by either vegetative extension or seed dispersal, will habitat quality allow the establishment and survival of viable populations (*sensu* Soulé 1987).

2) Does growth response depict a gradient in habitat conditions from field margin towards interior? Wales (1972), Bruner (1977), Ranney (1977), and others (*e.g.* Levenson 1981), have found distinct differences between the vegetation structure of forest edges and forest interiors. The width of forest edge alone, generally cited as *ca.* 15 m, is greater than the entire width of most farmland fencerows. Assuming at first that fencerows are edges without interiors, then no significant differences in phytometer growth response would be expected across the fencerow width. However, fencerow structure is not homogenous across its width, so an equally tenable assumption is that a zone, comparable to that of the forest edge-interior interface, results at the fencerow centre.

I addressed the question of habitat suitability (#1) by comparing phytometer response to treatments of edge type. The general hypothesis tested was that, if fencerows (FR) are structural extensions or analogs of forest edges (FE), then the response of the phytometer species transplanted to fencerows would not be significantly different from

response in forest edges. Statistical differences in response between fencerows and forest edges, or evidence for dependence of response upon edge type would lead to rejection of this hypothesis. Otherwise, a structural habitat affinity between edge types could be inferred.

To investigate the presence of an environmental gradient (#2) I compared phytometer response along transects in both edge types that extended from field margin towards interior. The relevant hypothesis here was that, if a gradient was evident, then the response curve along the gradient would be independent of edge type. Some contention arose whether the difference in width of edge in fencerows relative to forest edges would allow direct comparison, so two bases for parameter estimation and comparison were considered: actual (metric) distance, and relative (proportion of field margin-to-interior) distance. With this approach I could explore the notion that fencerows are spatially compressed structures relative to forest edges. However, if no gradient was detected in fencerows, then fencerows would effectively be all edge, at least at the scale of investigation.

Methods

Plant response has typically been quantified as morphometric change (*e.g.* leaf size or number) and biomass. Generally these responses are a function of environmental effects (factor complexes comprising availability of light, water, solutes and substrate), competitive interactions (intra- and interspecific) and genetic fitness of individuals. To control for differences in genetic fitness that may occur in wide-ranging populations, the experimental plants in this study were selected from relatively discrete populations.

The only attempt to control for competitive interaction was made at the time of initial transplanting to the experimental plots. By removing sufficient vegetation (primarily densely matted grasses at field margins) to expose the soil surface at points established along the transects, the transplants had an opportunity to re-establish themselves in the new locations before encountering the full brunt of any above-ground resource competition that might ensue.

Otherwise, plant response included the combined effects of environmental factors and any interactions with vegetation in the immediate vicinity. That the two effects may not be clearly distinguished in the experimental results should not bear on the satisfactory test of the hypothesis that fencerow structure provides plants a habitat that is indistinguishable from forest edges. Lack of habitat affinity due exclusively to differences in environmental conditions can only be determined in a much more intensive, controlled situation. My hypothesis is not so demanding, and looks at fencerows and forest edges as they really are, not as ideal structures.

Study Area

In farmland 30 km south of Ottawa, Ontario, 50 m sections of two fencerows and 2 edges of a single forest patch were used for the experiment. Fencerows (FR) were selected on a subjective assessment of overall structural development and on length sufficient to provide a minimum of 5 widthwise transects at 10 m intervals.

One fencerow (FR 1) was 10 to 11 m wide for the entire length used in the experiment. Tilled fields bordered both sides, but only the south side was in crop during the run of the experiment. This fencerow had no fence, though much piled rock and coarse woody debris had been piled towards the centre, elevating this part of the fencerow approximately 1 m from ground level at the field margin. Predominant vegetation consisted

of *Fraxinus americana*, *Ulmus americana*, and *Quercus alba* trees densely interspersed with *Crataegus* sp., *Prunus virginiana* and *Viburnum lentago* shrubs, and draped in *Vitis riparia* and *Parthenocissus vitacea* vines.

The second fencerow (FR 2) was 6 to 6.5 m wide for the length used in the experiment. A tilled and planted barley field bordered the east side, and an old field, recently opened to light grazing, bordered the opposite side. An electrified fence excluded livestock from this experimental site. At the centre of FR 2, a page wire fence was present along with some piled rock, but the centre was not as markedly elevated as in FR 1. Predominant vegetation consisted of *Fraxinus americana*, *Ulmus americana*, *Prunus serotina* and *Quercus alba* trees interspersed with dense clusters of *Crataegus*, *Prunus virginiana* and *Viburnum lentago* shrubs. Vines were a minor component in this fencerow.

The forest patch was a relict stand (5 ha) of *Acer saccharum* with a cornfield abutting the west margin and mixed hay field at the east margin. *Fraxinus americana*, *Ulmus* spp., *Tilia americana* trees dominated both edges, with abundant *Ostrya virginiana* in the west edge, and *Carpinus carolinianus* in the east edge. Shrubs included primarily *Cornus stolonifera*, *Prunus virginiana* and *Viburnum lentago*.

Transects from field margins towards the interiors were established at 10 m intervals along the length of each site. Forest edge transects extended 15 m towards the forest interior (cf. Wales 1972, Ranney *et al.* 1981). Fencerow transects traversed the entire fencerow width.

Planting points were established with numbered flags placed along transects at 0, 1.5, and 3 m from the field margin in all sites, with additional points in forest edges at 4.5, 6, 9, 12 and 15 m from the field margin. The additional forest edge points allowed a coarse test of the hypothesis that fencerows are compressed relative to forest edges--that is, if distance from field margin is a critical factor for phytometer response, then relative

distance (vs. actual distance) will be the effective distance. A total of 270 transplant points was established, plus at least 5 additional control points at the source of collection for each species.

Plant Selection

For this experiment I transplanted 3 herbaceous species along several transects in each of 2 fencerows and 2 forest edges. The contrasting growth forms and phenologies of the 3 phytometer species provided a conservative test of the hypothesis that fencerow habitat was not different than that of forest edges. The three herbaceous species were *Geum aleppicum*, abundant in a hummocky old field in the study area, and *Carex brunnescens* and *Sanguinaria canadensis*, both abundant within the maple woods used for this experiment. Hereafter, phytometers will be referred to by their generic names.

An individual of each of three phytometer species was transplanted to each point using plant material collected from naturally occurring populations within the study area. *Geum*, collected from an old field in full sunlight, was expected to respond primarily to light availability within the canopied edge types. *Sanguinaria* and *Carex*, collected in the maple woods, were expected to respond more to soil conditions, though the light intensity at the outer limits of the edges was expected to present a possible problem for these two more shade-tolerant woodland species.

Geum individuals having 5 to 7 leaves with maximum length of 15-20 cm were taken up with a bulb planter. This allowed extraction of a 5 cm diameter root ball with soil intact to a standard depth of 10 cm. *Carex* was collected as an entire mat of turf from which "plugs" of approximately 20 shoots with a standard length of 15-20 cm were separated out. *Sanguinaria* individuals with leaf diameter 15-20 cm and an intact, undehisced seed capsule were collected by carefully excavating the rhizomatous tuber and

attached roots with trowel and fingers.

Transplanting was carried out and completed during the third week of May 1989, under overcast to rainy weather conditions. Plants were transplanted within 5 hr of collection, and pairs of sites (e.g. FR 1 and FE 1) were fully planted with a given species the same day. All plants were replanted to the same approximate depth at which they were found.

After planting, no further treatment was provided (e.g. water or fertilizer). Over the first 30 days after planting, transplants were monitored to see whether replacement was necessary. Plants with apparent shoot death were replaced from "nursery" stocks established at the sources of collection. Nursery plants were all dug up and replanted in their original sites, and at least 5 of these nursery plants were used as experimental controls. Of a total of 820 phytometers, 12 individuals required replacement within three weeks of transplanting. No experimental plants were replaced after 21 June.

Data Collection

The morphometric response (Table 18a) of each individual plant was measured at 30 day intervals, beginning 21 June, over the course of the 1989 growing season. As *Sanguinaria* leaf dimension and shoot height did not change measurably, only the qualitative response variable, "condition" was recorded in 1989. For all three species, shoot condition was scored as an ordinal response. For *Carex*, the number of flower-bearing culms was the sole variable considered for morphometric response.

In measuring *Geum*, only entirely or mostly green leaves (≥ 1 cm length) were considered in determining leaf number. Partially eaten or wilted leaves that met this former criterion were included in counts. Length, width and area were measured from the largest leaf of each individual plant. A grid of 0.5 cm² cells on clear acetate placed over the

flattened leaf allowed estimation of leaf area (cf. Winter *et al.* 1956). Leaf and shoot lengths were measured from soil surface, and width was measured at the widest part of the leaf perpendicular to the midrib.

Data for 1990 include the number of phytometers surviving over winter and biomass estimates (Table 18b). All surviving phytometers were harvested 21 June 1990, with each entire individual plant being collected in a brown paper bag for transport to laboratory for biomass assessment. Estimates of shoot and root fresh weights were taken within 5 hr of harvest. During the subsequent shoot drying period (48 hr at 105°C), all plant roots were returned to sites of origin and replanted.

The recorded shoot dry weights include various shoot elements, depending on species. *Sanguinaria* shoot weight consisted of the leaf-stem plus the seed pod-stem components. *Carex* seed weight was incorporated into shoot weight. Seed weight was not a factor of concern with *Geum* at time of harvest as only a few individuals had flowered. All quantitative data were normalized with log-transformation prior to analyses.

Analyses

Multivariate analyses of variance (MANOVA), using transect means for each dependent variable (Tables 18) as input, found no evidence for response differences between opposite sides of either fencerow, or between forest edges. This preliminary analysis suggested it would be appropriate to pool data from opposite sides of fencerow and forest edge sites to increase sample sizes. Data for each dependent variable were first summarized as frequencies (shoot condition and survival) and mean values (morphometric and biomass measures) by transect to obtain a measure of variability across the different edge types. These summary data were then used as independent estimates of phytometer response along the length of each site. The resultant sample sizes then were FE = 22 and

FR = 38 (consisting of pooled FR 1 = 22 and FR 2 = 16).

The experiment was run in two opposite edges of a single forest site, and across the entire width of two fencerow sites. In tests that consider edge type as the main effect, the two forest edges are pooled together, as are the four fencerow sides. This results in an unbalanced design due to the lack of a forest replicate. So determination of whether edge type was the sole main effect required comparisons of all pairs of sites, within as well as between edge types.

Sample points across fencerow widths were not directly commensurable with those in forest edges due to the narrower widths of fencerows. In tests for differences between edge types in gradient response (field margin toward interior), direct comparisons included only points at equal distances from field margins. This eliminated forest edge points > 5 m from field margins. A complementary test of gradient response based on proportional distance allowed inclusion of the more interior forest edge points in comparisons. In both tests, data input consisted of mean response estimates for each edge type from pooling of transplant points that were a common distance from field margins.

In MANOVA, when edge type was shown to significantly affect the multivariate phytometer response (*i.e.* the combined responses of shoot persistence, morphometric and biomass variables), univariate F-ratios were examined to determine which particular variables were most affected. Correlation coefficients were calculated for response by distance from field margins, and MANOVA testing for an effect of distance were based on a multiple regression model (Norusis 1985).

Results

As the three phytometer species in the experiment have contrasting growth forms and phenology, the response of each species is here addressed separately. Experimental results are based on comparisons of phytometer response relative to the main effect, edge type. Responses considered include shoot persistence and morphometry over the 1989 season, shoot regeneration after winter, and biomass in June 1990 (Table 18).

Carex brunnescens

Carex shoots may persist in a relatively dormant state beneath snow cover and so have functioning leaves very early in spring. The assimilates of these leaves go to expanding the shoot mass through tillering and production of new shoots throughout the season. So the longer a shoot persists, the better for the growth and development of the plant as a whole.

The persistence of *Carex* shoots over the 1989 growing season was independent of edge type ($\text{Chi}^2 = 5.45$, $\text{DF} = 3$, $p = 0.143$) until September when a highly significant reduction in number of remaining shoots was observed in fencerows ($\text{Chi}^2 = 40.66$, $\text{DF} = 1$, $p = 0.0001$) relative to forest edges which maintained ca. 95% of the *Carex* phytometers there (Figure 11a). No significant differences occurred in monthly shoot loss between fencerows.

