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COMPOSITION AND STRUCTURE OF FOREST EDGE IN BEECH-SUGAR
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COMPOSITION AND STRUCTURE OF FOREST EDGE IN BEECH-SUGAR MAPLE AND OAK FRAGMENTS IN CENTRAL LOWER MICHIGAN

By

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ABSTRACT

COMPOSITION AND STRUCTURE OF FOREST EDGE IN BEECH-SUGAR MAPLE AND OAK FRAGMENTS IN CENTRAL LOWER MICHIGAN

By

Brian Josef Palik

Edge-to-interior gradients of trees and shrubs were examined in four hardwood forest fragments. In general, edge forest was characterized by higher stem densities and a greater number and importance of less tolerant and disturbance-oriented species, relative to the interior. The development and depth of edge characteristics was dependent upon aspect, size, and the disturbance history of a site. Edge conditions were best developed in: 1) an old-growth fragment on the southern aspect; and 2) a very small fragment with a major disturbance in the northern aspect forest. In two formerly grazed fragments edge conditions were less well developed, presumably as a result of edge-species elimination during grazing. Landscape-level management plans should consider not only size, but disturbance history and successional status of a site when estimating the amount of interior forest present in a specific fragment.

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The refuge provided by my family throughtout my graduate career has kept me relatively sane and I am delighted that they will remain within reach during the next step. Finally, I thank Andrew and Josef, their love of trees has been my light in the forest.

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INTRODUCTION

The postsettlement history of land use in the eastern United States has been marked by large scale deforestation and landscape conversion. Within a span of two to three generations, the once contiguous Eastern Deciduous Forest has been reduced to a patchwork mosaic of isolated forest fragments surrounded by agricultural and urbanized land (Hill 1985; Whitney & Somerlot 1985).

Forested areas normally are influenced by natural disturbances ranging from individual treefalls (Bray 1956; Runkle 1982; Donnelly 1986) to fire, catastrophic blowdown, and insect infestation (Heinselman 1973; Pickett 1979; Dunn et al. 1983; Sprugel 1984). None of these, however, have the impact that human-induced deforestation and landscape conversion have on ecosystem stability and preservation (Curtis 1956; Burgess & Sharpe 1981; Wilcove et al. 1986).

The value of forested areas often involves qualities that are difficult to measure. These include watershed stability, climate modification, erosion control, habitat and species diversity, and aesthetic appeal (Bormann & Likens 1979; Hill 1985). Futhermore, forests provide direct economic contributions through lumber, pulpwood, fuelwood and recreation (Kittredge 1948; Curtis 1956; Hill 1985).

Remnant forest fragments are the last strongholds in much of the eastern United States for the ecosystems that once dominated the landscape. Any hope of preserving present landscape characteristics and recovering some degree of presettlement landscape characteristics must focus on the vegetation that remains. Therefore, a thorough understanding of forest fragments is vital.

One of the ways in which the effects of fragmentation are manifest is through the development of edge forest (Ranney 1978). Studies focusing on the role of edge forest in the matrix created through landscape conversion have been limited. Because the effectiveness of potential landscape-level management plans that involving forest fragments may be dependent on an understanding of the role of edge forest in the matrix, additional research quantifying the characteristics and extent of edge forest are of value.

In its original context edge forest was viewed as beneficial, primarily with respect to wildlife management (Leopold 1933). Attainment of maximum animal species diversity in a given area could be accomplished by increasing habitat diversity. Since edge forest provides a transitional habitat between interior forest and the surrounding landscape, fragmentation of a large forest into several smaller fragments would increase edge habitat at the landscape level, and thereby increase species diversity. This has been demonstrated empirically for bird and butterfly communities (Karr 1968; Gates & Gysel 1978; Strelke & Dickson 1980; Lovejoy et al. 1986).

The use of numerous small terrestrial islands, with their high proportion of edge habitat, has been proposed as a possible management approach for maintaining high species diversity (Simberloff & Abele 1976). Unfortunately, this approach is biased towards edge species, i.e. those species that are either not characteristic of, or as abundant in, the original habitat type (Diamond et al. 1976). Further, the desirability of high species diversity must be questioned when applied to mature forests of eastern North America. Many of these ecosystems typically have low tree diversity (Levenson 1981; Middleton & Merrium 1985). If the optimal goal of a management strategy is the preservation of whole ecosystems characteristic of the presettlement landscape, edge habitat must be minimized. This requires recognition and understanding of the effects of edge. The present study examined edge-to-interior gradients in the tree and shrub strata of four small fragments of temperate deciduous forest located in the agricultural landscape of central lower Michigan.

Forest Islands and Edge

The analogy of isolated terrestrial ecosystems to oceanic islands has resulted in numerous attempts to explain their patterns of species diversity in terms of island biogeographic theory (MacArthur & Wilson 1967; Miller & Harris 1977; Lovejoy et al. 1983, 1986; Harris 1984; Wilcove et al. 1986). Although direct application of species-area relationships to the vegetation of forest fragments appears invalid (Helliwell 1976; Levenson 1981; Middleton & Mirriam 1983; Forman & Godron 1981), theories relating species diversity to a complex function incorporating habitat diversity, disturbance, area, age, heterogeneity of the surrounding landscape matrix, isolation and discreteness of boundaries seem more tenable (Forman & Godron 1981).

Fragmentation and continued reduction in forest island size is accompanied by an increase in perimeter/area ratio, increasing the amount of forest edge. This favors more shade intolerant plant species (Whitney & Somerlot 1985). Levenson (1981) found that fragments of the southern-mesic forest in Wisconsin were subject to retrogressive succession below 2.3 ha in area, becoming essentially all-edge forest, composed of intolerant and residual tolerant species. Ranney et al. (1981), also working in southern-mesic fragments in Wisconsin, found clear distinctions in composition between edge and interior forests. The edge forest, defined as successionally younger, was characterized by more intolerant species relative to the more closed, light-limited interior forest.

These findings point to the negative effects of size reduction, with its corresponding increase in edge effects, on the characteristic vegetation of a particular forest type. Further, the necessity of determining the minimum critical size of an ecosystem required to assure its dynamic equilibrium, or continued successional development, becomes apparent (Lovejoy & Oren 1981).

Two important components of forest fragmentation, area reduction and isolation, may combine to facilitate edge forest development (Wilcove et al. 1986). As interfragment distance increases, the pattern of seed input into a fragment may be altered (Curtis 1956). Wind- and mammal-dispersed species become increasingly disadvantaged compared to bird-dispersed species, because of the relatively low mobility of these dispersal mechanisms (Auclair & Cottam 1971).

This suggests that diaspore input into isolated forest fragments may be disproportionately biased towards edge species, a high percentage of which are bird-dispersed (Ranney 1978). Fragment size reduction, with a corresponding increase in edge habitat, assures the availability of safe sites for the bird-dispersed edge species. Conversely, if characteristic interior species are not bird-dispersed their establishment in earlier successional forests may be limited or impossible given large interfragment distances and a minimal availability of interior safe sites (Levenson 1980).

There are two important exceptions to the edge species-bird-dispersed species scenario not addressed by the above authors. Propagules of American beech (Fagus grandifolia Ehrh.[1]), an important interior species in beech-maple forests (Ranney et al. 1981), are dispersed up to 4 km by bluejays (Johnson & Adkisson 1985). Acorns of some species of oak (Quercus spp.) are dispersed up to 1.9 km by bluejays (Darley-Hill & Johnson 1981). The classification of oaks as edge or interior species is dependent on the forest type in question, e.g. in a beech-maple forest, red oak (Q. rubra L.) might be considered an edge species (Wales 1972; Ranney 1978), however in mesic oak sites the species is important in the interior forest. These exceptions suggest that, at least for some species, isolation by itself may not present a major barrier to dispersal.

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[1] Nomenclature follows Gleason & Cronquist 1963.

The Microclimatic Gradient

Edge Effects

Although all forests are strongly influenced by the surrounding climatic regime, the impact is greater on isolated forest fragments as a consequence of their increased perimeter/area ratios (Ranney et al. 1981). There is increased penetration of light into the edge forest relative to the interior resulting from a large lateral exposure (Hutchinson & Matt 1976a, 1977). The edge forest may thus be subjected to greater net radiation or higher temperature than the interior, two conditions which in general can increase evapotranspiration (Salisbury & Ross 1969; Rosenberg et al. 1983). Wind can also increase evapotranspiration (Rosenberg et al. 1983), although the lowering of air and soil temperature by wind may somewhat dampen the increase (Geiger 1965). Differing wind velocities between edge and interior forest may thus contribute to microclimatic differences. These effects may combine to establish a complex microclimatic gradient (Whittaker 1975) from outside the fragment to its interior. Wales (1972) and Ranney et al. (1981) state that since different species respond characteristically to different microclimates, a corresponding vegetational gradient may develop. The applicability of gradient analysis to such studies led Whittaker to describe the edge-interior forest transition as a microecocline (Wales 1972).

The microclimatic gradient may involve both varying light and moisture regimes from the edge to the interior, such that edge forest might be categorized as being less light-limited and more xeric relative to interior forest. The gradient develops as a consequence of decreasing exposure to wind and light, from edge-to-interior, rather than topographic or soil differences within the fragment.

A further consequence of the large lateral exposure of the edge forest is the mechanical effects of the wind. Edge tree crown geometry is more characteristic of open grown trees than of streamlined, slender interior trees. The edge trees are buffeted by wind which may cause increased incidence of branch breakage (Moen 1979). Branch breakage may result in decreased vigor and increased mortality. The potential for catastrophic windthrow and windsnap is increased at the forest edge (DeWalle 1983; Franklin & Forman 1987). In Amazonian forest fragments of Brazil an increased incidence of tree fall at the forest edge has been reported (Lovejoy et al. 1986). Even small gaps at that forest edge may provide increased habitat for opportunistic species, above that already provided by the edge condition. Species which are best able to adapt to the increased disturbance regime of the edge may be more important in the edge forest.

Aspect Effects

The amount of solar radiation and wind to which an edge is exposed varies with aspect (Wales 1972). The non-uniformity of climatic conditions on the different aspects of a forest fragment suggests that the magnitude of the proposed microclimatic gradient from edge-to- interior may also vary with aspect.

Past studies have demonstrated that vegetational composition varies on north and south slopes within a forest (Cantlon 1953; Zager & Pippen 1977). Although these researchers were not examining edge effects, clearly the analogy of slope to aspect can be made.

Empirical Evidence for the Microclimatic Gradient

Although the existence of a microclimatic gradient may be intuitively obvious, studies which specifically examined microclimatic variation along edge-to-interior forest gradients have been limited. The data however, do support the existence of microclimatic differences between edge and interior forest.

Wales (1967) examined several microclimatic variables on the north and south borders, and in the interior, of an oak-hickory forest in New Jersey. He found that the greatest accumulations of snow occurred within the first 25 meters of the forest on the northern aspect. Further, snow melt was most rapid in the southern border forest. This may translate into seasonal variations in soil moisture and temperature regimes between different areas of a forest. Both maximum and minimum air temperatures, in a profile 5 cm to 2 m above the forest floor, were highest at the boundary of the southern aspect forest. The difference was as great as 14^{o} C in the summer. Light penetration, as percent of full sunlight, generally decreased from the edge to 25 meters into the forest in the winter and spring leafless conditions. The pattern in the summer, subsequent to full leaf flush, was not demonstrative of a clear edge-to-interior gradient. However, in a similar study, August light intensities on the northern aspect of a shortleaf pine (Pinus echinata Mill.) stand were found to decrease

65% between the stand edge and 30 m into the forest (Oosting & Kramer 1946).

In the same shortleaf pine stand, available surface soil moisture (to 15 cm depth) increased between the stand edge and points 4 m and 15 m into the forest on the northern aspect, although the differences between the measurement points were not significant (Oosting & Kramer 1946). This may reflect the more mesic condition of the northern aspect forest, whereas in the forest on the southern aspect, a steeper moisture gradient would be expected.

Studies examining wind profiles in forests have shown that wind velocities may be reduced 5-15% at the the forest boundary (Kittredge 1948; Hutchison & Matt 1976b). Reifsnyder (1955) found reductions of 30-50% at 50 m into the forest (depending on temperature conditions, height above the forest floor and original wind velocity), in a small ponderosa pine stand (Pinus ponderosa Dougl.). Although not directly measured, an edge-to-interior gradient is implied in these studies. In the Amazonian forest fragments referred to previously, Lovejoy et al. (1986) report increases in relative humidity of 5-20% and decreases in air temperature of 4-5° C between boundary forest and interior forest.

The Vegetational Gradient

Studies focusing on the edge-to-interior vegetational gradient that develop in response to the microclimatic gradient in forest fragments have been limited in number. Gysel (1951) studied edge-interior distinctions in several sugar maple-beech fragments in

Michigan. While both north and south aspects were examined no distinction between them was made in the analysis. He reported that edge conditions extended 2-12 m into the forest, and were characterized by a higher sapling density, relative to the interior.

Additionally, there were numerous compositional distinctions between edge and interior forest, such as the restriction of hawthorn (*Crataegus* spp.), yellow-poplar (*Liriodendron tulipifera* L.) and sassafras (*Sassafras albidum* (Nutt.) Nees) to the edge forest, and American beech to interior forest. Many species had a higher frequency of occurrence in the edge forest including: bitternut hickory (*Carya cordiformis* (Wang.) K. Koch); pignut hickory (*C. glabra* (Mill.) Sweet); white ash (*Fraxinus americana* L.); black cherry (*Prunus serotina* Ehrh.); red oak; and basswood (*Tilia americana* L).

Gysel found that edge-interior compositional differences were also evident in the shrub community. Gooseberry (*Ribes cynosbati* L.), staghorn sumac (*Rhus typhina* L.), and three species of *Rubus* were restricted to edge forest, while the converse was true of witch-hazel (*Hamamelis virginiana* L.) and mapleleaf viburnum (*Viburnum acerifolium* L.).

Gysel described the open growth crown geometry of edge trees, some of which had low-growing horizontal limbs extending 10 meters in the direction of the forest boundary. The increased crown growth response of trees bordering forest openings has been examined in detail by subsequent researchers (Trimble & Tryon 1966; Runkle & Yetter 1987). Finally, similarities in composition between edge forest and recovering gaps were noted. This may reflect a parallel in resource availability in the two situations.

Wales (1972), in a study that compared north edge, south edge and interior forest in a mature oak-hickory stand, found that edge forest extended approximately 20 m into the fragment on the southern aspect, and 10 m on the northern aspect. Like Gysel (1951), he noted a similarity between edge forest and recovering gaps in horizontal and vertical structure. Total tree density, and densities and basal areas of many individual canopy species were highest at or near the edge. These included species characterized as shade intolerant or those capable of vegetative reproduction, such as white ash, sassafras, black oak (_Quercus_ _velutina_ Lam.), black cherry and shagbark hickory (_Carya_ _ovata_ (Mill.) K. Koch). The latter two species were not found as large individuals in the interior forest.