The results were somewhat different for individual *Carex* leaves. From July to August 1989, the phytometers in fencerows lost 50% of the total number of leaves without replacement, whereas only 20% such leaf loss occurred in forest edges. Assuming leaf assimilates go to tillering and new shoot development, then fencerows appeared to be much less suitable for generating new shoots. This was corroborated by the significantly

lower number of shoots remaining in fencerows in September.

Edge type did not affect the multivariate response in morphometry and biomass ($F = 1.814$, $DF = 3,56$, $p = 0.155$). However, evidence for an effect of site was found in comparisons between forest edges and individual fencerows, as well as between fencerow sites (Table 19a). Mean values for *Carex* morphometry and biomass were all significantly higher in forest edges than in either fencerow (Table 20a). The difference between the two fencerows was attributed to lower values for response variables in FR 2, particularly the number of flower-bearing culms.

If *Carex* productivity in a previous season is critical to plant survival and shoot regeneration after winter, then it may be expected that forest edges would show a significantly greater number of phytometers regenerating shoots in spring 1990. The number of *Carex* plants surviving over winter (ca. 50% of total transplants, Figure 11a) was independent of edge type--and thus of the previous season's growth--except for a marginally greater number of shoots returning in forest edges (Fisher's Exact Test, $p = 0.039$).

Although *Carex* in forest edges produced more flowering culms than the control group, forest edge biomass in the subsequent season was much less than that of the controls (Table 19a), as was *Carex* biomass in fencerows. No significant difference in biomass occurred between the two fencerows--the significant effect of site here ($F = 136.942$, $DF = 3,37$, $p = 0.0001$) was due entirely to morphometry, particularly the number of flowering culms which contributed most to the difference between edge types.

For *Carex*, the hypothesis of no habitat difference between fencerows and forest edges was not rejected due to the absence of a detectable difference between edge types in the multivariate response of the phytometers.

Geum aleppicum

The leaves of free-growing species like *Geum* export assimilates directly to new leaf production. There is a constant and relatively high rate of leaf turnover. Phenological development in July results in assimilates becoming directed to the reproductive shoot and its attendant organs. The observed patterns in shoot condition were similar in both edge types: a steady but gradual decline in the number of healthy shoots from June to September (Figure 11b).

Across the entire 1989 season, *Geum* shoot persistence was independent of edge type (Figure 11b). After substantial shoot loss at the end of July in both fencerows and forest edges, this decline continued in fencerows, whereas healthy shoots persisted in forest edges into September. Thus a difference in shoot persistence occurred between edge types only in August (Fisher's Exact Test, $p = 0.03$). The marginally higher losses in fencerows were due to a significantly lower number of healthy shoots remaining in FR 2.

Geum flower production in the two edge types was not compared as fewer than 1% of the test plants produced flowering shoots, even though all controls had flowered by August 1989. The number of *Geum* phytometers that survived over winter and generated new shoots was independent of edge type, although both fencerows and forest edges suffered nearly 50% mortality.

Edge type had a significant effect ($F = 21.816$, $DF = 6,53$, $p = 0.0001$) on the multivariate response of *Geum* (Table 19b). As this response was indistinguishable between FR 1 and forest edges ($F = 1.677$, $DF = 6,47$, $p = 0.154$), the difference between edge types was due entirely to the significantly lower response values in FR 2 (Table 20b). Response values for both edge types were lower than those of the control group.

The low number of returning plants, and the lower values for both morphometric

and biomass responses than controls suggest that neither edge type provides habitat amenable to prosperous growth of this species. Still, the differences between the two edge types in the response of *Geum* leads to rejection of the hypothesis of no difference between habitats.

Sanguinaria canadensis

The shoot of *Sanguinaria* emerges in early spring, often before snow cover has completely disappeared. All *Sanguinaria* plants used as phytometers had flowered before transplanting, so the shoot portion of transplants consisted of a single leaf and the fruiting peduncle. The seed pods had invariably dehisced by the end of June, while leaves maintained a healthy appearance through July 1989, becoming yellow and withered by August. After flowering, larger and longer-lasting leaves confer greater advantages on the subsequent season's shoot production as assimilates are directed to below ground storage organs. As phytometer selection controlled for initial leaf size, shoot persistence alone remains the factor of interest for 1989 response.

The overall trend in *Sanguinaria* shoot condition was similar in both edge types, with continuous and increasing loss of healthy shoots across the season (Figure 11c). However, shoot persistence was highest in forest edges ($\text{Chi}^2 = 14.43$, $\text{DF} = 2$, $p = 0.001$) up until September 1989 when no site had any remaining shoots. The difference between edge types earlier on (June and July) was attributed to the significantly lower number of shoots remaining in FR 2 (Fisher's Exact Test, $p = 0.0001$ for both months) determined by comparing the two fencerows. By August, both fencerows sites had less than 5% remaining shoots. This contrasts with comparisons between the two forest edges which showed no significant differences in *Sanguinaria* shoot loss in June and July, though shoots did persist in FE 2 into August (Fisher's Exact Test, $p = 0.0001$)

when the number of remaining shoots in FE 1 dropped to the low levels observed in both fencerow sites. From these results, the export of assimilates to storage then can be reasonably inferred to have been greater in forest edges.

Edge type did not affect the number of *Sanguinaria* phytometers generating new shoots after winter (Fisher's Exact Test, $p = 0.429$), nor the number of shoots produced in addition to the expected single shoot (Fisher's Exact Test, $p = 0.171$). Most (70%) of the *Sanguinaria* phytometers surviving over winter generated only a single new shoot in the spring of 1990. Assuming that *Sanguinaria* had "fixed" reproductive information prior to transplanting, then the probability of differences occurring between forest edges and fencerows in the number of new shoots produced in the following season would be expected to be a function of edge type. In this case, even the early shoot senescence in FR 2 did not entail the production of fewer shoots in the following season. Virtually all surviving plants (ca. 90% of total transplants overall) produced flowers and fruit in the spring of 1990.

Edge type had a highly significant effect on *Sanguinaria* biomass in June 1990 ($F = 17.600$, $DF = 4,55$, $p = 0.0001$). Differences between fencerows and forest edges were significant for all response variables (Table 19c), but shoot fresh weight was most strongly correlated with the discriminant function. Subsequent MANOVA, in concert with summary statistics for biomass variables (Table 20c), showed that the difference in biomass between edge types was due primarily to lower biomass in FR 2. Only FR 1 produced biomass comparable to that of the control group, and the biomass response in FR 1 was not significantly different from forest edges ($F = 2.443$, $DF = 4,39$, $p = 0.063$).

Sanguinaria, then, experienced earlier and significantly higher shoot loss in fencerows over the 1989 season. This appeared not to affect the number of plants

surviving over winter, or subsequent regeneration and growth of new shoots in spring of 1990--no evidence was found for differences between edge types for these responses. Biomass in June 1990 was significantly different between edge types. The consistently lower values for all response variables in FR 2 suggest that this difference is not due to the effect of edge type, but rather to a particular site. Unexpectedly, this woodland species produced significantly greater biomass in FR 1 than in forest edges, suggesting that FR 1 offers habitat capable of supporting healthy growth and regeneration of *Sanguinaria*.

Summary

No clear relationship was found between phytometer shoot persistence and either concurrent shoot morphometry or subsequent season's shoot regeneration and biomass. Edge type appeared not to affect *Carex* shoot persistence, morphometry or the number of shoots returning in 1990, yet all of these were strongly correlated ($r \geq 0.63$, $p < 0.001$) with biomass, the sole response that indicated that edge type may be a significant factor (Table 21a). The previous season's growth, not edge type, influenced the fate of these phytometers in the spring of 1990. In this case, a study of longer duration may be worthwhile.

Geum showed correlations (Table 21b) clearly consistent with the MANOVA results. The number of shoots persisting in July, 1989 was strongly correlated with the number of shoots returning in the spring, 1990 ($r = 0.85$, $p < 0.001$), and both of these variables were found to be independent of edge type. Also, 1989 morphometry was correlated with 1990 biomass ($r = 0.47$, $p < 0.001$), and both of these responses were significantly greater in fencerows than in forest edges. Plant growth and numbers of plants were unrelated.

Sanguinaria showed some confounding relationships. Two variables (number of July

shoots and biomass) that showed an effect of edge type were both strongly correlated with variables that were unaffected by edge type, namely the number of regenerating shoots and the increase in shoot number in spring, 1990 (Table 21c).

Considering the evidence for each phytometer species then, the hypothesis of no difference between edge types must be rejected. Shoot persistence data taken alone tends to support habitat affinity between fencerows and forest edges in general, primarily due to the negligible differences in the number of overwintering survivors for all phytometer species. Shoot persistence over the preceding season also suggests affinity between edge types, except for *Sanguinaria* which persisted longer in forest edges. However, this species also showed significant differences within each edge type.

Morphometry and biomass for two of the three phytometer species were both significantly different between fencerows and forest edges. That FR 1 was least different from forest edges suggests that FR 1 may have habitat affinity to forest edges. FR 2, possibly experiencing greater exposure to sun and wind due to its narrow width and north-south axis, was shown to be unique in all tests.

Discussion

If plants generally experience fencerows and forest edges differently, then phytometers would be expected to show this. As species of contrasting growth forms and life histories were used as phytometers, the differences may be expected to manifest themselves in different ways. The experimental results have considered shoot persistence and morphometry in 1989, overwinter survival, shoot regeneration and biomass in June 1990.

Only *Sanguinaria canadensis* demonstrated differences between edge types in shoot persistence in July (and consistently across the season), as well as within each edge type. This may indicate that *Sanguinaria* is a particularly sensitive phytometer--it had suffered the highest shoot loss in both edge types. My previous horticultural experience at Rockway Gardens, Kitchener (1985-87), suggests that *Sanguinaria* can adapt quickly to situations that would be expected not to support this species. Plants transplanted from shaded habitats with rich organic soil to sandy soil with full sun exposure survived and produced new shoots and flowers in subsequent seasons. At the end of the 1989 season for the experiment presented here, several *Sanguinaria* plants at the field margin of FR 1 had been ploughed under, yet these all managed to produce flowering shoots the following spring. I conclude then that the differences in shoot persistence between edge types shown by *Sanguinaria* are due to habitat differences rather than to phytometer sensitivity.

The number of healthy shoots persisting into July for *Carex brunnescens* and *Geum aleppicum* phytometers showed response to fencerow and forest edge habitats were not different. The differences in the relative number of phytometers generating shoots after surviving over winter suggests that habitat conditions of the two edge types are not easily distinguished. Only for *Carex* was number of returning phytometers associated with edge type. Nevertheless, it is notable that the two woodland phytometers showed differences

in shoot persistence between fencerows and forest edges.

Because the relationships between edge type and both shoot persistence and return after winter are not generally consistent, the morphometric and biomass data must also be considered in determining whether fencerows and forest edges present different habitats to plants. Both morphometry and biomass are functions of shoot dimension which is determined in primordial development (Milthorpe 1956). As events influenced by habitat structure can affect the rate of production of primordia and the number of their constituent cells, morphometry and biomass should be appropriate indices of significant habitat differences between forest edges and fencerows.

The phytometers were transplanted late enough in spring to not interrupt leaf development appreciably. Thus the morphometric response in July 1989 may be construed as dependent mainly upon the accessibility and quality of limiting resources such as water, light and nutrients. Biomass in the following year would be more influenced by adverse conditions experienced in early development of re-emerging phytometer shoots--there would be no appreciable recovery from impeded leaf growth even with subsequent favorable conditions (Milthorpe 1956).

Carex and *Sanguinaria*, as woodland species, were used to determine if fencerows provide environmental conditions suitable for sustaining woodland plants. The expectation was that if fencerows have structural affinity to forest edges, then the consequent fencerow habitat should support typically woodland species. The differences in morphology and phenology of these two species were expected to provide a way of assessing habitat affinity more fairly than with a single species.

As one of the earliest woodland herbs to appear, *Sanguinaria* depends upon the high concentrations of soil nutrients and solar energy that are available before spring runoff and canopy closure for rapid shoot growth and flower production. After flowering, the rest

of its shoot life goes into transforming relatively low light filtering through the forest canopy to its single, broad reniform leaf into storage tissue below ground for regeneration and/or vegetative reproduction next season. As the phytometers had already completed shoot growth and flower formation prior to being transplanted, the main environmental factors measured by these plants were light intensity and soil moisture.

In this perennial, the shoot for the present season is predetermined in, and developed at the expense of assimilates stored in the previous year--that is, the assimilates exported from the present shoot are not immediately reinvested, but pass time in a "non-interest bearing deposit account" (Harper 1989). So there is no difference in the carbon value to the plant whether a young shoot or an old shoot produces the assimilates. But shoots lasting longer into the season continue to contribute assimilates to storage, even if at a reduced rate. It may be expected then that shoots lasting longer into the present season effect higher biomass in the subsequent season.

The early occurrence of high shoot loss in *Sanguinaria* in fencerows relative to persistence in forest edges suggests a difference in the habitat qualities of the two edge types. On the other hand, virtually no difference occurred in the number of plants returning to produce shoots, nor the number of additional shoots produced, after winter. Evidently, fencerow habitat conditions were adequate to support high phytometer returns. Indeed, the highest values for *Sanguinaria* biomass occurred in FR 1, and these values were comparable to those of the woodland controls.

Factors likely responsible for the losses observed during the previous season would be light intensity and soil moisture. Both would be affected by the width of the fencerow, as well as by the vegetation structure. The narrowness of a fencerow would be expected to provide more opportunity for light and wind to reach the interior through the canopy or fencerow sides at lower angles. Resulting higher temperatures and diminished humidity of

fencerow habitats would be adverse to species of mesic woodlands, as the experiment has shown with earlier *Sanguinaria* shoot senescence in fencerows. But later senescence in forest edges appeared to confer no advantage on biomass production the following season. This suggests that fencerows can support *Sanguinaria*.

Carex, although also returning relatively early in the spring, persists into the fall, producing new shoots and flower-bearing culms continuously throughout the season. Growth is not as rapid as that of *Sanguinaria*. The very narrow, blade-like leaves can function adequately at various light intensities and temperatures, so the critical effect on this phytometer probably relates to soil properties.

Carex showed no difference between edge types in the number of shoots persisting into July 1989. Overwinter survival was shown to be only marginally higher in forest edges, so it appears that fencerows are at least capable of supporting *Carex*. Even the highest response values for morphometry and biomass in fencerows, when compared to forest edges, suggest however that this support is tenuous.

Geum, from the open, hummocky old field, was expected to provide mainly a measure of light quality. Shoot persistence was poor and not detectably different between edge types, and the negligible number of plants flowering, relative to the phytometer controls in open habitat, indicates growth and development were hampered. Neither did morphometric nor biomass responses show differences between FR 1 and forest edges. The differences that *Geum* did show appear wholly due to FR 2 where *Geum* phytometers fared least well. This site was not as wide as FR 1, and it appeared to be less developed in terms of vegetation and soil characteristics. Under these conditions, light quality in FR 2 would be expected to be closer to that of open habitats than that of the other experimental sites. That the phytometers did not positively respond to greater incidence of light in FR 2 suggests that soil conditions were inadequate there. Soil in FR 2, particularly on the west

side, was considerably drier and sandier than in FR 1.

Both 1989 morphometry and 1990 biomass strongly suggest that fencerows and forest edges indeed present different habitats to plants. Previous chapters have shown significant structural differences between edge types in vegetation composition and architecture. The experiment has shown that these structural differences may functionally constrain movement of plants along fencerow corridors.

That edge type had no effect on phytometer response in comparisons of forest edges and FR 1 suggests habitat affinity may rely upon structural characteristics. Phytometer response has pinpointed FR 2 as a distinctly different habitat from the other two sites. Differences sensed by a plant generally found in open habitats (*Geum aleppicum*) suggest that differences between edge types would be associated with light intensity, wind and humidity. The narrow width of FR 2 would be expected to permit more light to reach the mid-section, and at greater intensity due to its solar aspect. This, coupled with the effect of wind passing through rather than being diverted up and over, would have a desiccating effect on the fencerow interior.

In conclusion, the observed differences in the response of three phytometer species have led to the rejection of the hypothesis that there is no difference in habitat conditions between fencerows and forest edges. Despite the significant differences observed in phytometer response, the experimental evidence does suggest that fencerows have the capacity to sustain woodland plants that have been able to become established in fencerows. There is no indication, however, that new plants arriving in fencerows will be able to establish other than ephemeral populations. Population persistence would be required for fencerows to effectively link woodland plant populations.

Synthesis and Conclusions

Fencerow networks in farmland are threatened with removal by farm mechanization and urban expansion. Increased efficiency of agriculture has induced profound effects on all aspects of rural landscapes. Fewer and larger farms, corporate ownership, and inflation of land prices around urban centres all influence landscape pattern as well as the way people view rural areas. Furthermore, rural areas are under increasing development pressure to supply housing for urban commuters. The fragmentation of such landscapes through regional development has resulted in disruption of demographic and genetic flows between ecosystems, flows which now persist only through tenuous links such as fencerows, riparian strips and road verges.

My research sought a structural basis for plant movement from forest edges into fencerows--none was found. The three components of my research have led to rejection of the hypothesis that fencerow structure is analogous to the structure of the edges of remnant forests occurring in the same agricultural landscape. A similarity between fencerows and forest edges was expected as they both have anthropogenic origins and are both subject to comparable manipulation.

Vegetation structure, architectural structure and ground layer habitat quality in fencerows were all significantly different from those in forest edges. The low statistical power of hypothesis tests due to small sample sizes may have precluded detecting fine scale differences; however, results from all three data sets indicate that the differences between fencerows and forest edges are substantial.

The clearest distinction between fencerow and forest edge vegetation was made on the basis of the abundance of dominant canopy species, even though mean stem diameter showed no difference between edge types. If the difference in abundance is

solely due to the amount of time each edge type has had to develop, then fencerows should eventually become more similar to established forest edges through successional changes. Neither the ages of fencerows nor of the forest edges were accounted for in this study; the general appearance of structural development was considered representative of age. There may be less structural difference between edges of comparable age.

Other clear differences in vegetation show that fencerows do not extend forest edges: the greater structural diversity of fencerow canopies due to co-dominant species; mainly biotically dispersed species in all fencerow strata; dominance of fruit-bearing shrubs and dense grasses in lower strata of fencerows, and the fewer numbers of woodland species in fencerows. Forest edges, in contrast, had canopies dominated by a single species; disproportionate abundance of wind-dispersed and shade tolerant species, and more woodland species, particularly in ground flora. Fencerows, then, may not be effective corridors for plants, as the vegetation composition and architecture of fencerows are not structural extensions of forest edges. Woodland herbs in fencerows are likely relict--some of the woodland species in fencerows were absent from the nearby forests.

The differences in vegetation were complemented by those found in architecture, most notably the dominance of dense grasses in fencerow ground vegetation, which would partly explain the poor representation of woodland species there. But grasses were generally restricted to outer margins; the fencerow interiors often lacked the herbaceous ground cover found in the forest edges. Instead, the innermost part of fencerows consisted of coarse woody debris, piled rock and low woody species. Of the woodland species that did occur in fencerows, *Asarum canadense* and *Sanguinaria canadensis* had large, healthy populations located within the limits defined by the dense grasses. Neither of these woodland herbs was found in forest edges.

Although canopy trees, and dense shrub and vine foliage created an interior quality

that appeared, felt and smelled similar to forest, the response of the woodland phytometers showed no difference between this inner zone and the field margin. But fencerow habitat quality was distinct from that in forest edges. Foliage cover was adequate to filter intense sunlight, as the results have shown, so the limiting factor was likely soil quality.

The phytometers also showed that woodland species can grow in fencerows once they get there somehow. The question then arises--if woodland species can grow in fencerows, why were these species so poorly represented in fencerow ground flora? The answer requires appraisal of structural and functional connections between source populations and fencerows. Studies previously cited have shown functional connections for animals only. This study has shown the lack of structural connection between fencerows and forest edges, that is, the two edge types are structurally distinct.

Further research should consider whether the woodland species occurring in fencerows represent remnant populations from a time prior to forest clearing for agriculture. This question assumes that at least some of the contemporary fencerow structure existed as part of a woodland and was not removed with subsequent clearing. The trend of clear-cutting by agricultural pioneers suggests that this is not the case. Still, local herb populations may have continued to exist in a suppressed state after clearing to emerge once conditions improved with the structural development of the vegetation associated with established fencelines.

European studies suggest these plants may have colonized fencerows at a later time. If forest clearing removed all viable populations, recolonization could only occur by either vegetative growth extending from adjacent remnant patches, or seed dispersal and germination success. Seeds of the species previously mentioned are ant-dispersed, so repopulating a fencerow by seed dispersal would rely on the same physical proximity as does the vegetative expansion of populations.

All evidence points to substantial structural differences between edge types and by inference, resulting habitat quality. From this, I conclude that fencerow corridor value to plants is conditional. Woodland species present in fencerows persist in marginal habitat. It was not determined when these plants arrived, or where they came from. Hutchinson (pers. communication) believes patch populations of woodland species, such as the ones in fencerows, are not new, but rather surviving populations. Middleton and Merriam (1983), however, assert that woodland species have always had to deal with spatial discontinuity of habitat and so have evolved mechanisms for dispersal that allows populations to establish in new habitats as they arise. Fencerows, then, would be likely movement corridors for these species.

Recommendations for further research include investigations of genetic relationships among disjunct plant populations in fencerows; historical research into the ecological effects of land fragmentation; an extended experiment with phytometers in a larger sample of fencerows; an experiment testing the seed germination ability of woodland species in fencerows; a survey of ant fauna that may act as seed dispersers to fencerows, and examination of the hypothetical gradient from field margin toward interior with computer aided design (CAD) to make fencerow width commensurable with forest edges.

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MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS
STANDARD REFERENCE MATERIAL 1010a
(ANSI and ISO TEST CHART No. 2)

TABLES

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TABLE 1: Sampling information for vegetation survey of fencerows and forest edges.

Edge Type	Forest (FE)	Fencerow (FR)
Sample Size	3	7
Transect Number	14	34
Length (m)	15	6-12 ^a
Quadrat Number		
Ground (1 X 1 m)	112	293
Shrub (3 X 3 m)	56	103
Tree (10 X 10 m)	14	34 ^b

^a Transects extended across the entire width of all fencerows. These numbers represent the range of fencerow widths in the sample (See Table 4).

^b FR tree plots were 10 m X FR width. Mean width = 9.29 m, std deviation = 2.13.

TABLE 2: Species richness in forest edges (FE) and fencerows (FR).

	Species Richness					Fisher's Exact	Jaccard's
	Total	FE	n	FR	n	Test, p	Similarity
Canopy trees	19	12	14	17	34	0.062	0.53
Shrub layer	37	29	56	28	103	0.500	0.54
Ground vegetation	75	58	112	61	293	0.590	0.59
All strata	87	65	182	70	430	0.234	0.55

Fisher's Exact Test for association between species number and edge type. Jaccard's Similarity coefficient is the ratio of the number of species co-occurrences to the total number of species in both edge types. Sample sizes were the number of plots surveyed in each edge type.

TABLE 3: The effect of fencerow width on richness (S) and frequency (f) of woodland species in fencerow ground vegetation. Mean richness (S), frequency (f) and standard errors of means (SE) are based on log-transformed data for n (number of transects sampled) = 5 for all widths. F-ratios (DF = 4,24) and significances (p) are from tests for an effect of width on S and f. Coefficients of determination (R²) for variability in dependent variables with fencerow width have n = 25; all R² values were ns at p < 0.05. All Woodland Species includes woody species. Woodland species occurring in fencerows included: *Acer saccharum*, *Actaea pachypoda* & *A. rubra*, *Asarum canadense*, *Corylus cornuta*, *Equisetum pratense*, *Fraxinus americana*, *Geranium robertianum*, *Geum canadense*, *Maianthemum canadense*, *Quercus alba*, *Ribes cynosbati*, *Ulmus americana* & *U. rubra*.