In addition to the differences in extent of edge forest between aspects, other aspect distinctions included: a greater abundance of less tolerant species on the southern aspect relative to the northern aspect; more than three times higher densities of oak seedlings and saplings in the southern edge forest than on the northern aspect, or in the interior forest; and higher cover values for blackberry (_Rubus_ _allegheniensis_ Porter) and Japanese honeysuckle (_Lonicera_ _japonica_ Thunb.) in the first 15 m of forest on the southern aspect.

Ranney _et_ _al_. (1981) found that in beech-maple forest fragments of southeastern Wisconsin, edge forest extended approximately 10 m into the interior on the northern and eastern aspects, and 20 m on the southern and western aspects. The edge forest supported up to 50% more basal area than the interior and had higher stem densities. Although these findings do indicate structural variation along the gradient, they should not be misconstrued as suggesting superior site quality of the edge forest because no comparison of tree heights, volumes or biomass differences between edge and interior was given.

Community index values (Curtis 1959) were lower in the edge forest relative to the adjacent interior. This was the result of an edge-to-interior gradient of decreasing importance values for intermediate and intolerant species such as basswood, smooth serviceberry (Amelanchier laevis Wieg.), red oak, white oak (Quercus alba L.), bur oak (Q. macrocarpa Michx.), roundleaf dogwood (Cornus rugosa Lam.), hawthorn spp. (Crataegus), hickory spp. (Carya), willow spp. (Salix), trembling aspen (Populus tremuloides Michx.), boxelder (Acer negundo L.), slippery elm (Ulmus rubra Muhl.) and ash spp. (Fraxinus), and increasing importance values for very tolerant sugar maple and beech and intermediate red maple (Acer rubrum L.).

Although they provided no direct evidence Ranney et al. (1981) stated that edge forest on the southern and western aspects provided a permanent xeric habitat as a result of greater exposure to drying microclimatic conditions, relative to the northern and eastern aspects, in an otherwise mesic fragment. They concluded that this condition allowed species of more xeric habitats, such as hawthorn, bur oak, hickory and prickly-ash (Zanthoxylum americanum Mill.) to exist in the fragment. This distribution, rather than being in response to soil moisture differences, may be more of a reflection of the shade intolerance of these species, thus they were more abundant in edge forest because it is less light-limited than interior forest.

The results of the above study, which are often cited in the literature, and those of Gysel (1951), are potentially misleading in regards to the extent of edge forest penetration. Values reported were averages derived from numerous fragments, sites which the authors stated were relatively homogeneous in terms of management history and present condition. Personal observation indicates that in an urban-agricultural matrix it is unlikely that this is true, thus warranting an individualistic approach to edge analysis. Examining the influence of different fragment histories and conditions on edge forest characteristics may be requisite for determining how variable is edge forest across a landscape.

Whitney and Runkle (1981) examined edge-interior forest distinctions in an old-growth beech-maple forest in Ohio. They found that species composition in the first 10 m of edge forest on the western aspect of the old-growth forest had greater similarity to the interior of an adjacent second-growth forest than to the interior of the old growth forest itself. Compositional characteristics of edge forest included higher densities and basal areas of red oak, shagbark hickory, blue-beech (Carpinus caroliniana Walt.), basswood, white ash and ironwood (Ostrya virginiana (Mill.) K. Koch), relative to the interior forest. The converse was true for sugar maple and beech. No attempt was made to examine aspect differences.

None of the above studies sampled beyond 30 meters from the forest boundary, and although Gysel (1951), Wales (1972) and Whitney & Runkle (1981) did compare edge plots with those of the interior, more extensive linear sampling along the edge-to-interior gradient is necessary to firmly establish the extent of edge conditions in specific forest fragments.

Fragment Disturbance and Edge History

An examination of an edge-to-interior gradient must consider the effects of disturbance, both natural and anthropogenic, on the composition and structure of the vegetation. Wales (1972) described treefall gaps and paths as "noise" with the potential to mask edge effects in gradient analysis. Donnelly (1986) found that black cherry and yellow-poplar (Liriodendron tulipifera L.) were associated with areas of more open canopy, such as steep slopes and poorly-drained depressions, in a beech-sugar maple forest in southern Michigan. The presence of these internal edges may account for edge species in the interior forest, particularly in fragments below a minimum critical size where no area is very far from edge forest, and consequently the seed rain into the interior may be dominated by edge species (Ranney et al. 1981).

The management history of a fragment or its edge may influence the composition and structure of the gradient (Gysel 1951; Wales 1972). For example, grazing and selective tree removal, by reducing competition and creating a more open habitat in a fragment large enough to normally support interior forest, provide conditions favorable to opportunistic species and may promote the development of edge-like conditions throughout (Auclair & Cottam 1971), thus obscuring any gradient of forest structure and composition. Whether or not interior conditions can redevelop may depend on the magnitude of the disturbance and the size of the fragment. In newly created edge that exposes interior forest to edge conditions for the first time, it may take several decades for edge species to become established and structural distinctions to develop.

Heterogeneity of the Landscape Matrix

In addition to variability induced by individual site history, the characteristics of the surrounding landscape matrix may influence edge structure and composition (Forman and Godron 1986). In an agricultural landscape, pesticide and herbicide use, artificial tile drainage, and irrigation practices may influence the development and persistence of forest edge in a site specific manner. Natural features of the surrounding matrix including soil structural and drainage characteristics (i.e., rocky or poorly drained soils) and topographic features may also influence edge structure and composition. Corridors and windbreaks adjacent to a fragment may alter the biotic and abiotic influences acting on a site, relative to an isolated fragment without these structures (Forman and Godron 1986). Heterogeneity of the landscape matrix may therefore introduce a variable, additional to site specific disturbance and management history, with the potential to influence edge and fragment characteristics.

Research Hypotheses and Objectives

This research examined edge-interior forest differences in four forest fragments in central lower Michigan. The fragments differed in forest type and management history. The composition and structure of the tree and shrub strata along edge-to-interior gradients on north and south aspects were analyzed. Soil moisture and light penetration were examined on the north and south aspects in one of the fragments.

Hypotheses

1. There exists a vegetational gradient from edge-to-interior that develops in response to an assumed microclimatic gradient. At the extremes of this gradient, separate edge and interior forest communities will be distinguishable compositionally and structurally.

The edge forest will be distinguished by a greater abundance of less tolerant or disturbance-oriented species relative to the interior.

2. Given the relatively slow growth rates and long life spans of many dominant canopy species, it is probable that fragments of second-growth forest are of an insufficient age for the composition of the canopy to reflect an edge-interior forest distinction (Hill 1985; Whitney & Somerlot 1985). Therefore, any trend will be most evident in subcanopy strata that established subsequent to formation of the present fragment boundaries.

3. The edge forest on the northern aspect of a fragment will tend to be narrower, and of different composition and structure, relative to the edge forest on the southern aspect.

For this study the assumption was made that in temperate forests of eastern North America, eastern and western aspects are intermediate to northern and southern aspects with respect to edge conditions.

4. There is a minimum critical size of fragment below which interior conditions will fail to be maintained, resulting in an all-edge forest.

5. The disturbance regime or management history to which a fragment or its edge has been exposed will influence the composition, structure and extent of the edge-to-interior gradient.

Specific research objectives include:

1) the quantification of soil moisture and light levels along the edge-to-interior in a forest fragment;

2) the quantification of the diversity and distribution of woody species relative to the edge-to-interior gradient;

3) the quantitative description of community structure from the edge to the interior;

4) the quantitative determination of the extent of edge forest;
5) a comparison of the edge-to-interior gradients on northern and southern aspects;

6) a determination of the effect of fragment size on gradient composition, structure and extent;

7) an examination of the effects of fragment disturbance and edge management history on gradient composition, structure and extent;

8) comparison of edge characteristics in beech-sugar maple and oak forest fragments.

METHODS

Site Selection

This research utilized four previously studied forest fragments, two each of oak and beech-sugar maple, located in Ingham and Clinton counties in central lower Michigan (Figure 1; APPENDIX A). Dodge (1984) classified these fragments to forest type and determined that they occurred on sites of similar climate, topography, geomorphology, soil, and substratum. The adjacent matrix was agricultural for all sites, consisting of either pasture, corn, or fallow fields (see Appendix B for site diagrams). The potential influence of matrix structure and management history, as well as that of adjacent non-agricultural vegetation, on edge characteristics was not addressed by this research.

Criteria pertinent to stand selection required that: 1) all vegetational strata were present, i.e. ground layer, shrub layer, understory, and canopy; 2) the fragment was a remnant of original vegetation, not a newly established stand, or one with newly established edges; and 3) fragments had linear edges facing north and south (+/- 10 degrees). Individual sites were chosen for this study specifically for the particular management history and present condition they represented.

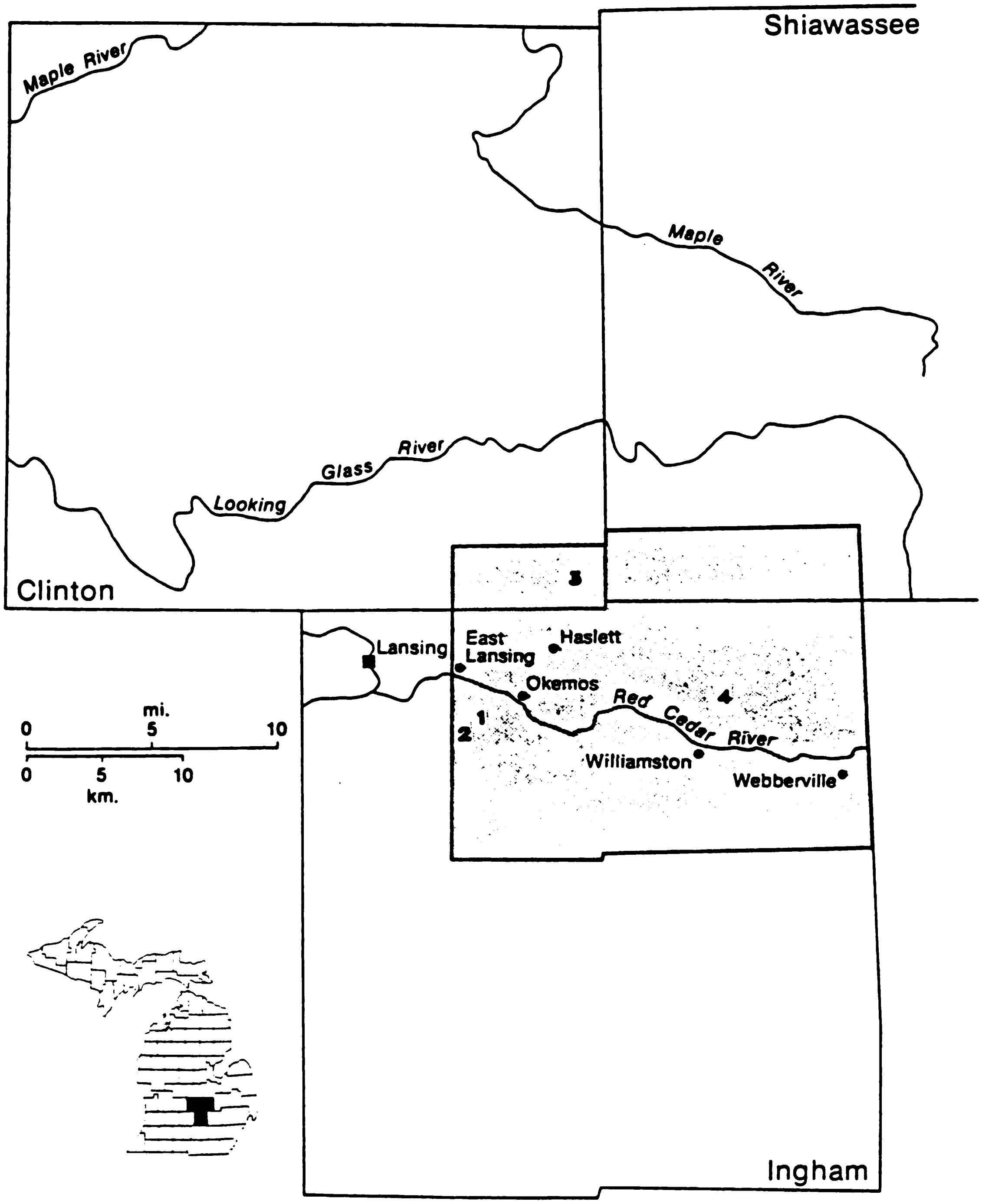

Figure 1. Location of study area and sites. Adapted from Dodge (1984).

Sites 1 and 2 were located on the campus of Michigan State University. Site 1, Toumey Forest, was an old-growth undisturbed beech-sugar maple forest (Schneider 1963). Actual area of the forest was 6.07 ha but only the upland 4.68 ha was studied (APPENDIX B). Linear dimensions of the sampled forest were 195 m (north-south) x 240 m (east-west). Both the western and eastern aspects of the entire forest were bounded by planted mixed conifers. Site 2, Clever Woodland, was a second-growth beech-sugar maple fragment approximately 2.7 ha in size. Linear dimensions were 150 m (north-south) x 180 m (east-west). The site was formerly grazed by cattle (L. Kramer, former M.S.U. agricultural land manager, personal communication). Age determination, based on growth rings, of individuals of an even-sized subcanopy of sugar maple saplings indicated that grazing was discontinued 18-20 years ago. A fenced off northwest extension of the site was actively grazed at the time of this study (APPENDIX B). Interviews with past and present M.S.U. farm managers revealed that selective tree removal for firewood from the edge forest was a common practice in the early to mid part of this century in this site. There was no evidence of recent cutting in the forest.

Site 3 was a 3.6 ha second-growth oak forest located within the Michigan Department of Natural Resources Rose Lake Wildlife Research Station. Linear dimensions were 240 M (north-south) x 150 m (east-west). This site was released from sheep grazing approximately 45 years ago (S. Dodge, Dept. of Gepgraphy, Georgia State Univ., personal communication). There apparently was a limited amount of past tree removal as evidenced by a small number of decomposing stumps. The western aspect of the site was bounded by a hiking path, followed by a

10 m-wide strip of ponderosa pine (APPENDIX B). Site 4 was a 1.5 ha second-growth oak forest located approximately 18 km east of East Lansing, Michigan. Linear dimensions were 150 m (north-south) x 100 m (east-west). There was no evidence of any recent artificial disturbance in the site. However, there was a large (20 x 20 m) patch of bracken fern (Pteridium aquilinum (L.) Kuhn), containing little woody vegetation, in the north central portion of the forest, which may suggest a past fire. The site had a strip of forest vegetation approximately 35 m-wide, extending 100 m eastward from the southeast corner of the fragment (APPENDIX B).

Sampling Methods

Transect Location

In each site a series of three to five, 10 m-wide transects was established on the northern and southern aspects. Transects ran 50 m into the forest in a north-south direction. A transect began at the outer boundary of shrub vegetation, the pre-mantel of Wilmanns & Brunhool (1982; Figure 2). In all sites, transects began interior to the canopy drip line (Bruner 1977). This reflects the management history of the edges, in which there has been no recent advancement of vegetation into the surrounding matrix.

The number of transects per aspect, which depended on linear edge length, numbered five in Sites 1-3 and three in Site 4. The location of the first transect in each site was determined randomly by choosing a number that corresponded to a point on the east-west compass line.

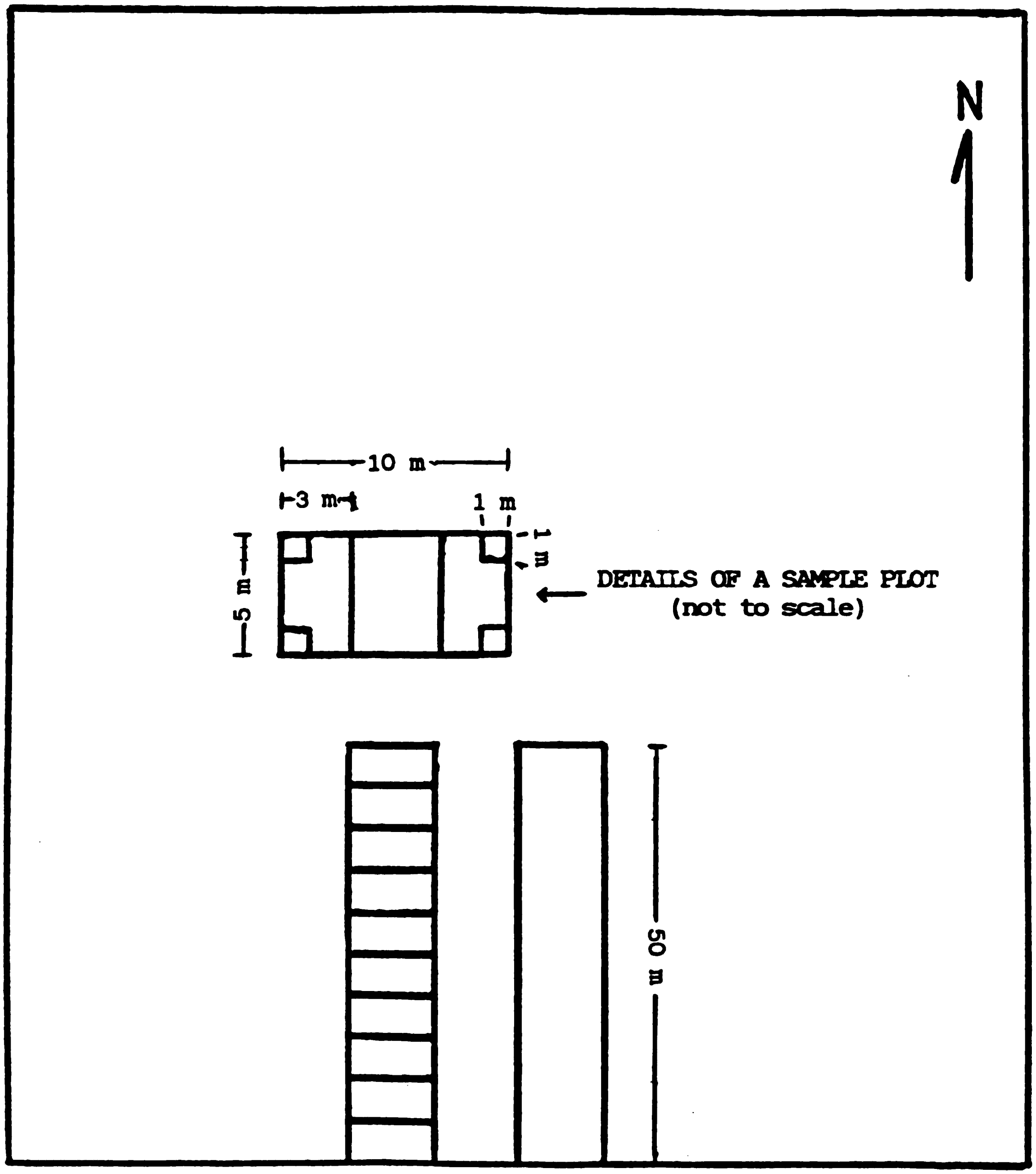

Figure 2. Transect location and sampling design for a hypothetical forest fragment. Trees (> 10 cm dbh) and saplings (2.5 cm ≤ dbh ≤ 10 cm) were sampled in the 10 x 5 m plots, shrubs and small trees (<2.5 cm dbh and taller than 1 m) were sampled in the 5 x 3 m subplots, the woody ground layer (< 1 m tall) was sampled in the 1 x 1 m subplots. Three to five 50 m transects were sampled on both the northern and southern aspects of a site. Transects were located at least 40 m interior of the western and eastern edges. Three to five plots located 50 m interior of all edges were also sampled in each site.

The location of this point, which was restricted to a position 40 m inside of the eastern and western forest boundaries, located the transect centerline. Subsequent transect centerlines were placed 20 m apart in whichever direction provided adequate room.

This procedure was followed in Sites 1-3, but was not possible in Site 4, because of its small size. In this site the three 10 m x 50 m transects were placed immediately adjacent to one another, with only a 35 m buffer on the eastern and western aspects. This design violated the procedure of random sampling, and may have concurrently introduced edge effects from the eastern and western aspects into the sampling. However, this was the only way to adequately sample a potentially interesting fragment.

Vegetation

The vegetation was sampled using a series of nested plots to measure woody ground layer, shrub, understory and canopy strata. Each 10 x 50 m transect was divided into ten 5 x 10 m plots, referred to as transect positions (e.g. 0-5, 5-10 ... 45-50) in the Results and Discussion sections. Trees (> 10 cm dbh), and saplings (2.5 cm $\leq$ dbh $\leq$ 10 cm), were sampled in the entire 5 x 10 m plot. Shrubs[2] (< 2.5 cm dbh, > 1 m) were sampled in 3 x 5 m subplots located on either end of the larger plot. The woody ground layer (< 1 m tall) was sampled in four 1 x 1 m subplots located in each corner of each 10 x 5 m plot (Figure 2). In each plot, species, stem densities of all strata, and

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[2] The shrub size class included individuals of tree species that were of the specified size, in addition to true shrubs.

diameter at breast height (1.4 m) of trees were recorded. The interior forest of each site was sampled using 10 x 5 m plots like those described above. These plots were located randomly in an area 50 m or more from all forest boundaries. The number of interior plots corresponded to the number of transects in that site. These plots are referred to as the "interior" in the subsequent Results and Discussion sections. The size of each fragment was determined from U. S. Geological Survey maps.

Soil Moisture and Light

Measurements of soil moisture and light were made in Site 2. Gradients on both the northern and southern aspects were examined. To determine soil moisture, three 1.5 cm-wide soil cores (to 12 cm depth) were removed from the middle and end points of a 1 m line located parallel to the long axis in the center of each 5 x 10 m plot on four transects. Additionally, samples were collected from an area immediately outside of the forest boundary at the beginning of each transect and in four interior plots. The three cores from each plot were composited and stored in plastic bags for transport to the laboratory. Determinations of percent moisture by weight were made gravimetrically following Brower & Zar (1977). Soil moisture was measured on three different dates: 30 April, 1987; 31 July, 1987; and 7 September, 1987.

Light penetration, as a percentage of full sunlight, was measured using a Li-cor quantum photometer under calm, cloudless conditions. Measurements were recorded along three of the established transects at

5 m intervals, beginning just inside the forest boundary (meter zero) to the 50 m point in the forest, for a total of 11 measurement points per transect. Measurements were taken at each point on the three transects by walking the length of the first transect in one direction, the next adjacent transect in the opposite direction, etc., repeating this procedure until 12 measurements had been recorded for each point. Measurements were taken 10 cm above the forest floor, avoiding any obvious light gaps and sun flecks. This technique gives an approximate measure of diffuse light in the forest (Wales 1967). The procedure, which took approximately one-half hour per aspect, was initiated at 11:00 hrs on 20 August, 1987 and 10:30 hrs. on 4 September, 1987, for the southern and northern aspects, respectively.

Data Analysis

Vegetation

Direct gradient analysis was used to examine patterns in: 1) total density and tree basal area; 2) individual species density or abundance (number of individuals in the total sampled area at each transect position); 3) species richness (total number of species); 4) individual species distributions; and 5) synthetic importance values (Curtis & McIntosh 1951) of potential canopy dominant species in each stratum, as a function of transect position (i.e. distance from the edge) and aspect. Importance values were sums of relative density, relative frequency and relative basal area for trees, and relative density and relative frequency for subcanopy strata.

When requirements of parametric statistics could be met, ANOVA or t-tests were used to test transect position and aspect effects on the various parameters examined[3]. Unless stated otherwise all data sets analyzed using parametric statistics were square root-transformed in order to meet the assumptions of normality and homogeneity of variances. Graphs and tables report untransformed data.

Individual transect position differences were examined in one of two ways: 1) orthogonal contrasts of a specific position mean relative to the mean of all positions interior to it combined on that aspect (excluding the interior position); 2) Dunnett's test for pair-wise comparison with a control (in this case the interior mean) when the interior position mean was substantially different from the majority of positions on one or both aspects.

Many of the individual species data sets did not meet the assumptions of parametric statistics, even with transformations, because of an excessive number of zeros in the data (i.e., >20%; J. Gill, Dept. of Animal Science, Michigan State Univ., personal communication). Further, non-parametric ANOVA with multiple comparisons could not be used to examine position effects because sample sizes were too small (Sokal & Roth 1981). In these cases, Welch's approximation, a test of means robust against non-normal data with heterogeneous variances (Gill 1978) was used to examine aspect effects alone.

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[3] Statistical methods follow Gill (1978).

Soil Moisture and Light

Soil moisture differences between aspects were analyzed by comparing means derived by using the 10 position means on each aspect. Specific comparisons of transect positions against the interior position mean were made using Dunnet's pair-wise comparison with a control (i.e. the interior position).

Log-transformed light measurements were analyzed using one way ANOVA, separately for each aspect. Specific position differences were analyzed using Bartholomew's test of ordered alternatives (Bartholomew 1961). Since the time and date of measurements on the two aspects were different, no direct statistical comparison was attempted. Regression equations and coefficient were derived for the light measurements, as a function of transect position.

Determination of Edge Depth

The criterion used to determine the depth of edge forest penetration on the northern and southern aspects of each site was the location of transitional events along the edge-to-interior gradient. A transitional event was defined as a relatively abrupt change in a measured attribute within a 5 m interval along the gradient. Attributes included: total stem densities and basal areas (of trees and saplings) in each stratum; individual species distribution or abundance in each stratum; species richness in each stratum; importance percentages of potential canopy dominant species in each stratum; and in Site 2, soil moisture and light values. The 5 m interval with the greatest accumulation of transitional events, relative to the remainder of the gradient, was used to designate the depth of edge forest penetration. A transitional event was attributed to the 45-50 m position if the value of the measured feature was higher of lower in the interior, relative to the final gradient position. Characterization of a species as an indicator of edge or interior forest conditions was made a posteriori based on observed distribution and/or abundance patterns. The characterization was substantiated by examining ecological and life history traits of the species (e.g. does it occur in disturbed habitats; is it shade tolerant) and by comparison with characterizations from Gysel (1951), Wales (1972), Ranney (1978), Ranney et al. (1981), and Whitney and Runkle (1981). The distribution and abundance of edge indicator species in the interior helped to determine if edge conditions penetrated throughout the sampled area of a fragment.

RESULTS

Soil Moisture and Light

Soil Moisture

The soil moisture profile for April in Site 2 is illustrated in Figure 3. Percent moisture by weight was significantly greater on the northern aspect than the southern aspect ($P < .05$, ANOVA; Table 1). This relationship also held without the inclusion of the outside position in the ANOVA. Moisture differences along the edge to interior gradients on both aspects were minimal. Only the southern exterior position and position 5-10 m on the southern aspect were significantly lower than the interior mean (Table 2). The July moisture profile depicts both overall lower soil moisture relative to April (Table 1), and a stronger position effect (Figure 3). On the southern aspect, percent moisture was significantly lower than the interior in the positions between the edge and 25 m into the forest (Table 2). On the northern aspect percent moisture was significantly lower than the interior in the first 15 m of the forest (Table 2). Aspect differences were not significant (Table 1). The September soil moisture profile (Figure 3) depicted an overall increase in moisture relative to July, but not quite back up to April levels (Table 1). Total moisture was significantly higher on the northern aspect, both

Figure 3. Soil moisture profiles (percent of wet weight; to 12 cm depth) from the edge to 50 m on the northern and southern aspects in Site 2. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges; OUT = 1 m outside of the edge. The y-axis values are means +/- se; n=5.