Width (m)	n	All Woodland Species			Herbaceous Species		
		Mean S	(SE)	Mean f	(SE)	Mean S	(SE)
12	10	2.40	(0.81)	3.60	(1.29)	1.00	(0.45)
11	10	3.64	(0.31)	6.57	(0.28)	0.95	(0.18)
9	10	4.20	(0.58)	8.20	(0.97)	1.80	(0.20)
8	10	3.44	(0.15)	5.75	(0.79)	1.61	(0.17)
6	8	2.00	(0.45)	2.50	(0.22)	0.25	(0.19)
F-ratio (p)		3.02	(0.043)	6.15	(0.002)	3.71	(0.020)
Adjusted R ²		0.0293		0.0405		0.0147	
						5.90	(0.003)
						0.0475	

TABLE 4: The effect of distance from nearest forest on richness (S) and frequency (f) of woodland species in fencerow ground vegetation. Distance classes are: 0 = directly connected to forest; 1 = 0.2-0.5 km; 3 = >0.5 km. Mean richness (S) and frequency (f) are based on log-transformed data for n (number of transects sampled) = 5 for all widths. F-ratios (DF = 2,12) and significances (p) are from tests for an effect of distance on S and f. Coefficients of determination (R²) for variability in dependent variables with distance class have n = 15; all R² were ns at p = 0.05. All woodland species includes woody species. Woodland species occurring in fencerows are listed in Table 3.

Distance Class	n	All Woodland Species		Herbaceous Species	
		Mean S	Mean f (SE)	Mean S (SE)	Mean f (SE)
0	5	4.80	8.20 (0.73)	2.60	5.20 (0.58)
1	5	1.88	2.40 (0.05)	0.27	0.27 (0.03)
2	5	3.83	6.78 (0.23)	1.23	1.83 (0.21)
F-ratio (p)		24.26 (0.0001)	112.82 (0.0001)	139.15 (0.0001)	159.08 (0.0001)
Adjusted R ²		-0.4384	-0.0594	0.3378	0.0524

TABLE 5: Similarity and diversity indices for species composition in forest edges (FE) and fencerows (FR). The t-statistic and significance (p) tests for differences between FE and FR in the diversity of species abundances.

a) Shannon's Diversity, H'

	FE	FR	t	DF	p
Canopy Trees					
Cover	1.32	1.96	1.35	198	0.179
Density	1.73	1.92	0.42	198	0.675
Dominance	1.03	1.58	1.32	198	0.188
Importance	1.42	1.85	0.92	199	0.359
Shrub Layer					
Cover	2.39	2.35	0.11	199	0.913
Frequency	2.82	2.72	0.29	197	0.772
Importance	2.65	2.58	0.17	197	0.865
Ground Vegetation					
Cover	2.57	2.35	0.35	196	0.727
Frequency	3.16	3.06	0.25	197	0.803
Importance	2.93	2.78	0.28	197	0.780

b) Evenness of distribution of Importance Values

	$H'_{\max}$		J'		Cuba's X	
	FE	FR	FE	FR	FE	FR
Canopy trees	2.48	2.77	0.53	0.71	0.36	0.41
Shrub layer	3.30	3.09	0.80	0.83	0.55	0.57
Ground vegetation	3.61	3.64	0.71	0.65	0.55	0.49

TABLE 6: Canopy tree abundance summary for forest edges and fencerows. All relative abundance (%) values are based on 10 X 10 m plots in FE, and plots 10 m X FR width in fencerows. n = number of plots in sample. Importance value (IV) is the mean of all abundance measures for a species. Only species with IV > 1.0 are shown; a complete listing appears in Appendix 2a. Absence of values means species was not present. F-ratio (DF = 1,46) and significance (p) are for comparisons of dominance between edge types.

Species	Forest Edges (n = 14)				Fencerows (n = 34)				F-ratio	p
	Cover	Density	Dominance	IV	Cover	Density	Dominance	IV		
<i>Acer saccharum</i>	57.67	30.83	63.17	50.56	1.06	1.53	0.33	0.97	64.97	<0.0001
<i>Ostrya virginiana</i>	15.73	23.79	22.93	20.82	0.26	0.25	0.00	0.17	52.54	<0.0001
<i>Fraxinus americana</i>	16.06	25.98	10.47	17.51	33.37	29.66	39.34	34.12	0.32	0.574
<i>Tilia americana</i>	3.07	5.98	1.58	3.54	6.11	3.47	4.85	4.81	0.85	0.360
<i>Carpinus carolinianus</i>	3.73	4.85	0.92	3.17					12.60	0.0009
<i>Ulmus rubra & U. americana</i>	1.13	2.73	0.13	1.33	5.14	5.00	1.15	3.76	0.72	0.401
<i>Prunus serotina</i>	1.06	1.59	0.28	0.98	3.18	2.46	0.81	2.15	0.53	0.469
<i>Crataegus</i> sp.	0.34	1.06	0.23	0.54	22.90	28.64	25.45	25.67	5.81	0.020
<i>Viburnum lentago</i>	0.07	0.53	0.04	0.21	7.42	12.46	15.69	11.86	11.38	0.0015
<i>Quercus alba</i>					14.17	10.93	10.97	12.02	11.38	0.0015
<i>Acer negundo</i>					1.99	1.53	0.81	1.44	0.83	0.369

TABLE 7: Shrub layer abundance summary for forest edges and fencerows. Relative abundance (%) values are based on transect means for 3 X 3 m plots. n = number of transects in the sample. Importance value (IV) is the mean of cover plus frequency. Only species IV > 1.0 in at least one edge type are presented here. No value means species was absent. A complete listing is given in Appendix 2b. F-ratio (DF = 1,80) and significance (p) are for comparisons of cover between edge types.

Species	Forest Edges (n = 14)			Fencerows (n = 68)			F-ratio	p
	Cover	Frequency	IV	Cover	Frequency	IV		
<i>Acer saccharum</i>	23.42	13.53	18.47	1.01	1.90	1.46	57.68	<0.0001
<i>Fraxinus americana</i>	22.14	11.94	17.04	1.58	4.70	3.14	19.60	<0.0001
<i>Viburnum lentago</i>	9.50	8.77	9.13	16.86	11.36	14.17	10.13	0.002
<i>Tilia americana</i>	8.21	7.70	7.95	1.56	2.44	2.00	11.59	0.001
<i>Prunus virginiana</i>	7.12	8.21	7.66	16.35	12.78	14.63	11.71	0.001
<i>Ostrya virginiana</i>	4.16	5.83	5.00				60.46	<0.0001
<i>Vitis riparia</i>	3.35	5.31	4.33	9.49	5.77	7.66	1.12	0.294
<i>Cornus stolonifera</i>	3.71	4.78	4.24	7.14	6.30	6.75	1.10	0.267
<i>Carpinus carolinianus</i>	4.19	3.97	4.08				33.51	<0.0001
<i>Ulmus americana</i> & <i>U. rubra</i>	2.64	4.98	3.51	1.97	3.69	2.83	0.13	0.717
<i>Ribes cynosbati</i>	0.51	5.83	3.17	1.42	6.84	3.42	2.53	0.100
<i>Rubus occidentalis</i>	1.92	3.45	2.68				116.40	<0.0001
<i>Rubus idaeus</i>	2.66	2.38	2.52	6.14	9.81	8.00	6.08	0.016

TABLE 8: Ground vegetation abundance summary for forest edges and fencerows. Relative abundance (%) values are based on transect means for 1 X 1 m plots. n = number of transects in the sample. Importance value (IV) is the mean of cover plus frequency. Only species IV > 1.0 in at least one edge type are presented here. No value means species was absent. A complete listing is provided in Appendix 2. F-ratio (DF = 1,80) and significance (p) are for comparisons of cover between edge types.

Species	Forest Edges (n = 14)			Fencerows (n = 68)			F-ratio	p
	Cover	Frequency	IV	Cover	Frequency	IV		
<i>Acer saccharum</i>	34.25	15.15	24.70	0.43	0.99	0.71	168.70	<0.0001
<i>Fraxinus americana</i>	6.72	9.43	8.07	1.51	1.93	1.72	12.02	0.0009
<i>Prunus virginiana</i>	4.80	7.75	6.28	7.87	7.50	7.69	6.02	0.016
<i>Viola</i> spp.	5.39	6.57	5.98	3.11	4.43	3.77	0.51	0.478
Gramineae	8.55	2.69	5.62	41.41	12.86	27.14	33.16	<0.0001
<i>Rubus idaeus</i>	6.35	3.37	4.86	9.58	9.74	9.66	10.99	0.0014
<i>Tilia americana</i>	3.98	4.88	4.43	0.24	0.47	0.35	40.68	<0.0001
<i>Solidago</i> sp.	5.26	3.04	4.15	2.84	4.06	3.45	0.03	0.864
<i>Carex</i> spp.	2.48	4.88	3.68				141.00	<0.0001
<i>Circaea quadrisulcata</i>	3.78	3.20	3.49				46.25	<0.0001
<i>Fragaria vesca</i>	2.74	4.03	3.38	2.18	5.89	4.03	1.41	0.236
<i>Ulmus rubra</i> & <i>U. americana</i>	1.01	3.53	2.27	0.13	0.52	0.33	18.13	0.0001
<i>Parthenocissus vitacea</i>	1.40	3.04	2.22	8.34	13.54	10.94	25.51	<0.0001

TABLE 8: continued

Species	Forest Edges (n = 14)		Fencerows (n = 68)		F-ratio	p
	Cover	Frequency	Cover	Frequency		
<i>Ostrya virginiana</i>	1.01	3.37	2.19		78.99	<0.0001
<i>Rubus occidentalis</i>	2.59	1.51	2.05		10.99	0.001
<i>Ribes cynosbati</i>	1.19	2.36	1.78	2.34 4.58 3.46	3.52	0.064
<i>Vitis riparia</i>	1.46	2.03	1.74	1.56 1.30 1.43	0.17	0.686
<i>Cornus stolonifera</i>	1.31	2.03	1.67	3.72 4.74 4.23	1.90	0.171
<i>Viburnum lentago</i>	0.75	2.52	1.64	2.00 4.69 3.34	4.79	0.032
<i>Carpinus carolinianus</i>	0.62	1.51	1.06		26.16	<0.0001
<i>Crataegus</i> sp.				1.16 2.08 1.62	5.84	0.018
<i>Maianthemum canadense</i>	0.32	1.67	1.00	0.34 0.99 0.66	0.57	0.454
<i>Lactuca canadensis</i>	0.50	1.51	1.00	0.55 3.44 1.99	0.29	0.591
<i>Asarum canadense</i>				2.77 1.15 1.96	2.20	0.142
<i>Clematis virginiana</i>				2.34 1.46 1.90	2.62	0.120

TABLE 9: Foliage height distribution (FHD) in fencerows and forest edges. FHD is based on the total of the mean cover for all species in each layer. FHD is the sum of inverse proportion of total cover ($1/p_i^2$) in all layers.

a) All vegetation layers

Vegetation Layer	Forest Edges		Fencerows	
	Percent of Total Cover	$1/p_i^2$	Percent of Total Cover	$1/p_i^2$
Canopy	38.91	4.17	40.51	3.84
Shrub	45.82	3.84	52.55	3.50
Ground	15.27	2.11	6.93	10.26
FHD (Total)		10.12		17.60

b) Canopy and shrub layers only

Vegetation Layer	Forest Edges		Fencerows	
	Percent of Total Cover	$1/p_i^2$	Percent of Total Cover	$1/p_i^2$
Canopy	45.92	3.79	43.53	4.22
Shrub	54.08	4.18	56.47	3.83
FHD (Total)		7.97		8.05

TABLE 10: Discriminant analysis results for fencerow vegetation. FR # = Individual fencerow sample. F-ratios and significances between pairs of fencerows (DF = 9,19).

FR	1	2	3	4	5	6
2	24.6273 0.0024					
3	4.6224 0.0024	6.9265 0.0002				
4	10.307 <0.0001	8.5468 <0.0001	15.126 <0.0001			
5	6.1042 0.0005	2.7268 0.0314	8.1004 0.0001	11.654 <0.0001		
6	2.7713 0.0294	5.5372 0.0008	3.1538 0.0168	14.342 <0.0001	4.4157 0.0031	
7	5.6909 0.0007	2.2197 0.0687	7.4478 0.0001	8.0806 0.0001	1.1775 0.3625	4.0210 .0051

The accepted significance level for these multiple tests was adjusted to $p \leq 0.002$.

TABLE 11: Stem frequency comparisons for five species present in fencerows in Ohio and Ontario. FE = Forest Edge, FR = Fencerow.