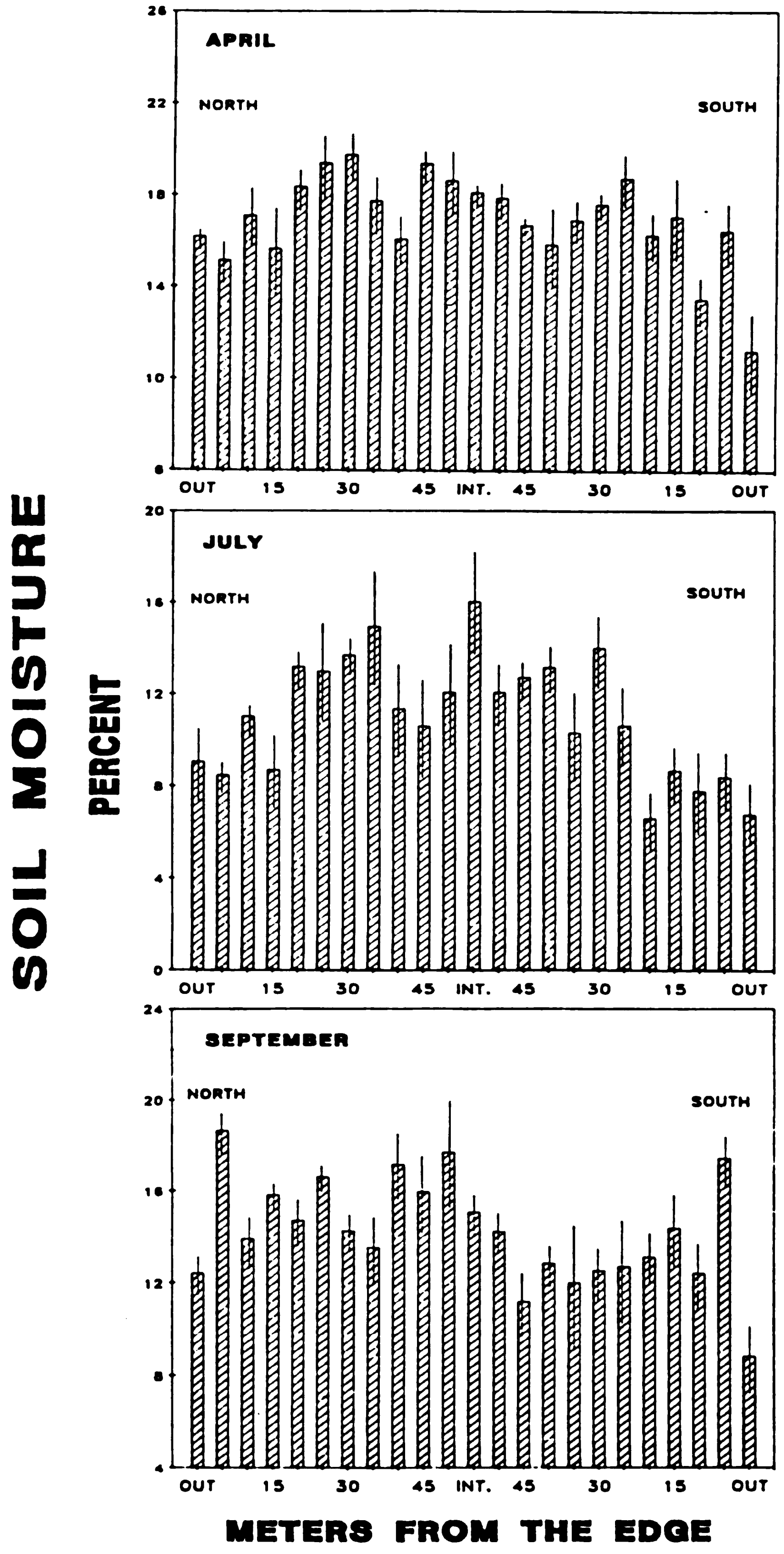
SOIL MOISTURE
PERCENT
APRIL
NORTH
SOUTH
26
22
18
14
10
6
OUT 15 30 45 INT. 45 30 15 OUT
JULY
NORTH
SOUTH
20
16
12
8
4
0
OUT 15 30 45 INT. 45 30 15 OUT
SEPTEMBER
NORTH
SOUTH
24
20
16
12
8
4
OUT 15 30 45 INT. 45 30 15 OUT
METERS FROM THE EDGE

Table 1. Soil moisture (to 12 cm depth) by aspect and date in Site 2.

	Aspect	
	North	South
April, 1987	17.72 (.41)*	16.60 (.38)
July, 1987	11.72 (.56)	10.47 (.54)
September, 1987	15.84 (.42)***	13.29 (.50)

Each value is a mean (percent wet weight) of 10 measurements (at 5 m intervals from the edge to 50 m) on each aspect +/- (se).

* P <.05, *** P <.001 indicates a significantly greater moisture content than the corresponding aspect.

Table 2. Dunnett's pair-wise comparisons between soil moisture values along the edge to interior gradients (0-50 m) on the northern and southern aspects and in the interior (50 m from all edges) in Site 2.

		Meters From the Edge										
	Aspect	Ext.[a]	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50
April 1987	North	---	---	---	---	---	---	---	---	---	---	---
	South	***	---	**	---	---	---	---	---	---	---	---
July 1987	North	**	**	---	**	---	---	---	---	---	---	---
	South	***	**	***	**	***	*	---	*	---	---	---
Sept. 1987	North	---	---	---	---	---	---	---	---	---	---	---
	South	**	---	---	---	---	---	---	---	---	---	---

[a] One meter exterior of the fragment edge.

* $P < .10$, ** $P < .05$, *** $P < .01$ indicates that the mean at that distance was significantly lower than the interior mean.

with ($P < .001$, ANOVA), and without the inclusion of the outside position. Position effects were negligible, with significantly lower moisture only in the exterior position on the southern aspect (Table 2).

Light

Northern and southern aspect light gradients are illustrated in Figure 4. The decrease in diffuse light from edge-to-interior was logarithmic, and was best described by the following regression equations for the northern and southern aspects respectively:

$$\log(Y*100)=2.25-0.55(\log X+10);$$

$$\log(Y*100)=3.12-2.09\log(x+10);$$

where Y is percent of full sunlight and X is distance from the edge in 5 m intervals.[4] The coefficients of determination for the two equations were .935 and .732 respectively ($P < .001$, f-test).

Bartholomew's test of ordered alternatives was used to examine differences in percent light by position. The use of this test requires that: 1) the differences of interest are quantitative, (e.g. percent of full sunlight); and 2) the alternative hypotheses can theoretically be restricted to sequentially increasing or decreasing values, although in reality some variability may be present, (e.g. a decrease in light levels from the edge to the interior). In such

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[4] Coding Y by multiplication with 100 avoids negative logs; coding X by the addition of 10 avoids the log of zero at the edge position.

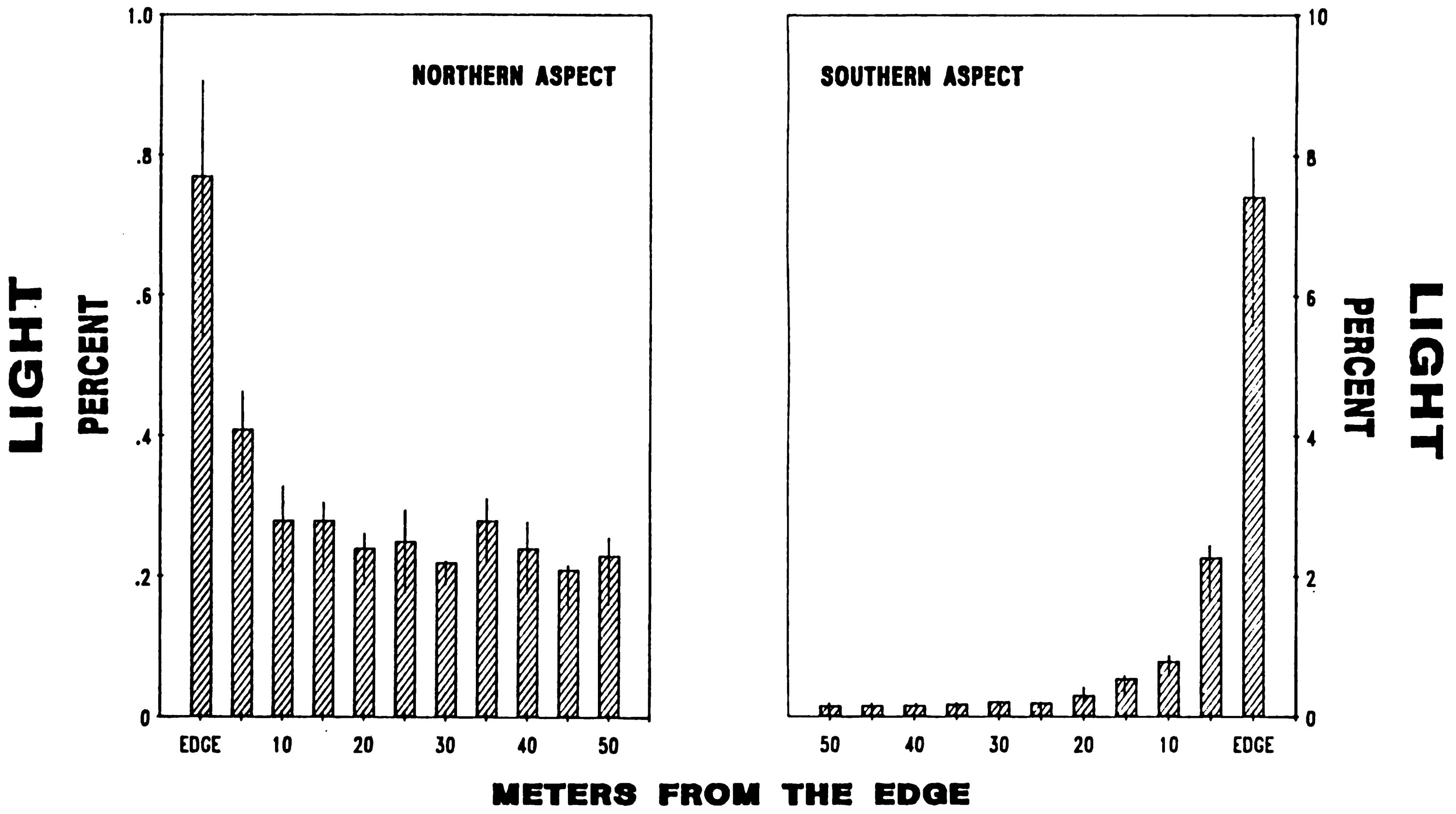


Figure 4. Light profiles (percent of full sunlight) from the edge to 50 m on the northern and southern aspects in Site 2. The y-axis values are means +/- se; n=12. Note the difference in y-axis scale on the two aspects.

cases one gains power by using Bartholomew's test (J. Gill, Department of Animal Science, Michigan State Univ., personal communication).

The test functions as a series of ANOVA's, in which the existence of significant position differences is determined in the first ANOVA, followed by the sequential exclusion of treatments with each successive comparison. The tests of significance of the ordered alternative comparisons allows one to infer at what position into the forest light levels were no longer significantly higher than the remainder of the positions interior to it. On the southern aspect the analysis indicated that there was a significant gradient of decreasing light levels from the edge to 20 m into the forest (Table 3). On the northern aspect, light levels were significantly greater in the first 10 m of the forest (Table 3).

General Edge Structure

Beech-Sugar Maple Fragments

Site 1 (4.68 ha)

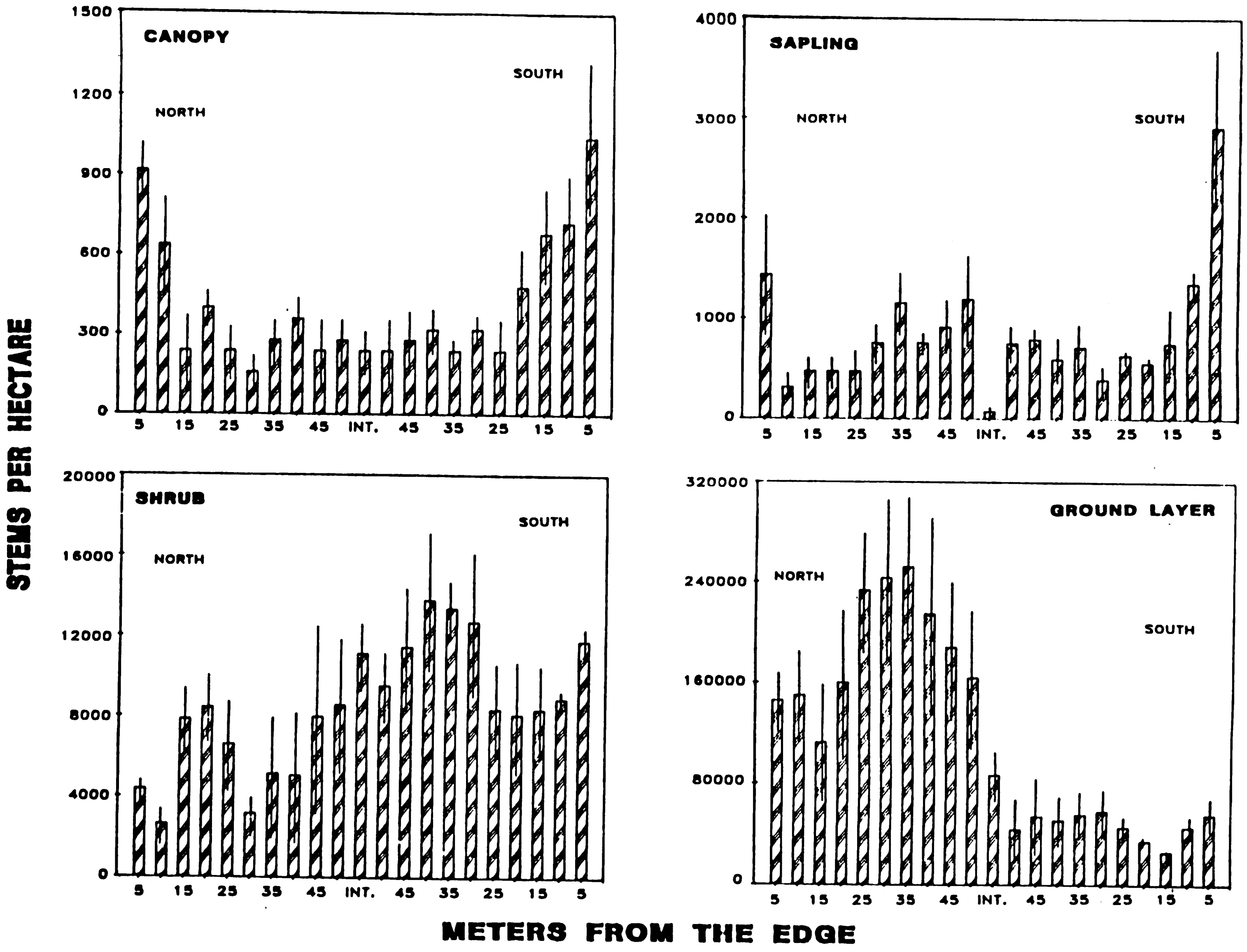
Canopy and sapling stem densities were highest at the edge on both aspects (Figure 5). Canopy density decreased from the edge to 50 m on both aspects but higher densities extended farther into the forest on the southern aspect (Figure 5). Contrasts of individual transect position means against the combined mean of the remainder of the aspect interior to that position showed significantly greater densities in the canopy at positions 0-5 m and 5-10 m north, and 0-5 m through 10-15 m south ($P < .01$, orthogonal contrasts on untransformed

Table 3. Bartholomew's test of ordered alternatives for light values along the edge to interior gradients (0-50) on the northern and southern aspects in Site 2.