Species	Ohio Fisher's Exact		Ottawa		Fisher's Exact Test, p ²
	FR	Test, p ¹	FR	FE	
<i>Prunus serotina</i>	173	0.0001	10	3	0.0001
<i>Fraxinus americana</i>	76	0.0001	172	49	0.033
<i>Ulmus americana</i> & <i>U. rubra</i>	28	0.261	23	5	0.189
<i>Acer saccharum</i>	8	0.381	6	59	0.0001
<i>Quercus alba</i>	5	0.0001	53	0	0.0001
<i>Quercus</i> spp. ³	71	0.188	53	(not applicable)	
<i>Ostrya virginiana</i>	0	ns	0	52	0.0001
Miscellaneous ⁴	68	0.0001	214	28	0.0001
Total Stems (n)	259		478	203	

1 The first test is for differences between Wayne County, Ohio fencerows (data in Whitney & Somerlot 1985) and Ottawa fencerows in the present study.

2 The second test is for association between stem frequency and edge type in Ottawa fencerows and forest edges.

3 Includes *Quercus alba*, *Q. palustris*, *Q. rubra* and *Q. velutina* from the Ohio study.

4 Miscellaneous = species reported as such in Whitney & Somerlot (1985) and were present in Ottawa fencerows. These species include: *Tilia americana*, *Populus tremuloides*, *Crataegus* sp., *Acer negundo*, *Pyrus malus*.

TABLE 12: Horizontal foliage density in fencerows and forest edges. Means and standard errors of means (SE) are based on mean foliage density per transect, and n = the number of transects sampled in each edge type. For height greater than 2 m, the parameter estimates represent mean frequencies of foliage density > 20% only. All F ratios have degrees of freedom = 1,53.

a) Summary statistics by height interval

Height (m)	FE (n = 15)		FR (n = 40)		F ratio	p
	Mean	(SE)	Mean	(SE)		
> 2	5.07	(0.52)	7.20	(0.40)	8.732	0.005
1.5-2	27.42	(5.44)	46.04	(3.10)	7.191	0.010
1-1.5	34.17	(6.20)	42.28	(3.12)	1.071	0.305
0.5-1	34.54	(4.49)	44.20	(2.03)	5.734	0.020
< 0.5	47.96	(4.81)	65.15	(2.47)	8.529	0.005

b) Multivariate tests for an effect of edge type on foliage density profiles.

<u>MANOVA statistics</u>			<u>Discriminant function statistics</u>		
Test ^a	F ratio	p	Eigen value	Canonical r^2	Wilk's λ
1	383.42	0.0001	0.828	0.673	0.547
2	457.32	0.0001	0.764	0.658	0.567

a The first test included foliage density at all heights, giving $DF = 5,49$ for the significance of F in MANOVA. Foliage density above 2 m was removed from the second test, giving $DF = 4,50$ for the significance of F in MANOVA.

TABLE 13: Habitat heterogeneity (HH) of horizontal foliage density in fencerows (FR) and forest edges (FE).

Height Interval (in)	Habitat Heterogeneity	
	FE	FR
> 2	0.0670	0.0195
1.5-2.0	0.0338	0.0343
1.0-1.5	0.0111	0.0170
0.5-1.0	0.0019	0.0033
< 0.5	0.0013	0.0012
Total	0.1151	0.0753

TABLE 14: Mean frequency of architectural elements in forest edges and fencerows. Means and standard errors of means (SE) are based on mean frequency in each transect, except for rock and litter which are based on percent cover/m². n = number of transects sampled in each edge type. Significance of F-ratio (*) was accepted at $p \leq 0.002$ in adjusting for multiple tests of the effect of edge type. ns = not significant.

Variable	Height (m)	Forest Edges (n = 15)		Fencerows (n = 41)		Signif F
		Mean	(SE)	Mean	(SE)	
Tree	> 7	6.27	(0.57)	3.80	(0.45)	ns
stems and	3.5-7	6.80	(0.34)	6.05	(0.41)	ns
branches	1.5-3.5	4.47	(0.34)	4.93	(0.35)	ns
	0.5-1.5	1.33	(0.30)	2.59	(0.27)	ns
	< 0.5	1.20	(0.31)	1.61	(0.18)	ns
Shrub	> 7	0.00	(0.00)	0.02	(0.02)	ns
stems and	3.5-7	0.20	(0.14)	0.76	(0.25)	ns
branches	1.5-3.5	5.60	(0.34)	6.02	(0.44)	ns
	0.5-1.5	7.67	(0.13)	7.10	(0.32)	ns
	< 0.5	7.53	(0.19)	6.90	(0.25)	ns
Vines	3.5-7	0.00	(0.00)	0.73	(0.26)	ns
	1.5-3.5	0.47	(0.19)	2.15	(0.43)	ns
	0.5-1.5	0.80	(0.33)	2.66	(0.43)	ns
	< 0.5	1.53	(0.40)	5.17	(0.43)	*

continued...

TABLE 14: continued

Variable	Height (m)	Forest Edges (n = 15)		Fencerows (n = 41)		Signif F
		Mean	SE	Mean	SE	
Coarse woody debris	1.5-3.5	0.40	(0.16)	0.66	(0.17)	ns
	0.5-1.5	1.53	(0.45)	1.59	(0.28)	ns
	< 0.5	5.80	(0.50)	4.83	(0.35)	ns
Grasses	0.5-1.5	0.67	(0.13)	3.83	(0.34)	*
	< 0.5	3.40	(0.45)	4.59	(0.33)	ns
Forbs	0.5-1.5	0.87	(0.19)	1.73	(0.22)	ns
	< 0.5	5.33	(0.52)	5.29	(0.31)	ns
Mosses	< 0.5	7.47	(0.22)	6.66	(0.26)	ns
Rock	< 0.5	10.50	(2.20)	9.47	(1.57)	ns
Litter	< 0.5	93.24	(2.00)	88.38	(1.91)	ns

TABLE 15: Habitat heterogeneity (HH) of the frequency of architectural elements present in fencerows (FR) and forest edges (FE).

a) HH by architectural element

Architectural Element	Height Interval (m)	Mean HH	
		FE	FR
Tree stems & branches (T)	0 - > 7	1.1720	1.1955
Shrub stems & branches (S)	0 - > 7	1.1558	1.2567
Vines (V)	0 - 7	2.7880	1.6424
Coarse woody debris (CWD)	0 - 3.5	1.2305	1.6027
Grasses (G)	0 - 1.5	0.7015	0.1249
Forbs (F)	0 - 1.5	0.5409	0.5060
Mosses (M)	< 0.5	0.0032	0.0120
Rock (R)	< 0.5	0.4187	0.3683
Litter (L)	< 0.5	0.0001	0.0008
Total		8.0107	6.7093

continued...

TABLE 15: continued.

b) HH by height

Height Interval (m)	Architectural Elements ^a	Mean HH	
		FE	FR
> 7	T,S	0.0987	0.6276
3.5-7	T,S,V	1.1502	1.4696
1.5-3.5	T,S,V,CWD	1.7803	1.7988
0.5-1.5	T,S,V,CWD,G,F	3.2605	1.9065
< 0.5	T,S,V,CWD,G,F,M,R,L	1.7210	0.9067
	Total	7.9207	6.7092

a See Table 19a for key to architectural elements.

TABLE 16: The relative contribution of architectural elements to structure of fencerows and forest edges: Mean class frequencies by edge type. CWD = coarse woody debris.

* indicates variables contributing to significance of F in MANOVA.

Variable	Forest Edges	Fencerows
	(n = 15)	(n = 42)
	Mean (SE)	Mean (SE)

Tree diameter	0.29 (0.06)	0.37 (0.05)
Shrub density	2.07 (0.11)	1.81 (0.07)
Gap size	2.38 (0.11)	1.93 (0.08) *
Rock size	0.46 (0.10)	0.50 (0.08)
CWD size	1.04 (0.15)	0.89 (0.06)
CWD condition	1.79 (0.18)	1.61 (0.10)
CWD position	0.85 (0.08)	1.04 (0.11)

TABLE 17: Habitat heterogeneity (HH) of the relative contribution of architectural elements to structure in fencerows (FR) and forest edges (FE).

Architectural Element	Mean HH	
	FE	FR
Tree stem diameter	0.3777	0.2978
Shrub density	0.0109	0.0222
Sub-canopy gap size	0.0050	0.0210
Rock size	0.4200	0.4476
Coarse woody debris:		
Size	0.0707	0.1020
Condition	0.0566	0.0810
Position	0.0541	0.1207
Total	0.9950	1.0923

TABLE 18: Phytometer response variables.

Gm = *Geum aleppicum*; Cx = *Carex brunnescens*; Sg = *Sanguinaria canadensis*.

---

a) Morphometry (June-Sept 1989)		Data	Species
<i>CND</i>	Shoot condition: poor, fair, good	(0,1,2)	All
<i>JL#</i>	Number of healthy shoots in July 1989	(n)	All
<i>LF#</i>	Number of green leaves per individual	ln(n)	Gm
<i>LEN</i>	Length of largest leaf, from tip to point of attachment	ln(cm)	Gm
<i>WID</i>	Width of largest leaf at widest point perpendicular to midrib	ln(cm)	Gm
<i>AREA</i>	Area of largest leaf, est. by overlay of 0.5 cm ² grid cells	ln(cm ²)	Gm
<i>CM#</i>	Number of flower-bearing culms per individual	(n)	Cx
<i>FL</i>	Flower: absence, presence	(0,1)	All
b) Biomass (21 June 1990)			
<i>RTN</i>	Plants generating shoots following winter: no, yes	(0,1)	All
<i>SHT</i>	Shoot fresh weight	ln(g)	All
<i>DRY</i>	Shoot dry wt	ln(g)	All
<i>POD</i>	Seed pod dry wt (undehisced)	ln(g)	Sg
<i>REP</i>	Number of new shoots produced	(n)	Sg

TABLE 19: Multivariate tests (MANOVA) of combined phytometer response variables by edge type (FE = Forest Edges, FR = Fencerows) and by site (FR # = individual FR). 1 Dependent variables for which univariate F-ratios indicated a significant effect ($p < 0.05$) in each test. 2 Response which was most strongly correlated with the discriminant function in each test. The multivariate response includes morphometry (July 1989: M) and biomass (June 1990: B). Sample size: FE = 22; FR = 38: (FR 1 = 22), (FR 2 = 16).

Comparison	F	DF	p	Univar Sig ¹	Discrim Corr ²
<i>a) Carex brunnescens</i>					
FE vs FR	1.814	3,56	0.155	SHT	B
FE vs FR 1	8.706	3,40	0.0001	ALL	M,B
FE vs FR 2	47.754	3,34	0.0001	CM#	M
FR 1 vs FR 2	13.942	3,34	0.0001	CM#	M
<i>b) Geum aleppicum</i>					
FE vs FR	21.816	6,53	0.0001	ALL	M
FE vs FR 1	1.677	6,37	0.154	-	-
FE vs FR 2	12.489	6,31	0.0001	ALL	M
FR 1 vs FR 2	9.507	6,31	0.0001	ALL	M
<i>c) Sanguinaria canadensis</i>					
FE vs FR	17.600	4,55	0.0001	ALL	B
FE vs FR 1	2.443	4,39	0.063	NOT POD	B
FE vs FR 2	20.521	4,33	0.0001	ALL	B
FR 1 vs FR 2	19.264	4,33	0.0001	ALL	B

TABLE 20: Summary of phytometer morphometric (July 1989) and biomass (June 1990) responses. Means and standard errors of means (SE) are based on log-transformed transect means. FE = Forest Edges, FR = Fencerows, FR# = individual FR site. n = number of transects in sample. Variables: CM# = number of flower-bearing culms per individual; SHT = shoot fresh weight (g); DRY = shoot dry weight (g); LF# = number of green leaves per individual; LEN = length of largest leaf; WID = width of largest leaf; AREA = area of largest leaf; POD = seed pod (undehisced) dry weight (g).