	Meters From the Edge										
Aspect	Edge	5	10	15	20	25	30	35	40	45	50
South	**	**	**	**	**	ns	ns	ns	ns	ns	—
North	**	**	**	ns	ns	ns	ns	ns	ns	ns	—

** P <.01 indicates that percent of full sunlight at that distance was significantly greater than the remainder of the distances interior to it.

Figure 5. Stem density profiles from the edge to 50 m on the northern and southern aspects in Site 1. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=5.


CANOPY
NORTH
SOUTH
1500
1200
900
600
300
0
SAPLING
NORTH
SOUTH
4000
3000
2000
1000
0
SHRUB
NORTH
SOUTH
20000
16000
12000
8000
4000
0
GROUND LAYER
NORTH
SOUTH
320000
240000
160000
80000
0
5 15 25 35 45 INT. 45 35 25 15 5
STEMS PER HECTARE
METERS FROM THE EDGE

data). Mean sapling density in the forest interior was markedly lower than most of the positions along either aspect; consequently, specific contrasts were made against the interior mean. Densities in fourteen of the 20 positions were significantly greater than in the interior (Dunnett t-test; Table 4). Although total density (the mean of the 10 positions) was not significantly different between the northern and southern aspects the canopy and shrub strata (Table 5), the Figure 5 does illustrate the greater penetration of edge conditions on the southern aspect. Canopy basal area showed no significant differences by aspect or distance from the edge (not illustrated). Shrub and ground layer densities showed no significant position trends; however, both strata did show strong differences by aspect (Figure 5). Total shrub density was highest on the southern aspect (P <.001, t-test on untransformed data), while ground layer density was highest on the northern aspect (P <.001, ANOVA; Table 5).

Site 2 (2.70 ha)

In general, density area trends for the canopy and sapling strata in Site 2 paralleled those of Site 1. An important difference was the extent of penetration of structural differences into the forest. Density was highest at the edge on both aspects (Figure 6) but significantly greater densities were found only at position 0-5 m south in both strata (P <.01, orthogonal contrasts). Canopy and sapling basal area showed no significany differences by distance from the edge or aspect (not illustrated). Shrub density showed no aspect trend (Figure 6) but density was significantly higher at position

Table 4. Dunnett's pair-wise comparisons between sapling stem densities along the edge to interior gradients (0-50 m) on the northern and southern aspects and the interior (50 m from all edges) in Site 1.

	Meters From the Edge									
Aspect	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50
North	***					**	***	**	**	***
South	***	***	*	*	*		*		***	***

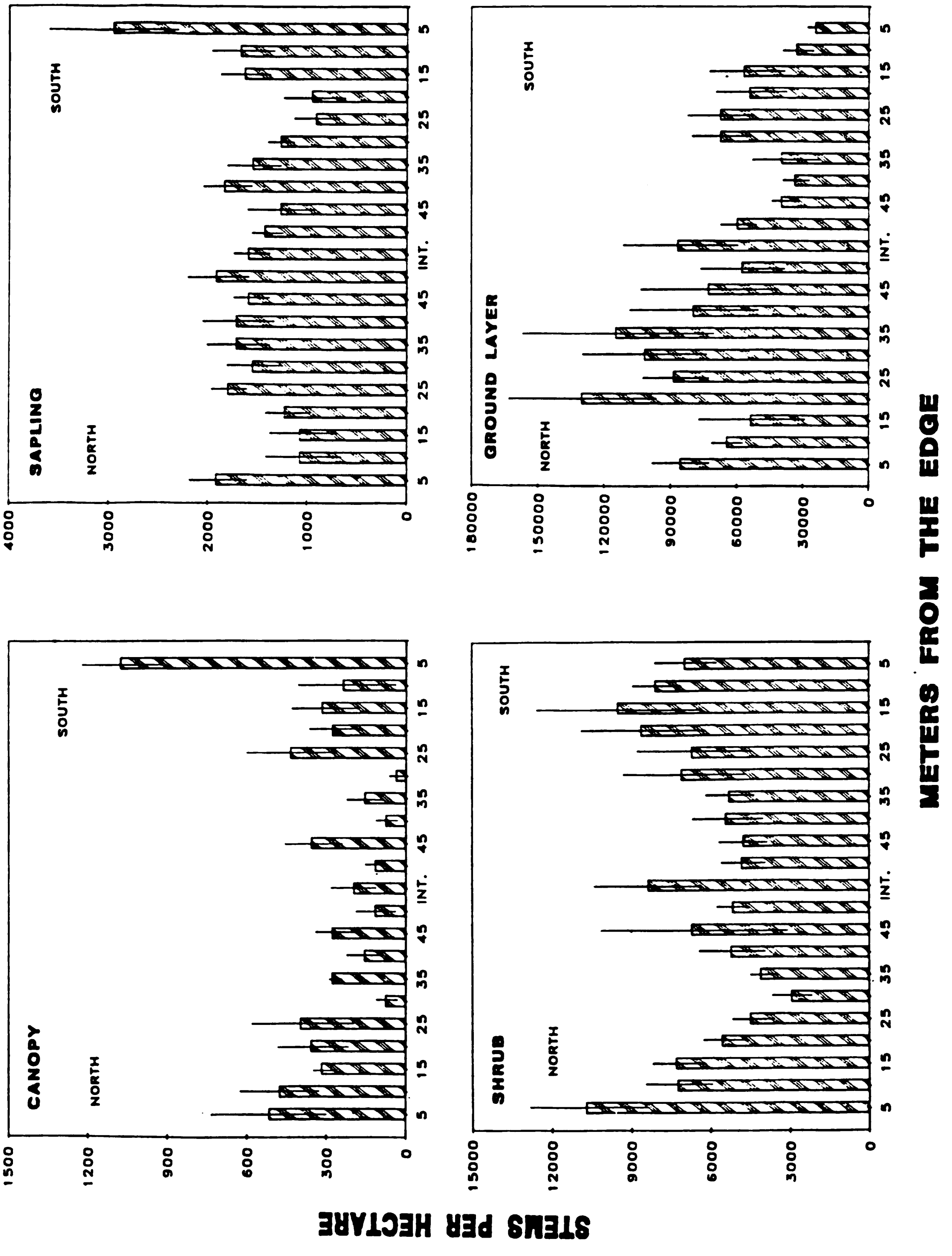
* P <.05, ** P <.01, *** P <.001 indicates that the mean at that interval was significantly greater than than the interior mean.

Table 5. Density per hectare by stratum on the northern and southern aspects (0-50 m) in Sites 1 through 4.

Site	Aspect	Canopy	Sapling	Shrub	Ground layer
1	north	376 (74)	800 (118)	6000 (698)	187100 (14986)**
	south	456 (86)	952 (233)	9707 (703)**	47850 (3275)
2	north	300 (47)	1564 (102)	5976 (687)	85250 (7841)**
	south	312 (94)	1556 (183)	6767 (522)	47800 (4863)
3	north	491 (45)	688 (70)	3480 (660)	41980 (3082)
	south	492 (53)	836 (80)*	7667 (1206)**	44450 (3847)
4	north	333 (54)	1093 (220)	10067 (1029)**	61500 (3759)**
	south	320 (81)	1593 (127)**	6045 (494)	41375 (2980)

Each value is a mean of 10 density measurements along the edge to interior gradient (5 m distance intervals from 0 to 50 m) on an aspect +/- (se).
* P <.05, ** P <.01 indicates significantly higher density than the corresponding aspect.

Figure 6. Stem density profiles from the edge to 50 m on the northern and southern aspects in Site 2. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=5.


CANOPY
NORTH
SOUTH
1500
1200
900
600
300
0
SAPLING
NORTH
SOUTH
4000
3000
2000
1000
0
SHRUB
NORTH
SOUTH
15000
12000
9000
6000
3000
0
GROUND LAYER
NORTH
SOUTH
180000
150000
120000
90000
60000
30000
0
5
15
25
35
45
INT.
45
35
25
15
5
STEMS PER HECTARE
METERS FROM THE EDGE

0-5 m north (P <.01, orthogonal contrasts). Ground layer density pattern paralleled that of Site 1, with a significantly higher total density on the northern aspect (P <.001, t-test; Table 5) and a lack of a strong position trend (Figure 6).

Oak Fragments

Site 3 (3.60 ha)

Canopy and sapling densities in Site 3 showed no significant position trends (Figure 7). However, total sapling density was significantly higher on the southern aspect (P <.05, ANOVA; Table 5). No significant aspect difference existed in the canopy stratum. Canopy basal area (not illustrated) was significantly higher at position 5-10 m north (P <.001, orthogonal contrast) but no other position or aspect trends were apparent. Shrub density showed strong position and aspect trends (Figure 7). Density at position 0-5 m north was significantly higher than positions in the remainder of the northern aspect (P <.01, orthogonal contrasts), as were all positions from 0 to 20 m on the southern aspect (P <.05, P <.10 for 10-15 m, orthogonal contrasts). Total density was significantly higher on the southern aspect (P <.001, ANOVA; Table 5). Ground layer density showed no significant position or aspect trends but position densities were highest exterior to 40 m (Figure 7).

Site 4 (1.5 ha)

Canopy density was greatest near the edge on both aspects (Figure 8). Density at position 5-10 m south was significantly

Figure 7. Stem density profiles from the edge to 50 m on the northern and southern aspects in Site 3. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=5.

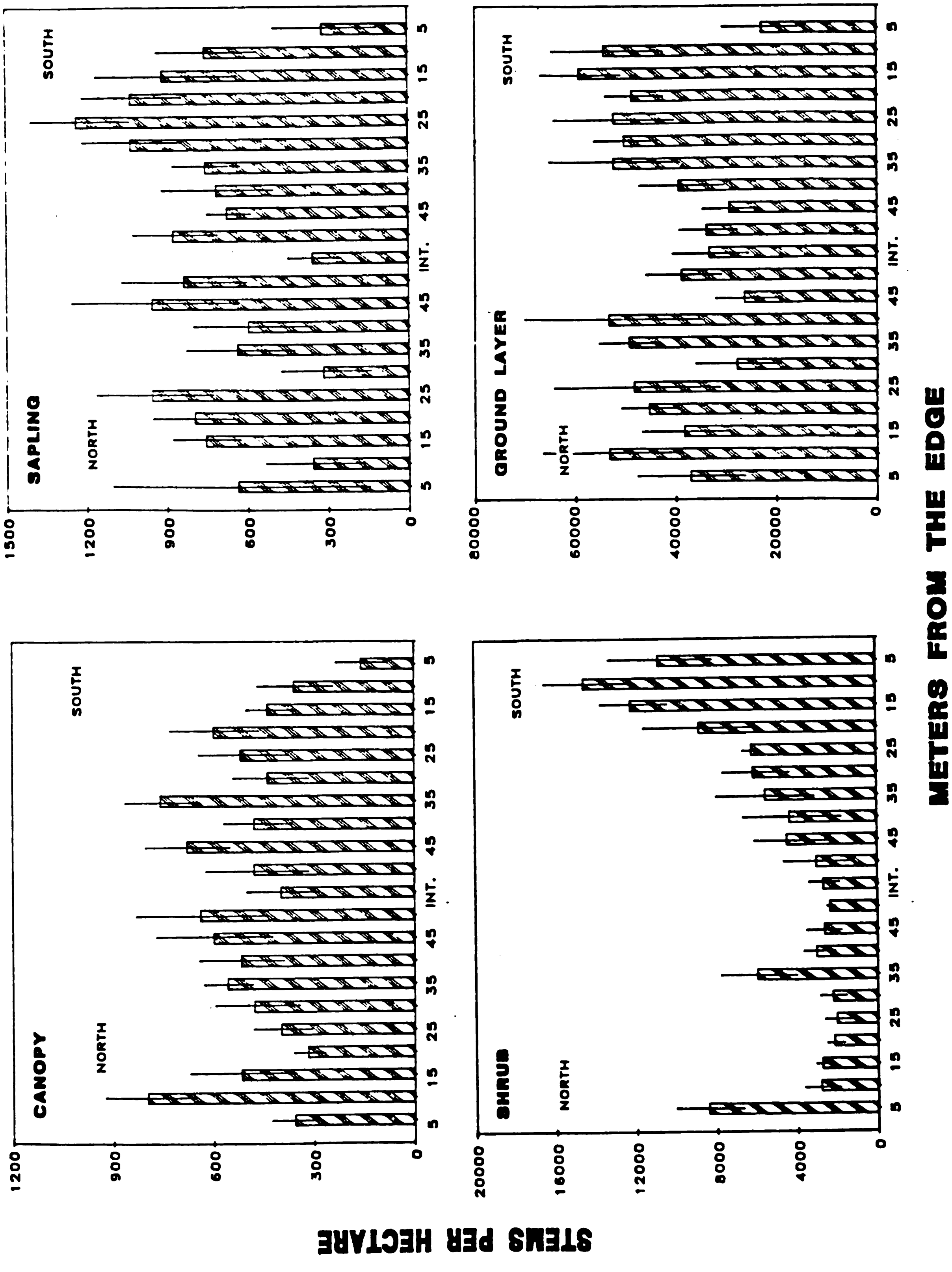
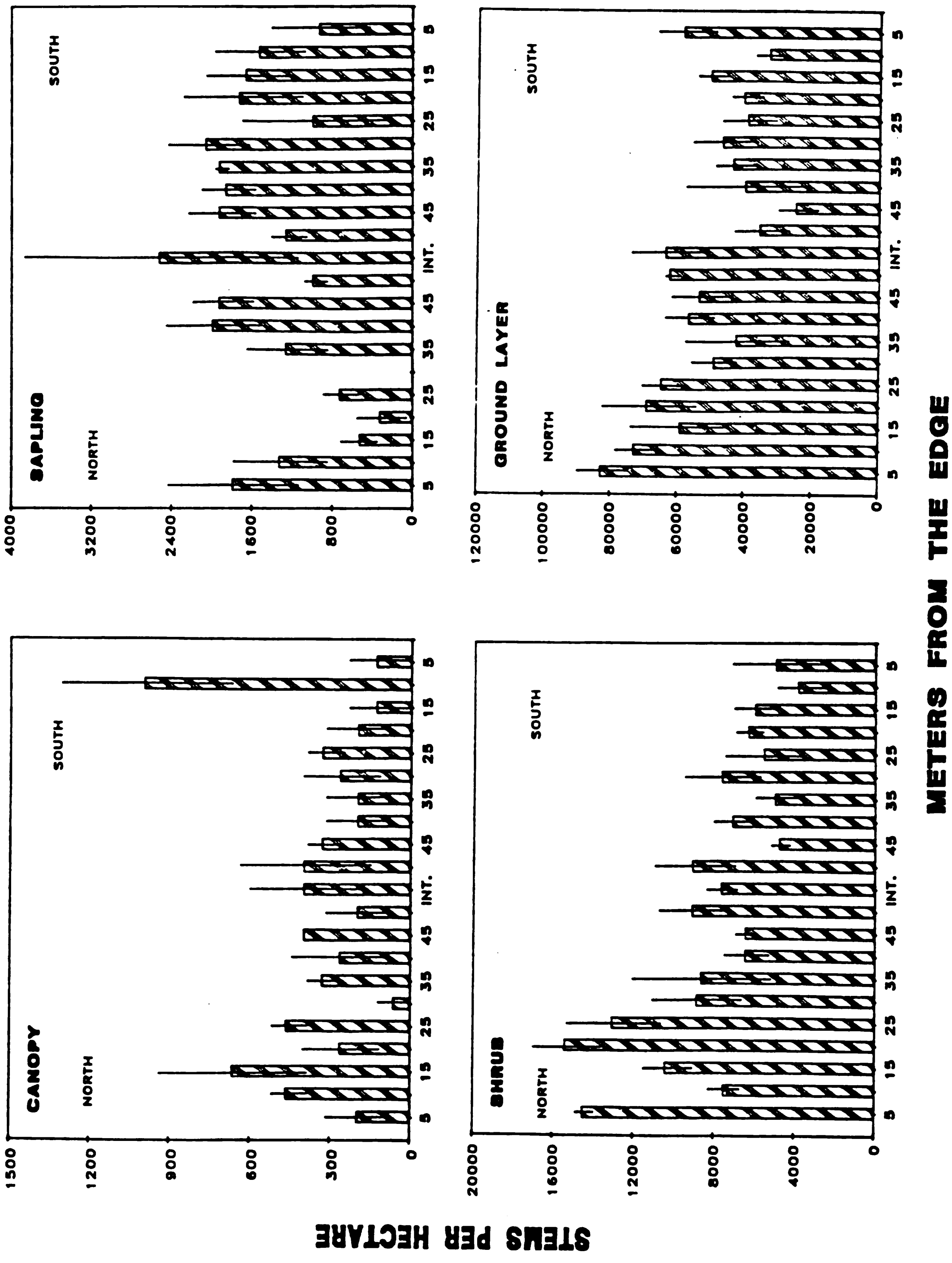