	FE (n = 22)		FR (n = 38)		FR1 (n = 22)		FR2 (n = 16)		Controls
Variable	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	(n = 5)
a) <i>Carex brunnescens</i>									
CM#	1.75	(0.11)	0.93	(0.11)	1.22	(0.10)	0.52	(0.11)	1.19
SHT	0.28	(0.04)	0.11	(0.02)	0.12	(0.02)	0.10	(0.04)	0.55
DRY	0.09	(0.01)	0.04	(0.01)	0.04	(0.01)	0.04	(0.01)	0.13
b) <i>Geum aleppicum</i>									
LF#	1.16	(0.05)	1.13	(0.05)	1.22	(0.06)	1.00	(0.06)	2.25
LEN	2.86	(0.09)	2.85	(0.10)	2.96	(0.16)	2.70	(0.09)	3.05
WID	1.99	(0.07)	1.95	(0.08)	2.01	(0.13)	1.87	(0.08)	2.24
AREA	3.49	(0.12)	3.54	(0.15)	3.67	(0.23)	3.37	(0.13)	4.24
SHT	0.61	(0.07)	0.60	(0.07)	0.69	(0.09)	0.47	(0.09)	1.62
DRY	0.23	(0.03)	0.24	(0.03)	0.27	(0.04)	0.20	(0.03)	0.78
c) <i>Sanguinaria canadensis</i>									
SHT	1.37	(0.07)	1.47	(0.09)	1.71	(0.10)	1.12	(0.05)	2.01
DRY	0.27	(0.01)	0.31	(0.03)	0.37	(0.03)	0.22	(0.02)	0.48
POD	0.16	(0.01)	0.15	(0.01)	0.18	(0.01)	0.12	(0.01)	0.16
TDRY	0.36	(0.02)	0.39	(0.03)	0.47	(0.04)	0.28	(0.02)	0.61

TABLE 21: Interdependence between phytometer response variables. Shown are correlation coefficients which represent the degree of linear association and 2-tailed probabilities (* 0.01; ** 0.001) between two response variables when FE and FR samples are pooled. The diagonal ([ ]) shows the direction of significant multivariate differences (MANOVA: * $p \leq 0.01$; ** $p \leq 0.001$; *** $p \leq 0.0001$) found between edge types for a given variable. FE = Forest Edges, FR = Fencerows, JL# = number of shoots persisting in July 1989, RTN = number of shoots regenerated after winter 1989-90, REP = number of additional shoots appearing in June 1990. N = 60 for all three species.

a) *Carex brunnescens*

JL#	[NS]			
MORPHOMETRY	0.733**	[NS]		
BIOMASS	0.670**	0.626**	[FE > FR]*	
RTN	NS	0.706**	0.879**	[NS]

b) *Geum aleppicum*

JL#	[NS]			
MORPHOMETRY	NS	[FE < FR]**		
BIOMASS	NS	0.470**	[FE < FR]*	
RTN	0.851**	NS	NS	[NS]

c) *Sanguinaria canadensis*

JL#	[FE > FR]***			
BIOMASS	NS	[FE < FR]***		
RTN	0.856**	NS	[NS]	
REP	0.816**	0.497*	0.943**	[NS]

FIGURE 1

Rarefaction curves for plant species richness in fencerows and forest edges. Sample size (n) is the number of individual observations included in calculation of the expected number of species, $E(S_n)$. (■) fencerows; (□) forest edges.

- a) Tree species richness
- b) Richness of woody species (includes tree and shrub species in all strata)
- c) Herbaceous species richness
- d) Richness of woodland interior species

a)

b)

FIGURE 2

Shrub layer richness as a function of edge length. Mean species richness (S) in shrub layers of forest edges and fencerows is calculated from mean richness per transect. Regression models and coefficients are based on S within a given length of edge. Error bars are ± 1 standard deviation from the mean. Data from both edge types fit the regression line well (from ANOVA, $p < 0.0001$). Adjusted R^2 represents how closely richness varies with variations in length.

a) Forest edges (n = 41).

b) Fencerows (n = 101).

FIGURE 3

Ground vegetation richness as a function of edge length. Mean species richness (S) in the ground layer of forest edges and fencerows. S is calculated from mean richness per transect. Error bars are ± 1 standard deviation from the mean. Regression models and coefficients are based on S within a given length of edge. Data from both edge types fit regression lines well (from ANOVA, $p < 0.0001$). Adjusted R^2 measures of how closely ground layer richness varies with variations in length.

a) Forest edges (n = 41).

b) Fencerows (n = 101).

FIGURE 4

Relative frequency (%) of modes of seed dispersal present in forest edge (FE) and fencerow (FR) vegetation. Dispersal modes: abiotic; biotic. Frequency is the number of plots in which each dispersal mode was present for each edge type. Abiotic dispersal here includes seeds dispersed primarily by wind. Biotic dispersal includes seeds dispersed by organisms other than the plant itself, particularly birds, mammals and ants. Dispersal modes based on Schopmeyer (1974) and Beattie & Culver (1981). Fisher's Exact Test for association of frequency of dispersal mode and edge type were significant at $p < 0.001$ in all strata. Sample sizes are given in parentheses below.

a) Canopy species (FE = 185, FR = 401)

b) Shrub layer species (FE = 265, FR = 459)

c) Ground layer species (FE = 300, FR = 315)

FIGURE 5

Relative frequency (%) of levels of shade tolerance in forest edge and fencerow canopy species. ● Tolerant; ◐ Intermediate; ○ Intolerant. Frequency is the number of plots in which each tolerance class was present for each edge type. Shade tolerance levels based on Fowells (1965). All G-tests ($DF = 2$) for association of shade tolerance with edge type were significant at $p < 0.0001$. Sample sizes are given in parentheses below.

- a) Canopy (FE = 185, FR = 401)
- b) Shrub layer (FE = 276, FR = 459)
- c) Ground layer (FE = 301, FR = 315)

FIGURE 6

Dendrogram of distance between fencerow (FR) and forest edge (FE) canopy vegetation. Squared Euclidean distance is shown, based on discriminant scores generated from combined abundance parameters for transects in each edge type. Discriminant analysis statistics were: eigenvalue = 123.00, Wilk's λ = 0.0081, and canonical r^2 = 0.996. Clusters were formed using average linkage between groups. Individual sites (FE #; FR #) are numbered and separated by horizontal lines.

FIGURE 7

Dendrogram of distance between fencerow (FR) and forest edge (FE) shrub layer vegetation. Squared Euclidean distance is shown, based on discriminant scores generated by differences between the two edge types in percent cover. Discriminant function statistics are: eigenvalue = 231.28, Wilk's λ = 0.0043, and canonical r^2 = 0.998. Clusters were formed using average linkage between groups. Main groups are labelled with site numbers (FE #; FR #).

FIGURE 8

Dendrogram of distance between fencerow (FR) and forest edge (FE) ground layer vegetation. Squared Euclidean distance is shown, based on discriminant scores generated by differences between the two edge types in percent cover. Discriminant function statistics were: eigenvalue = 86.78, Wilk's λ = 0.0114, canonical r^2 = 0.9943. Clusters were formed using average linkage between groups. Forest edge samples are labelled (*).

Distance

Site/Transect

FIGURE 9

Dendrogram of distance among fencerows (FR) in canopy structure. Squared Euclidean distance is shown, based on discriminant scores generated from combined vegetation abundance parameters. Clusters were formed using average linkage between groups. Individual sites are numbered (FR #).

a) Distance using discriminant scores determined in previous comparison with forest edge canopies.

b) Distance between discriminant scores generated on canopy abundance in fencerow samples. Discriminant function statistics were: eigenvalue = 9.276 for 50.04 percent of variance, Wilk's λ = 0.012 and canonical r^2 = 0.950. FR # = Individual fencerow sample.

a)

b)

FIGURE 10

Foliage density profiles in fencerow (FR) samples. Mean foliage density is plotted at the centre of each height interval. Means are based on transect means.

FR 1 (•), $n = 5$; FR 2 (+), $n = 5$; FR 3 (*), $n = 5$; FR 4 (□), $n = 7$;

FR 5 (X), $n = 5$; FR 6 (◇) $n = 5$; FR 7 (Δ) $n = 5$; FR 8 (○) $n = 6$.

FIGURE 11

Phytometer shoot persistence by month (1989) in fencerows (FR) and forest edges (FE).

Individual fencerow sites are shown (FR #).

FE , n = 162; FR 1 , n = 66; FR 2 , n = 40; Controls , n = 5.

a) *Carex brunnescens*

b) *Geum aleppicum*

c) *Sanguinaria canadensis*

APPENDICES

APPENDIX 1: Species list for the vegetation survey of fencerows and forest edges. Species are ordered by family. Nomenclature follows Gleason and Cronquist (1963).

Strata G S T	Botanical Name	Common Name	Habitat		Phenology
			1	2	
2	EQUISETACEAE <i>Equisetum pratense</i> Ehrh.	Horsetail	MW	W	PR
0	POLYPODIACEAE <i>Dryopteris marginalis</i> (L.) Gray.	Marginal Shield Fern	W	W	PR
0	<i>Athyrium filix-femina</i> (L.) Roth.	Lady Fern	UMW		PR
0	ARACEAE <i>Arisaema triphyllum</i> (L.) Schott.	Jack-in-the-Pulpit	MW	W	PC
2	CYPERACEAE <i>Carex</i> sp. L.	Sedge			
2	GRAMINEAE	Grasses			
1	LILIACEAE <i>Smilacina racemosa</i> (L.) Desf.	False Solomon's Seal	W	W	
2	<i>Maianthemum canadense</i> Desf.	Wild Lily of the Valley	MW	W	PR
0	<i>Polygonatum biflorum</i> (Walt.) Ell.	Solomon's Seal	MWE		PR
0	SALICACEAE <i>Salix bebbiana</i> Sarg.	Beaked Willow	E		
0	<i>Populus balsamifera</i> L.	Balsam Poplar	MWE		
1 1	<i>Populus tremuloides</i> Michx.	Trembling Aspen	Ds		
0 0	JUGLANDACEAE <i>Carya cordiformis</i> (Wang.) K.Koch	Bitternut	MW	W	

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APPENDIX 1: continued

Strata G S T	Botanical Name	Common Name		Habitat		Phenology
				1	2	
	CORYLACEAE					
2 2	<i>Corylus cornuta</i> Marsh.	Beaked Hazel		MWE	W	
2 2 2	<i>Ostrya virginiana</i> (Mill.) K.Koch.	Hophornbeam		W	W	
0 0 0	<i>Carpinus carolinianus</i> Walt.	Hornbeam		MW	W	
0	<i>Betula lutea</i> Michx. f.	Yellow Birch		MW	W	
0 0 0	<i>Betula papyrifera</i> Marsh.	White Birch		E		
	FAGACEAE					
2 2 1	<i>Quercus alba</i> L.	White Oak		MW	W	
	ULMACEAE					
2 2 2	<i>Ulmus americana</i> L.	White Elm		M		
2 2 2	<i>Ulmus rubra</i> Muhl.	Slippery Elm		MW	W	
	ARISTOLOCHIACEAE					
1	<i>Asarum canadense</i> L.	Wild Ginger		W	W	PR
1	<i>Rumex obtusa</i> L.	Bitter Dock		MDs		
	CARYOPHYLLACEAE					
1	<i>Cerastium arvense</i> L.	Mouse-eared Chickweed		UDs		P
2	<i>Silene cucubalus</i> Wibel.	Bladder Campion		UDs		
	RANUNCULACEAE					
2	<i>Ranunculus acris</i> L.	Buttercup		UDs		
1	<i>Clematis verticillaris</i> DC.	Mountain Clematis		W/Rock		
1	<i>Clematis virginiana</i> L.	Virgin's Bower		MWE		
2	<i>Actaea alba</i> (L.) Mill.	White Baneberry		W	W	P
2	<i>Actaea rubra</i> (Ait.) Willd.	Red Baneberry		W	W	P

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APPENDIX 1: continued

Strata G S T	Botanical Name	Common Name	Habitat		Phenology
			1	2	
0	BERBERIDACEAE <i>Caulophyllum thalictroides</i> (L.) Michx.	Blue Cohosh	MW	W	P
1 2	GROSSULARIACEAE <i>Ribes americanum</i> Mill.	Black Currant	MW	W	
2 2	<i>Ribes cynosbati</i> L.	Prickly Gooseberry	MW	W	
0	<i>Ribes lacustre</i> (Pers.) Poir.	Bristly Black Currant	MWE		
2 2	ROSACEAE <i>Spiraea alba</i> Du Roi	Narrow-leafed Meadow Sweet	M		
1 1	<i>Pyrus malus</i> Mill.	Apple	E		
2	<i>Fragaria vesca</i> L.	Wild Strawberry	U		P
2	<i>Potentilla recta</i> L.	Cinquefoil	ULsD		P*
1 1	<i>Amelanchier humilis</i> L.	Low Juneberry	D		
1 2 2	<i>Crataegus</i> sp. L.	Hawthorn	UDsWE		
2	<i>Geum aleppicum</i> Jacq.	Yellow Avens	MF		
2	<i>Geum canadense</i> (Mill.) K. Koch	White Avens	W	W	PR
2 2	<i>Rubus idaeus</i> Michx.	Red Raspberry	UDsWE		
2 2	<i>Rubus occidentalis</i> L.	Black Raspberry	WE		
0 0	<i>Rubus odoratus</i> L.	Flowering Raspberry	MWE	W	
0 0 2	<i>Prunus serotina</i> Ehrh.	Black Cherry	UDsE		
2 2 1	<i>Prunus virginiana</i> L. fil	Choke Cherry	UWE		
2	LEGUMINOSAE <i>Trifolium pratense</i> L.	Red Clover	UDs		P*
2	<i>Medicago lupulina</i> L.	Black Medic	UDs		*
1	<i>Lotus corniculatus</i> L.	Bird's Foot Trefoil	UDs		P*
2	<i>Vicia cracca</i> L.	Vetch	UDs		