CANOPY
SAPLING
SHRUB
GROUND LAYER
NORTH
SOUTH
1200
900
600
300
0
1500
1200
900
600
300
0
20000
16000
12000
8000
4000
0
80000
60000
40000
20000
0
5
15
25
35
45
INT.
45
35
25
15
5
STEMS PER HECTARE
METERS FROM THE EDGE

Figure 8. Stem density profiles from the edge to 50 m on the northern and southern aspects in Site 4. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=3.


CANOPY
SAPLING
SHRUB
GROUND LAYER
NORTH
SOUTH
STEMS PER HECTARE
METERS FROM THE EDGE
0
300
600
900
1200
1500
800
1600
2400
3200
4000
4000
8000
12000
16000
20000
20000
40000
60000
80000
100000
120000
5
15
25
35
45
INT.
45
35
25
15
5

greater than the remainder of the southern aspect (P <.01, orthogonal contrast). No significant position or aspect trends in canopy basal area were evident (not illustrated). Sapling density showed no strong position trends (Figure 8) but total density was significantly higher on the southern aspect (P <.01, ANOVA; Table 5). Total shrub density was highest on the northern aspect (P <.001, ANOVA; Table 5), a result opposite those of Sites 1-3. Significantly higher position densities were found at 0-5 m, 15-20 m and 20-25 m north (P <.05, orthogonal contrasts; Figure 8). Total ground layer density was highest on the northern aspect (P <.001, t-test; Table 5). Although not significant, highest densities were found at the edge positions on both aspects.

Individual Species Distributions and Abundance

The results presented below highlight those species whose distribution or abundance patterns illustrated position and/or aspect effects. The species composition for each site, separated into canopy and non-canopy components, is presented in Tables 6-9. It can be assumed that those species listed in the tables, but not treated below, either showed no position or aspect differences or were so rare that they had little impact on the analysis. Rare species were defined as those having a frequency of occurrence below 5% in sample plots. For many species mean density at a position was low but their distribution patterns were important in delineating edge-to-interior and aspect effects. For these species no attempt was made to indicate variability within a position; instead, the total number of individuals per position is reported.

Table 6. Species composition of Site 1.

Canopy species	
Acer nigrum Michx. f.	Black maple
A. saccharum Marsh.	Sugar maple
Carya cordiformis (Wang.) K. Koch	Bitternut hickory
Fagus grandifolia Ehrh.	American beech
Fraxinus americana L.	White ash
Prunus serotina Ehrh.	Black cherry
Tilia americana L.	Basswood
Quercus alba L.	White oak
Q. rubra L.	Red oak
Non-canopy species[a]	
Carpinus caroliniana Walt.	Hornbeam
Cornus florida L.	Flowering dogwood
C. alternifolia L.f.	Alternate-leaf dogwood
Crataegus punctata Jacq.	Dotted Haw
Crataegus sp.	Hawthorn
Hamamelis virginiana L.	Witch hazel
Lonicera dioica L.	Wild Honeysuckle
L. tatarica L.	Tartarian Honeysuckle
Ostrya virginiana (Mill.) K. Koch	Ironwood
Prunus virginiana L.	Choke-cherry
Ribes americanum Mill.	Wild black currant
R. cynosbati L.	Gooseberry
Rosa multiflora Thunb.	Rose
Rubus allegbaniensis Porter	Common blackberry
R. occidentalis L.	Black raspberry
Sambucus canadensis L.	Common elder
S. pubens Michx.	Red-berried elder
Ulmus rubra Muhl.	Slippery elm
U. thomasii Sarg.	Rock-elm
Viburnum opulus L.	European cranberry-bush
V. lantana L.	Wayfaring tree
Zanthoxylum americanum Mill.	Prickly ash

[a] Species that do not typically enter the canopy in the forests of the study region.

Table 7. Species composition of Site 2.

Canopy species	
Acer nigrum Michx. f.	Black maple
A. rubrum L.	Red maple
A. saccharum Marsh.	Sugar maple
Carya cordiformis (Wang.) K. Koch	Bitternut hickory
Fagus grandifolia Ehrh.	American beech
Fraxinus americana L.	White ash
Liriodendron tulipifera L.	Yellow poplar
Prunus serotina Ehrh.	Black cherry
Quercus rubra L.	Red oak
Tilia americana L.	Basswood
Non-canopy species[a]	
Carpinus caroliniana Walt.	Hornbeam
Celtis occidentalis L.	Hackberry
Cornus racemosa Lam.	Gray dogwood
Crataegus sp.	Hawthorn
Fraxinus quadrangulata Michx.	Blue ash
Ostrya virginiana (Mill.) K. Koch	Ironwood
Prunus virginiana L.	Choke-cherry
Ribes cynosbati L.	Gooseberry
Rubus allegheniensis Porter	Common blackberry
Sambucus canadensis L.	Common elder
S. pubens Michx.	Red-berried elder
Ulmus rubra Muhl.	Slippery elm

---

[a] Species that do not typically enter the canopy in the forests of the study area.

Table 8. Species composition of Site 3.

Canopy species

Acer *rubrum* L.	Red maple
A. *saccharum* Marsh.	Sugar maple
Carya *glabra* (Mill.) Sweet	Pignut hickory
C. *ovata* (Mill.) K. Koch	Shagbark hickory
Fraxinus *americana* L.	White ash
Juglans *cinerea* L.	Butternut
Prunus *serotina* Ehrh.	Black cherry
Quercus *alba* L.	White oak
Q. *rubra* L.	Red oak
Q. *velutina* Lam.	Black oak
Tilia *americana* L.	Basswood

Non-canopy species[a]

Acer *negundo* L.	Boxelder
Amelanchier *arborea* (Michx. f.) Fern.	Serviceberry
Celtis *occidentalis* L.	Common hackberry
Cornus *alternifolia* L. f.	Alternate-leaf dogwood
C. *racemosa* Lam.	Gray dogwood
Corylus *americana* Walt.	Hazel-nut
Crataegus sp.	Hawthorn
Elaeagnus *umbellata* Thunb.	Autumn olive
Hamamelis *virginiana* L.	Witch hazel
Lonicera *tatarica* L.	Tartarian Honeysuckle
Lonicera sp.	Honeysuckle
Malus *coronaria* L.	Wild crab apple
Prunus *virginiana* L.	Choke-cherry
Rhamnus *catharticus* L.	Buckthorn
Ribes *cynosbati* L.	Gooseberry
Rubus *allegheniensis* Porter	Common blackberry
Rosa *multiflora* Thunb.	Rose
Rosa sp.	Rose
Sambucus *canadensis* L.	Common elder
Sassafras *albidum* (Nutt.) Nees	Sassafras
Ulmus *rubra* Muhl.	Slippery elm
U. *thomasii* Sarg.	Rock-elm
Viburnum *acerifolium* L.	Mapleleaf dogwood
Viburnum *opulus* L.	European cranberry-bush
Unknown	

---

[a] Species that do not typically enter the canopy in the forests of the study region.

Table 9. Species composition of Site 4.

Canopy species

Acer rubrum L.	Red maple
A. saccharum Marsh.	Sugar maple
Carya cordiformis (Wang.) K. Koch	Bitternut hickory
C. glabra (Mill.) Sweet	Pignut hickory
C. ovata (Mill.) K. Koch	Shagbark hickory
Fagus grandifolia Ehrh.	American beech
Fraxinus americana L.	White ash
F. pennsylvanica Marsh.	Green ash
Juglans nigra L.	Black walnut
Liriodendron tulipifera L.	Yellow poplar
Prunus serotina Ehrh.	Black cherry
Quercus alba L.	White oak
Q. bicolor Willd.	Swamp white oak
Q rubra L.	Red oak

Non-canopy species[a]

Amelanchier arborea (Michx. f.) Fern.	Serviceberry
Carpinus caroliniana Walt.	Hornbeam
Celtis occidentalis L.	Common hackberry
Cornus alternifolia L. f.	Alternate-leaf dogwood
C. racemosa Lam.	Gray dogwood
Corylus americana Walt.	Hazel-nut
Crataegus sp.	Hawthorn
Elaeagnus umbellata Thunb.	Autumn olive
Hamamelis virginiana L.	Witch hazel
Lonicera tatarica L.	Tartarian Honeysuckle
Malus coronaria L.	Wild crab apple
Ostrya virginiana (Mill.) K. Koch	Ironwood
Populus deltoides Marsh.	Cottonwood
Prunus virginiana L.	Choke-cherry
Rhamnus catharticus L.	Buckthorn
Rhus typhina L.	Staghorn-sumac
Ribes cynosbati L.	Gooseberry
Rosa multiflora Thunb.	Rose
Rubus allegheniensis Porter	Common blackberry
Salix sp.	Willow
Sassafras albidum (Nutt.) Nees	Sassafras
Ulmus rubra Muhl.	Slippery elm
U. thomasii Sarg.	Rock-elm
Viburnum acerifolium L.	Mapleleaf viburnum
V. lentago L.	Nannyberry
V. opulus L.	European cranberry-bush
Zanthoxylum americanum Mill.	Prickly ash

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[a] Species that do not typically enter the canopy in the forests of the study region.

In all sites many of the individual species distribution and abundance patterns reflected differential success in response to position and/or aspect, in one or more strata. Certain species were restricted to, or were most abundant in, edge or interior forest, with many also showing aspect responses. This can be interpreted as an adaptation to a specific microclimatic condition created through the interaction of position and aspect.

Beech-Sugar Maple Fragments

Site 1 (4.68 ha)

In the canopy stratum sugar maple was distributed over the entire northern aspect and into the interior (Figure 9). Densities of the first two northern edge positions were significantly greater than the remainder of the aspect (P <.001, orthogonal contrasts of untransformed data). On the southern aspect this species was not found within 10 m of the edge (Figure 9). In the sapling stratum sugar maple was present in all plots throught the forest, however total density (the mean of the 10 positions) was significantly greater on the northern aspect (P <.05, ANOVA; Table 10), and density of position 0-5 m north was greater than the remainder of the northern aspect (P <.05, orthogonal contrast; Figure 9). In contrast, total density in the shrub layer was significantly greater on the southern aspect (P <.01, t-test; Table 10). This was due for the most part to high densities interior of 25 m on this aspect (Figure 10). Total density in the ground layer was significantly higher on the northern aspect (P <.001, ANOVA; Table 10). Low densities on the southern

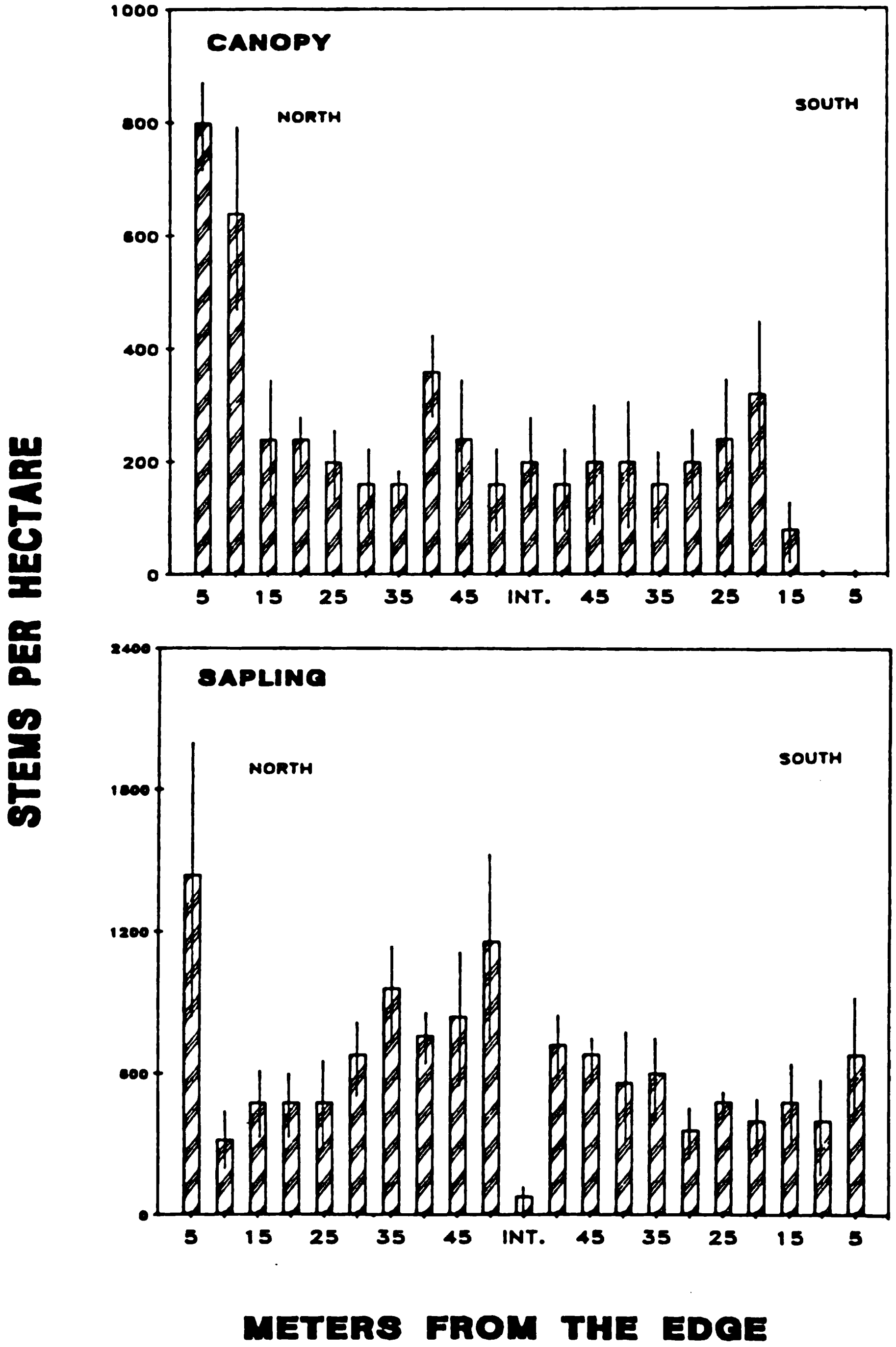


Figure 9. Sugar maple canopy and sapling density profiles from the edge to 50 m on the northern and southern aspects in Site 1. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=5.