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APPENDIX 1: continued

Strata G S T	Botanical Name	Common Name	Habitat		Phenology
			1	2	
2	OXALIDACEAE <i>Oxalis stricta</i> L.	Wood Sorrel	U		
2	GERANIACEAE <i>Geranium robertianum</i> L.	Herb Robert	MW	W	A
1 1 1	ACERACEAE <i>Acer negundo</i> L.	Box Elder	M		
1	<i>Acer nigrum</i> Michx.	Black Maple	M		
2 2 2	<i>Acer saccharum</i> Marsh.	Sugar Maple	MW	W	
2 2	RHAMNACEAE <i>Rhamnus alnifolia</i> L'Her	Buckthorn	M		
2 2	VITACEAE <i>Vitis riparia</i> Michx.	Frost Grape	MWE		
2 1	<i>Parthenocissus vitacea</i> (Knerr) Hitchc.	Virginia Creeper	MWE		
2 2 2	TILIACEAE <i>Tilia americana</i> L.	Basswood	M		
0	VIOLACEAE <i>Viola blanda</i>	Sweet White Violet	W	W	
0	<i>Viola emarginata</i>	Triangle-leaved Violet	WE		
2	<i>Viola pennsylvanica</i>	Smooth Yellow Violet	MWF		
2	ONAGRACEAE <i>Circaea quadrifida</i> (Maxim.) Franch. & Sav.	Enchanter's Nightshade	MW	W	P

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APPENDIX 1: continued

Strata G S T	Botanical Name	Common Name		Habitat		Phenology
		1	2	1	2	
1	UMBELLIFERAE <i>Daucus carota</i> L.	Queen Anne's Lace		UDs		B*
2 2 2	CORNACEAE <i>Cornus stolonifera</i> Michx.	Red-Osier Dogwood		UMWE		
1	PRIMULACEAE <i>Lysimachia ciliata</i> L.	Fringed Loosestrife		M		
2 2 2	OLEACEAE <i>Fraxinus americana</i> L.	White Ash		MW	W	
1	ASCLEPIADACEAE <i>Asclepias</i> sp. L.	Milkweed		UDs		
1	CONVOLVULACEAE <i>Convolvus arvensis</i> L.	Bindweed		UDs		•
2	LABIATAE <i>Prunella vulgaris</i> L.	Selfheal		UDs		P
1	PLANTAGINACEAE <i>Veronica officinalis</i> L.	Speedwell		DWF		P
1	RUBIACEAE <i>Galium</i> sp. L.	Bedstraw		U		

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APPENDIX 1: continued

Strata		Botanical Name	Common Name	Habitat		Phenology
G	S T			1	2	
1		CAPRIFOLIACEAE				
2	2	<i>Lonicera tatarica</i>	Tartarian Honeysuckle	WE		
2	2	<i>Viburnum lentago</i> L.	Nannyberry	MWEDs		
0		<i>Virburnum trilobum</i>	Highbush Cranberry	MW		
		COMPOSITAE				
2		<i>Solidago</i> sp. L.	Goldenrod	U		
0		<i>Aster prenanthoides</i> Muhl.	Crooked-stem Aster	MWE		PR
2		<i>Aster vimineus</i> Lam.	Small White Aster	MUDs		PR
2		<i>Aster</i> sp. L.	Aster			
2		<i>Erigeron philadelphicus</i> L.	Fleabane	UM		B
1		<i>Rudebeckia hirta</i> L.	Black-eyed Susan	UDs		B
1		<i>Achillea millefolium</i> L.	Yarrow	UDs		PR
2		<i>Chrysanthemum leucanthemum</i> L.	Ox-eye Daisy	UDs		PR*
2		<i>Cirsium arvense</i> (L.) Scop.	Canada Thistle	UDs		PR*
2		<i>Taraxacum officinale</i> Weber.	Common Dandelion	UDs		•
2		<i>Lactuca canadense</i> L.	Wild Lettuce	UDs		B

KEY:		Layer	Presence	Habitat affinity	Phenology
G	S				
Ground		0	Forest edge	1	Typical range of habitats
Shrub		1	Fencerow	2	Typically woodland specialists
Tree		2	Both	D	Dry, well drained
				Ds	Disturbed places
				E	Edges, fencerows, thickets
				F	Fields, meadows
				M	Moist, wet, poorly drained
				U	Ubiquitous, various habitats
				W	Woods, forests
				A	Annual
				B	Biennial
				P	Perennial
				•	Alien

APPENDIX 2a: Canopy vegetation summary for forest edges and fencerows. Means and standard errors of means (SE) for abundance measures are based on 100 m² plots. Disp = mode of seed dispersal, where A is abiotic and B is biotic; Tol = shade tolerance class, where 1 = tolerant, 0 = intermediate, -1 = intolerant.

Species	Disp Tol	Forest Edges (n = 14)						Fencerows (n = 34)					
		Cover		Basal Area (cm ²)		Density		Cover		Basal Area (cm ²)		Density	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<i>Acer saccharum</i>	A 1	61.79	6.72	14314.91	4940.22	4.07	1.74	1.18	.04	57.04	52.20	0.18	0.13
<i>Ostrya virginiana</i>	A 1	16.86	5.19	5196.01	3203.24	3.14	0.75	0.29	0.29	0.70	0.70	0.03	0.03
<i>Fraxinus americana</i>	A 0	17.21	3.82	2372.94	1118.29	3.43	0.1	37.06	5.06	6785.44	1507.29	3.50	0.55
<i>Tilia americana</i>	A 1	3.29	1.11	357.92	243.79	0.79	0.32	6.79	2.81	836.63	408.05	0.41	0.16
<i>Carpinus carolinianus</i>	B 1	4.00	2.16	208.19	125.17	0.64	0.34						
<i>Ulmus</i> spp.	A 0	1.21	0.76	30.33	15.74	0.36	0.17	5.71	1.67	197.81	86.43	0.59	0.13
<i>Prunus serotina</i>	B -1	1.14	0.77	64.25	34.48	0.21	0.11	3.53	2.02	139.60	90.15	0.29	0.19
<i>Cornus stolonifera</i>	B 1	0.79	0.71	3.72	2.54	0.14	0.10	0.74	0.52	4.19	3.64	0.06	0.04
<i>Crategeus</i> sp.	B -1	0.36	0.36	52.19	52.19	0.14	0.14	25.44	5.70	4388.78	1513.95	3.38	0.87
<i>Betula papyrifera</i>	A -1	0.36	0.36	46.21	46.21	0.14	0.14						
<i>Viburnum lentago</i>	B 1	0.07	0.07	9.48	9.48	0.07	0.07	8.24	3.76	2706.44	1814.98	1.47	0.69
<i>Prunus virginiana</i>	B -1	0.07	0.07	3.16	3.16	0.07	0.07	1.06	0.89	17.91	15.12	0.15	0.10
<i>Quercus alba</i>	B 0							15.74	3.38	1891.33	747.77	1.29	0.31
<i>Acer negundo</i>	A 1							2.21	1.25	139.88	114.28	0.18	0.15
<i>Pyrus malus</i>	B -1							1.47	0.86	38.95	26.12	0.09	0.05
<i>Populus tremuloides</i>	A -1							1.03	0.72	39.02	28.35	0.2	0.08
<i>Amelanchier humilis</i>	B 0							0.29	0.29	2.31	2.31	0.03	0.03
<i>Acer nigrum</i>	A 1							0.29	0.29	0.58	0.58	0.03	0.03
Total		107.15		22659.31		13.20		111.07		17246.61		11.80	

APPENDIX 2b: Shrub layer abundance summary for forest edges and fencerows. Percent cover and frequency are based on transect means for 3 X 3 m plots; n = number of transects in the sample. Importance value (IV) is the mean of relative cover plus relative frequency. No value means species was absent. Dispersal mode of seeds: A = abiotic; B = biotic.

Species	Dispersal Mode	Forest Edges (n = 14)				Fencerows (n = 68)			
		Cover	Frequency	Mean	SE	IV	Mean	SE	IV
<i>Acer saccharum</i>	A	29.45	6.04	3.64	0.13	18.47	1.46	0.61	0.32 0.14 1.46
<i>Fraxinus americana</i>	A	27.84	5.41	3.21	0.38	17.04	2.27	0.66	0.79 0.16 3.14
<i>Viburnum lentago</i>	B	11.95	4.99	2.36	0.36	9.13	24.27	3.21	1.91 0.19 14.17
<i>Tilia americana</i>	A	10.32	2.71	2.07	0.43	7.95	2.24	0.82	0.41 0.15 2.00
<i>Prunus virginiana</i>	B	8.95	2.29	2.21	0.33	7.66	23.53	2.79	2.15 0.17 14.63
<i>Ostrya virginiana</i>	B	5.23	2.14	1.57	0.62	5.00	0.00		0.03 0.03 0.09
<i>Vitis riparia</i>	B	4.21	2.61	1.43	0.34	4.33	13.65	2.78	0.97 0.23 7.66
<i>Cornus stolonifera</i>	B	4.66	1.68	1.29	0.30	4.24	10.27	2.07	1.06 0.21 6.75
<i>Carpinus carolinianus</i>	B	5.27	2.65	1.07	0.47	4.08			
<i>Ulmus</i> spp.	A	3.32	1.20	1.07	0.32	3.31	2.83	0.89	0.62 0.13 2.83
<i>Ribes cynosbati</i>	B	0.64	0.24	1.57	0.37	3.17	0.00		1.15 0.16 3.42
<i>Rubus occidentalis</i>	B	2.41	1.30	0.93	0.22	2.68	0.00		0.06 0.04 0.18
<i>Rubus idaeus</i>	B	3.34	1.78	0.64	0.36	2.52	8.83	2.11	1.65 0.21 8.00
<i>Crataegus</i> sp.	B	1.18	0.89	0.71	0.22	1.79	33.32	4.31	1.91 0.18 17.34
<i>Corylus cornuta</i>	B	2.34	1.25	0.43	0.17	1.73	5.04	1.45	0.50 0.16 3.25
<i>Quercus alba</i>	B	0.66	0.40	0.64	0.23	1.46	2.46	1.09	0.71 0.14 2.97

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APPENDIX 2c: Ground layer abundance summary for forest edge and fencerow vegetation. Percent cover and frequency are based on transect means for 1 X 1 m plots; n = number of transects in the sample. Importance value (IV) is the mean of relative cover plus relative frequency. No value means species was absent.

Species	Forest Edges (n = 14)				Fencerows (n = 68)			
	Cover		Frequency		Cover		Frequency	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<i>Acer saccharum</i>	25.53	5.19	6.43	0.40	24.70		0.38	0.17
<i>Fraxinus americana</i>	5.01	0.95	4.00	0.30	8.07		0.19	0.07
<i>Prunus virginiana</i>	3.58	1.18	3.29	0.51	6.28		0.37	0.07
<i>Viola</i> spp.	4.02	1.12	2.79	0.59	5.98		1.44	0.13
<i>Gramineae</i>	6.37	1.23	1.14	0.21	5.62		0.85	0.14
<i>Rubus idaeus</i>	4.73	1.78	1.43	0.37	4.86		2.47	0.15
<i>Tilia americana</i>	2.97	0.95	2.07	0.56	4.43		1.87	0.14
<i>Solidago</i> spp.	3.92	1.53	1.29	0.34	4.15		0.09	0.04
<i>Carex</i> sp.	1.85	0.56	2.07	0.47	3.68		0.78	0.11
<i>Circaea quadrisulcata</i>	2.82	1.14	1.36	0.43	3.49			
<i>Fragaria vesca</i>	2.04	0.70	1.71	0.44	3.38		1.94	0.40
<i>Ulmus</i> spp.	0.75	0.26	1.50	0.43	2.27		0.12	0.06
<i>Parthenocissus vitacea</i>	1.04	0.38	1.29	0.35	2.22		7.44	0.92
<i>Ostrya virginiana</i>	0.75	0.24	1.43	0.40	2.19			
<i>Rubus occidentalis</i>	1.93	0.92	0.64	0.25	2.05			
<i>Ribes cynosbati</i>	0.89	0.38	1.00	0.33	1.78		2.09	0.38
							0.88	0.12
								3.46

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APPENDIX 2c: continued.

Species	Forest Edges (n = 14)				Fencerows (n = 68)			
	Cover		Frequency		Cover		Frequency	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
IV								
<i>Prunella vulgaris</i>	0.06	0.04	0.21	0.11				
<i>Quercus alba</i>	0.10	0.09	0.14	0.10	0.31	0.18	0.15	0.05
<i>Carya cordiformis</i>	0.04	0.04	0.07	0.07				0.56
<i>Betula papyrifera</i>	0.04	0.04	0.07	0.07				
<i>Asarum canadense</i>					2.47	0.99	0.22	0.08
<i>Clematis virginiana</i>					2.09	0.75	0.28	0.08
<i>Crataegus</i> sp.					1.03	0.26	0.40	0.08
<i>Geum aleppicum</i>					0.26	0.06	0.35	0.07
<i>Vicia cracca</i>					0.37	0.15	0.22	0.07
<i>Polygonatum biflorum</i>					0.17	0.09	0.19	0.07
<i>Medicago lupulina</i>					0.29	0.14	0.10	0.04
<i>Trifolium repens</i>					0.13	0.07	0.13	0.05
<i>Rhamnus alnifolia</i>					0.35	0.21	0.07	0.03
<i>Acer negundo</i>					0.12	0.07	0.09	0.04
<i>Geranium robertianum</i>					0.15	0.08	0.07	0.03
<i>Achillea millefolium</i>					0.05	0.04	0.04	0.03
Total	74.53		42.44		89.16		19.20	

APPENDIX 3a: Horizontal foliage density in fencerows. Means and standard errors of means (SE) are based on mean foliage density per transect, and n = number of transects sampled in each fencerow. a Above 2 m, values represent mean frequency of samples with foliage density > 20%.

Height (m)	FR 1 (n = 5) Mean SE	FR 2 (n = 5) Mean SE	FR 3 (n = 5) Mean SE	FR 4 (n = 7) Mean SE	FR 5 (n = 5) Mean SE	FR 6 (n = 5) Mean SE	FR 7 (n = 5) Mean SE	FR 8 (n = 6) Mean SE
> 2*	10.00 0.00	8.20 0.37	5.20 0.58	4.43 0.78	6.60 0.68	9.40 0.51	5.60 0.24	10.67 0.33
1.5-2	47.80 4.20	68.82 1.65	60.50 8.63	21.34 6.06	45.13 8.82	42.17 4.93	47.17 8.39	44.72 3.41
1-1.5	37.20 3.05	61.78 3.18	61.50 5.67	12.57 3.02	44.87 7.24	43.42 5.10	46.83 9.97	41.81 1.94
0.5-1	36.50 2.80	61.29 3.37	47.50 4.55	32.97 5.14	45.50 4.12	47.25 4.86	38.50 5.72	51.53 0.84
< 0.5	45.70 5.82	70.17 3.19	61.17 2.91	86.41 3.49	55.75 6.43	63.42 6.71	64.67 3.62	65.56 6.74

APPENDIX 3b: ANOVA results for comparisons of foliage density among eight fencerows

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Height (m)	F ratio	p
> 2	17.089	<0.0001
1.5-2	5.211	0.0005
1-1.5	7.103	<0.0001
0.5-1	3.480	0.007
< 0.5	9.755	<0.0001

All F ratios have degrees of freedom = 7,32

APPENDIX 4a: Summary of architectural elements present in fencerows.

Var	FR 1 (n=5)		FR 2 (n=5)		FR 3 (n=5)		FR 4 (n=5)		FR 5 (n=5)		FR 6 (n=5)		FR 7 (n=5)		FR 8 (n=6)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
T5	1.60	1.03	0.60	0.40	3.20	0.86	2.00	1.38	5.80	0.80	8.20	0.37	4.80	0.37	4.17	0.91
T4	6.40	1.57	3.60	1.36	4.60	1.17	6.60	0.75	7.20	0.37	9.80	0.80	5.60	0.24	4.83	0.54
T3	5.20	1.24	0.40	1.81	4.00	1.05	5.60	0.40	4.80	0.97	6.80	0.97	4.40	0.51	4.33	0.49
T2	3.00	0.63	3.00	1.67	2.20	0.66	1.00	0.32	2.60	0.51	2.00	0.71	3.00	0.45	3.67	0.33
T1	1.60	0.24	1.40	0.75	1.00	0.45	0.60	0.24	1.60	0.40	1.40	0.60	2.80	0.49	2.33	0.21
S5	0.20	0.20	0.00		0.00		0.00		0.00		0.00		0.00		0.00	
S4	4.20	0.97	0.40	0.40	0.40	0.40	0.40	0.40	0.00		0.60	0.40	0.00		0.17	0.17
S3	9.80	0.49	7.40	0.68	5.20	0.49	1.80	0.66	5.20	1.24	8.40	1.44	5.20	0.37	5.33	0.33
S2	9.20	0.73	8.20	0.37	6.00	0.00	5.20	0.73	6.80	0.58	10.20	0.58	5.60	0.40	5.83	0.17
S1	8.20	0.58	8.20	0.20	5.80	0.20	6.60	0.51	6.20	0.58	9.40	0	5.40	0.40	5.67	0.21
V4	4.20	1.20	1.00	0.63	0.60	0.24	0.00		0.00		0.20	0.20	0.00		0.00	
V3	7.00	1.05	4.00	1.14	3.20	0.37	0.20	0.20	0.00		2.00	1.38	0.60	0.40	0.50	0.34
V2	5.80	0.86	4.80	1.16	2.80	0.49	2.00	1.30	0.80	0.58	4.00	1.70	0.60	0.40	0.83	0.48
V1	8.20	0.66	6.00	1.58	3.40	0.68	5.80	0.73	5.60	0.51	7.60	1.50	2.80	0.37	2.50	0.22
W3	1.20	0.73	0.40	0.40	0.00		0.40	0.40	1.80	0.80	1.00	0.55	0.20	0.20	0.33	0.21
W2	4.40	0.68	1.80	0.80	0.40	0.24	0.40	0.24	1.20	0.73	2.40	1.12	1.00	0.45	1.17	0.31
W1	8.60	0.75	6.40	0.68	1.80	0.37	4.80	0.37	4.60	1.17	4.60	0.51	4.00	0.32	4.00	0.26

APPENDIX 4a: continued.

Var	FR 1 (n=5)		FR 2 (n=5)		FR 3 (n=5)		FR 4 (n=5)		FR 5 (n=5)		FR 6 (n=5)		FR 7 (n=5)		FR 8 (n=6)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
G2	1.80	0.58	3.60	0.60	4.00	0.55	6.40	0.93	4.60	0.93	6.00	1.05	2.00	0.32	2.50	0.43
G1	3.80	0.37	3.80	.58	5.00	0.55	7.60	0.40	5.60	0.68	6.40	0.93	2.20	0.37	2.67	0.42
F2	0.80	0.49	1.80	0.58	2.00	0.45	1.80	0.58	0.20	0.20	3.60	0.93	1.40	0.40	2.17	0.31
F1	5.40	0.40	7.40	1.03	4.80	0.20	7.40	0.40	3.60	1.12	5.40	1.03	4.20	0.58	4.33	0.21
MS	7.60	0.68	8.60	0.40	5.60	0.40	6.80	0.37	5.20	0.73	8.40	0.68	5.60	0.24	5.67	0.21
RK	26.62	5.04	5.63	3.39	13.42	0.91	1.12	1.12	0.00		17.77	2.32	9.06	2.27	3.34	1.55
LT	70.34	9.38	98.38	1.35	81.77	5.08	84.65	3.17	91.63	2.91	89.97	2.86	93.58	2.82	95.33	1.64

Variables (Var): T = tree stems and branches; S = shrub stems and branches; V = vines; W = coarse woody debris; G = grasses; F = forbs; MS = mosses; RK = rock cover (%); LT = litter cover (%). Numbers in variables indicate height intervals (m): 5 = > 7 m; 4 = 3.5-7; 3 = 1.5-3.5; 2 = 0.5-1.5; 1 = < 0.5. Means and standard errors of means (SE) are based on transect mean frequency, and n is the number of transects sampled in each fencerow. Mean rock and litter cover are based on percent cover in 1 X 1 m plots along n transects in each fencerow.

APPENDIX 4b: Multiple tests for differences among fencerows in the frequency of architectural elements.

Height (m)	Coarse Woody									
	Trees	Shrubs	Vines	Debris	Grasses	Fu.bs	Mosses	Rock	Litter	
> 7	100.385*	5.167								
	<0.0001	0.640								
3.5-7	50.708	68.382	77.063							
	<0.0001	<0.0001	<0.0001							
1.5-3.5	13.713	70.874	97.917	16.830						
	0.057	<0.0001	<0.0001	0.019						
0.5-1.5	31.943	22.108	44.924	24.170	51.085	24.818				
	<0.0001	0.0024	<0.0001	0.001	<0.0001	0.0008				
< 0.5	29.221	15.014	18.867	35.154	61.701	50.367	34.541	75.628	35.291	
	0.0001	0.036	0.009	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	

a The upper numbers are Kruskal-Wallis χ^2 statistics, corrected for ties. Below is the significance of χ^2 . Separate contingency test results were the same as those presented above.

APPENDIX 5a: Summary of relative contribution of architectural elements to fencerow structure.

Var	FR 1 (n=5)		FR 2 (n=5)		FR 3 (n=5)		FR 4 (n=6)		FR 5 (n=5)		FR 6 (n=5)		FR 7 (n=5)		FR 8 (n=6)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
TRE	0.24	0.08	0.23	0.11	0.33	0.11	0.26	0.06	0.23	0.07	0.23	0.10	0.57	0.21	0.81	0.08
SHR	2.04	0.14	2.21	0.23	1.98	0.11	1.68	0.28	1.27	0.14	1.90	0.06	1.84	0.20	1.61	0.11
GAP	2.07	0.17	1.43	0.09	1.67	0.21	2.41	0.21	2.13	0.31	2.27	0.21	1.70	0.18	1.75	0.10
ROC	1.07	0.05	0.24	0.15	1.45	0.09	0.06	0.06	0.00		0.58	0.12	0.58	0.11	0.17	0.07
SIZ	1.30	0.09	0.88	0.14	0.49	0.14	1.07	0.11	0.70	0.25	0.52	0.06	0.99	0.12	1.08	0.21
CND	2.17	0.28	2.17	0.20	0.77	0.23	1.40	0.07	1.40	0.43	1.07	0.08	1.91	0.19	1.97	0.18
POS	2.24	0.21	1.90	0.15	0.51	0.16	0.73	0.15	0.75	0.28	0.58	0.11	0.66	0.06	1.03	0.22

Variables (Var): TRE = tree stems (> 0.5 cm dbh); SHR = shrub density; GAP = sub-canopy gaps; ROC = rock size; SIZ = diameter of coarse woody debris (CWD); CND = condition of CWD; POS = position of CWD. Class limits and measurement methods are discussed in the text. Means and standard error of means (SE) are based on mean contribution in each transect, and n = number of transects sampled in each fencerow.

APPENDIX 5b: Comparison of the contribution of architectural elements to structure among eight fencerows.

Architectural Element	Kruskal-Wallis Chi ²	p
Tree stem diameter	0.148	0.701
Shrub density	1.084	0.298
Sub-canopy gap size	15.071	0.0001
Rock size	19.124	<0.0001
Coarse woody debris (CWD) size	4.546	0.033
CWD condition	1.271	0.260
CWD position	1.376	0.241
Fence type	0.077	0.781

Kruskal-Wallis test statistics are corrected for ties.

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