Table 10. Density per hectare of selected species in the sapling, shrub, and ground layer (g.l.) strata on the northern and southern aspects (0-50 m) in beech-sugar maple fragments.

			Aspect	
Site	Species	Stratum	North	South
1	*Acer saccharum*	sapling	760 (93)*[a]	535 (52)
		shrub	5227 (625)	7380 (684)**
		g.l.	178300 (16645)**	17600 (4013)
	Fraxinus americana	sapling	47 (19)	627 (233)*
		g.l.	1300 (393)	18600 (2330)*
	Ulmus rubra	shrub	53 (20)	793 (201)*
	Carya cordiformis	g.l.	450 (137)	1650 (340)**
2	*Acer saccharum*	sapling	1330 (107)**	848 (109)
		g.l.	78017 (8192)	41900 (3742)**
	Fagus grandifolia	sapling	80 (29)	252 (66)*
	Ostrya virginiana	sapling	60 (20)	308 (59)**
	Prunus serotina	g.l.	2533 (554)**	600 (381)

[a] The mean of 50 sample plots per aspect +/- (se).

* P <.05, ** P <.01 indicates significantly higher density than the corresponding aspect (Welch's approximation).

aspect were not localized, but encompassed the entire 50 m gradient (Figure 10).

Abundance of American beech was greatest on the northern aspect in all strata (Table 10). Its distribution was confined to positions interior of 15 m and 20 m on the northern and southern aspects, respectively (Figure 11). Patterns of distribution and abundance for white ash and red oak were similar to one another (Figures 12 & 13). These species were confined to southern edge positions in the upper two strata. White ash distribution in the lower strata was expanded across the southern aspect, and into the northern edge positions (Figure 12). Total densities of white ash in the lower two strata were significantly higher on the southern aspect ($P < .05$, Welch's approximation; Table 10). In the lower two strata red oak distribution was somewhat expanded but was still not found interior of 35 m, and had highest abundance near the edge (Figure 13).

The distribution of slippery elm reflected edge and southern aspect affinities in all strata. Canopy and sapling individuals were found only in extreme edge positions on both aspects (Figure 14). Its distribution widened to 45 m on both aspects in the lower two strata but abundance was greatest near the southern edge (Figure 14). Total density was significantly greater on the southern aspect in the shrub stratum ($P < .05$, Welch's approximation; Table 10). In the upper three strata, basswood was distributed across the southern aspect, but was very rare on the northern aspect (Figure 15). In the ground layer, abundance was greatest on the northern aspect. Abundance in all strata was highest in the exterior portion of the gradient.

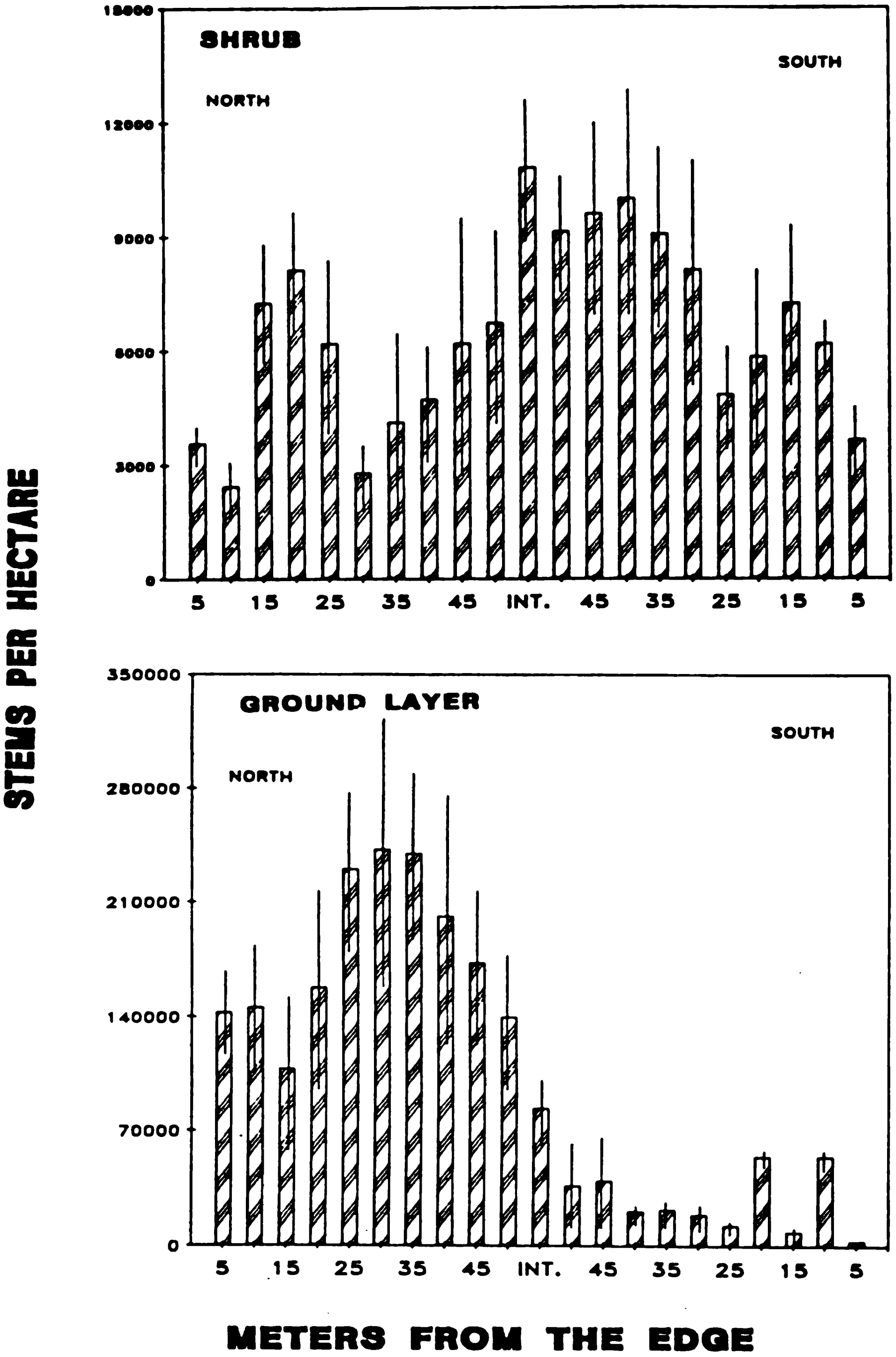


Figure 10. Sugar maple shrub and ground layer density profiles from the edge to 50 m on the northern and southern aspects in Site 1. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=5.

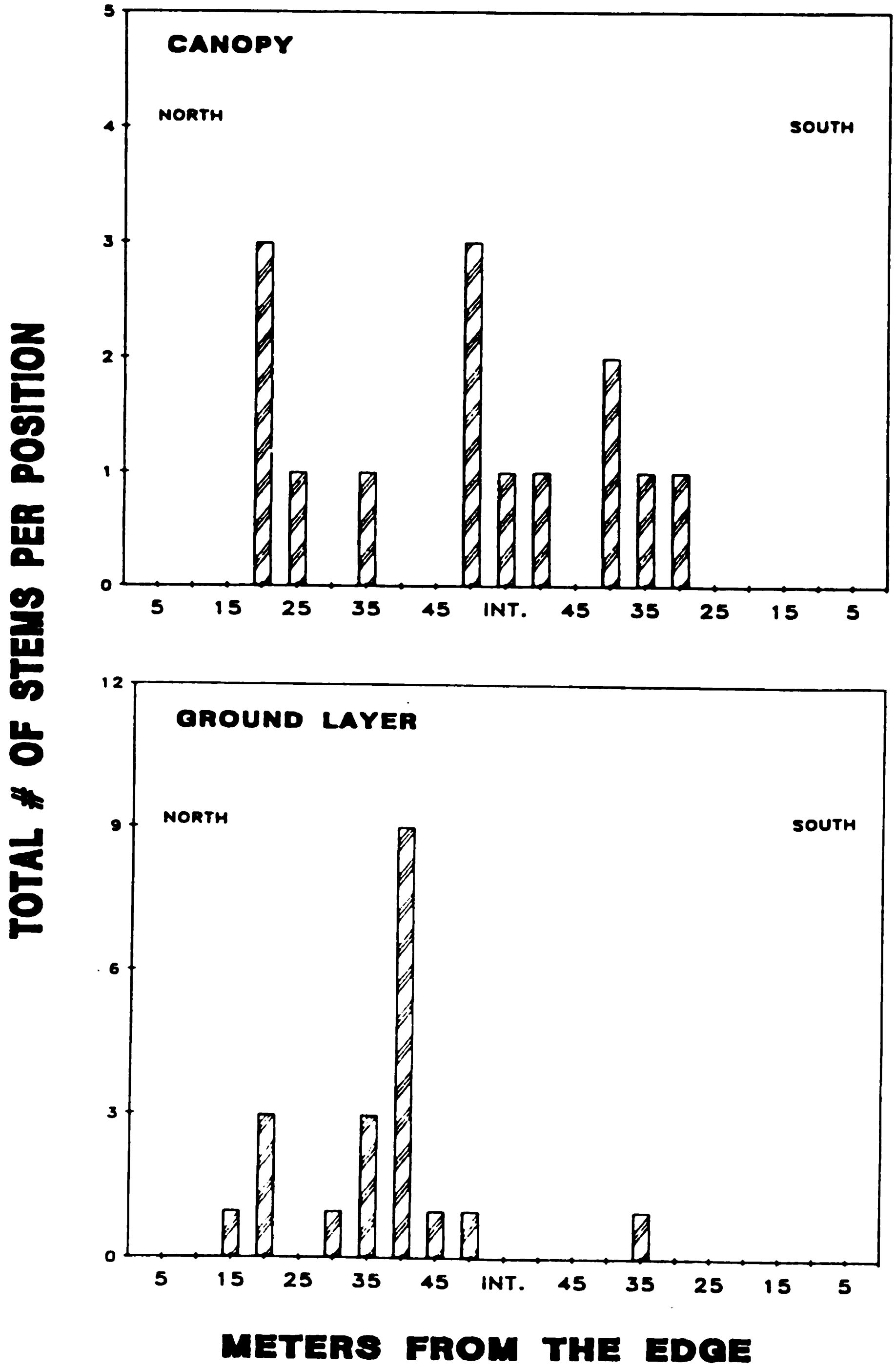


Figure 11. American beech canopy and ground layer abundance profiles from the edge to 50 m on the northern and southern aspects in Site 1. The x-axis values are upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number of stems encountered in each 5 m interval and in the interior. The sapling and shrub profiles were similar to the canopy and ground layer profiles respectively.

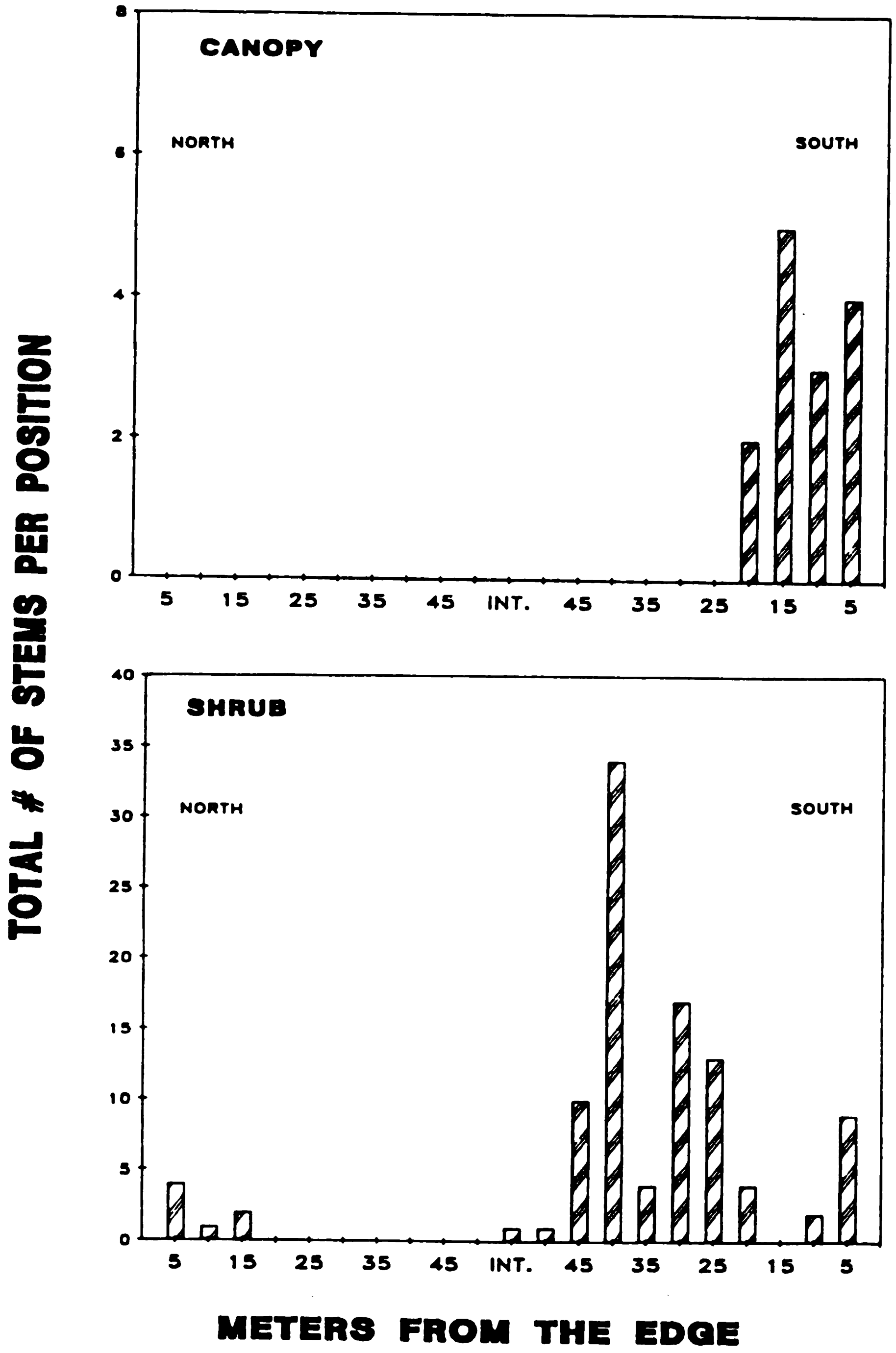


Figure 12. White ash canopy and shrub abundance profiles from the edge to 50 m on the northern and southern aspects in Site 1. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number of stems encountered in each 5 m interval and in the interior. The sapling and ground layer profiles were similar to the canopy and shrub profiles respectively.

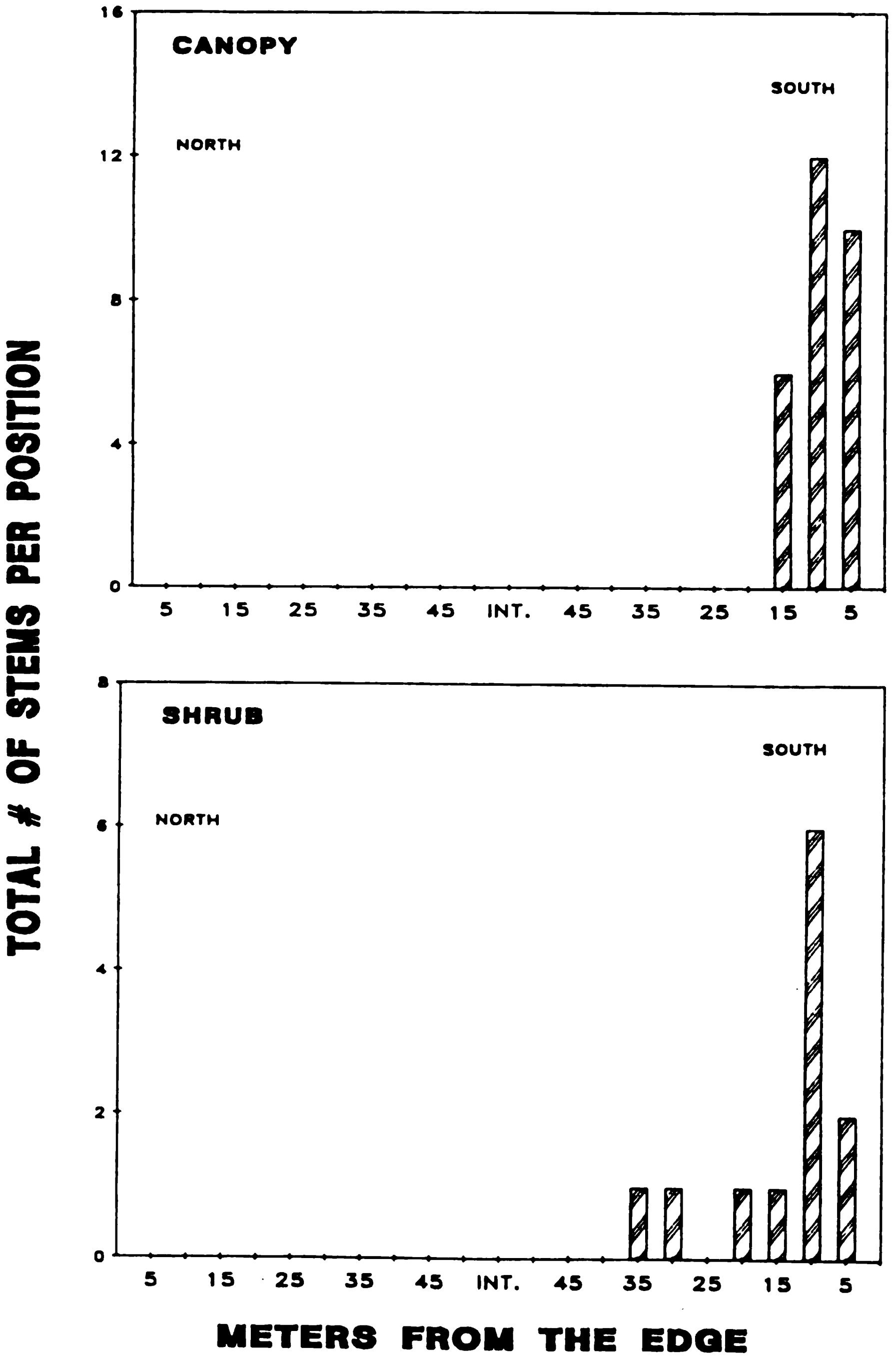


Figure 13. Red oak canopy and shrub abundance profiles from the edge to 50 m on the northern and southern aspects in Site 1. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number of stems encountered in each 5 m interval and in the interior. The sapling and ground layer profiles were similar to the canopy and shrub profiles respectively.

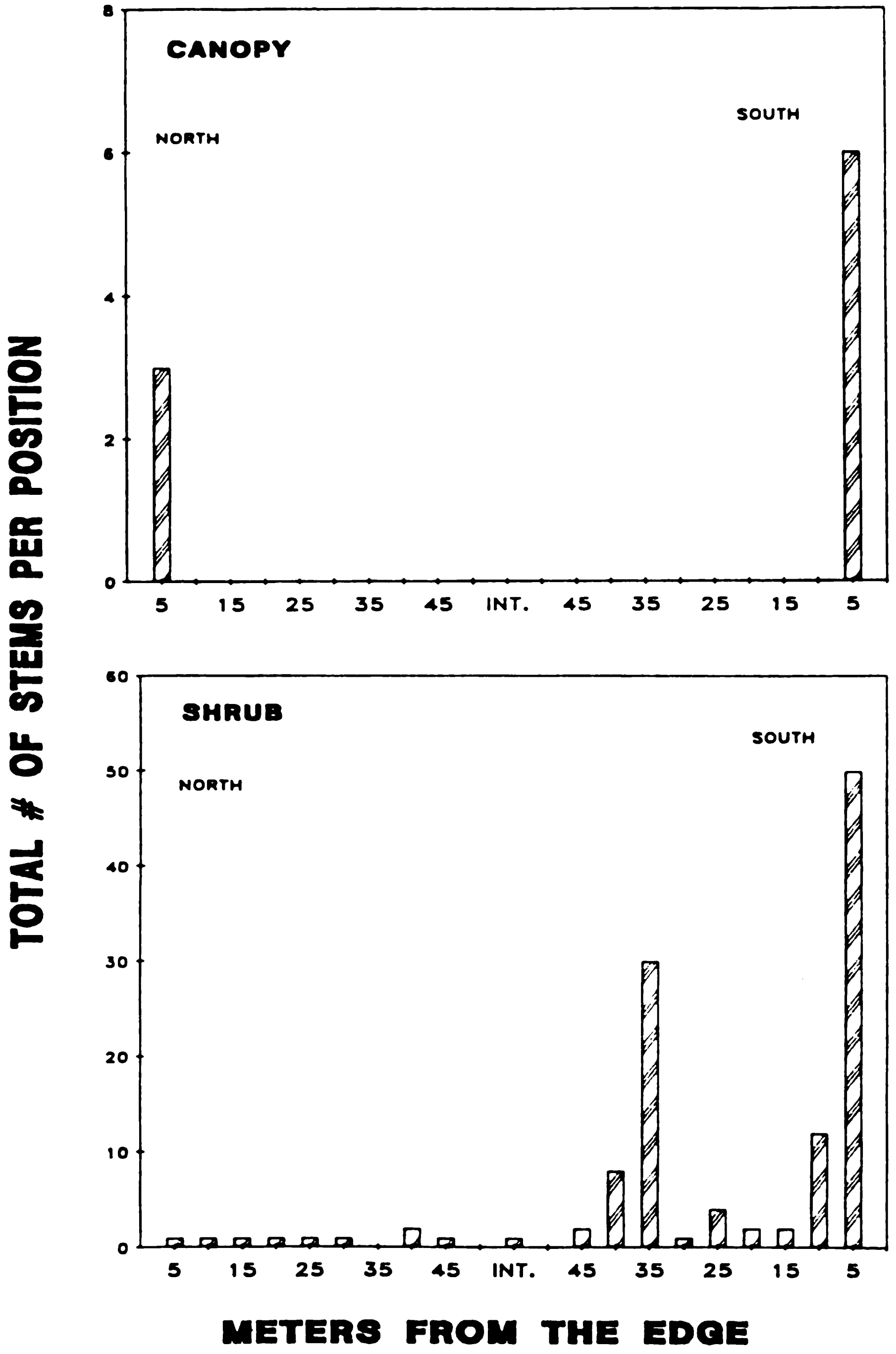


Figure 14. Slippery elm canopy and shrub abundance profiles from the edge to 50 m on the northern and southern aspects in Site 1. The x-axis values are the upper limits of 5 distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number of stems encountered in each 5 m interval and in the interior. The sapling and ground layer profiles were similar to the canopy and shrub profiles respectively.

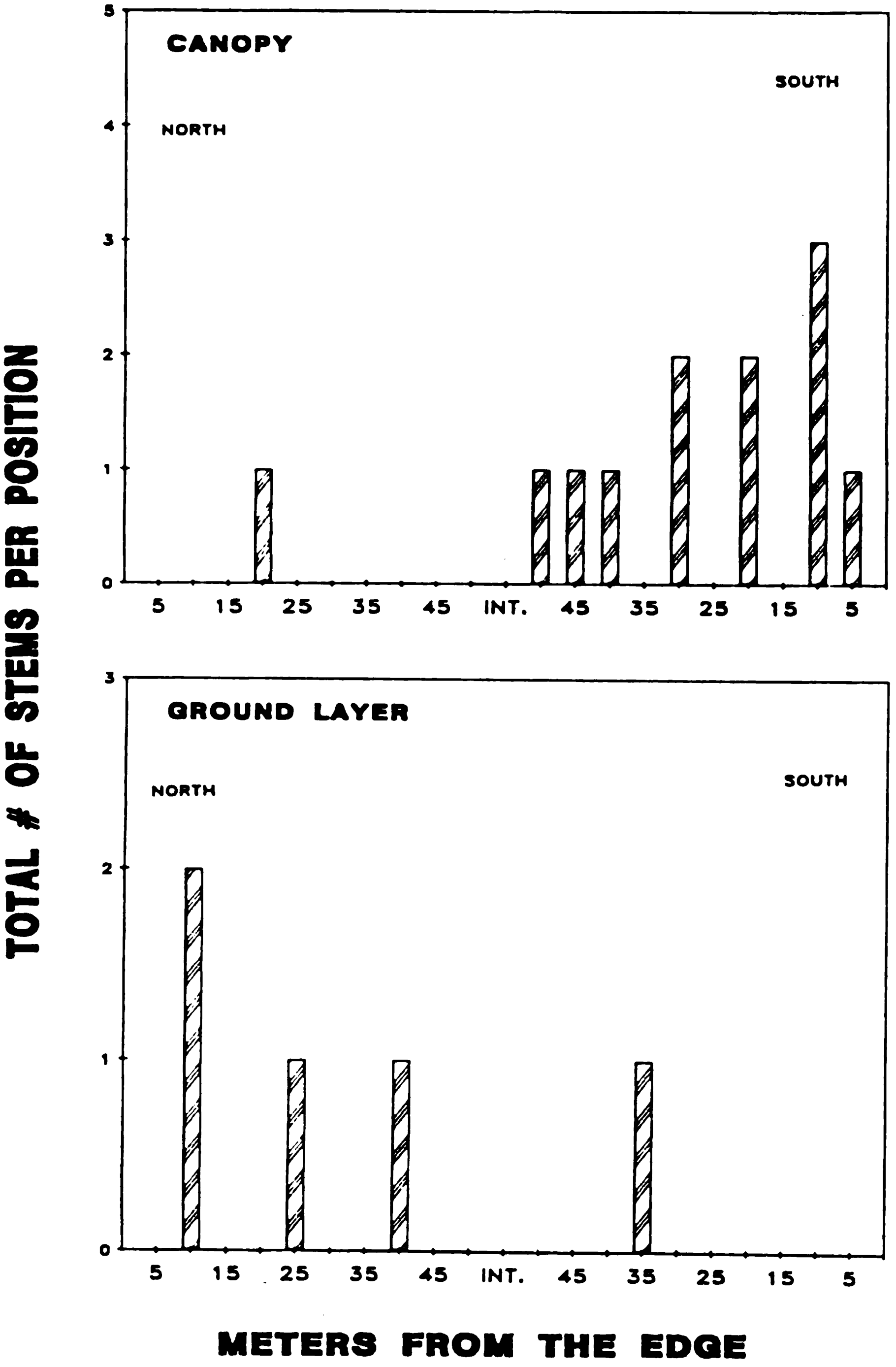


Figure 15. Basswood canopy and ground layer abundance profiles from the edge to 50 m on the northern and southern aspects in Site 1. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number of stems encountered in each 5 m interval and in the interior. The sapling and shrub profiles were similar to the canopy profile.

Additional species distributions of interest but not illustrated, included ironwood, which was found throughout the forest on the southern aspect only, and black cherry, canopy individuals of which were found only on the southern aspect. In the subcanopy strata, black cherry abundance was greatest on the southern aspect, with a distribution extending 45 m into the forest. The same general pattern was also found for bitternut hickory. Additionally, total ground layer density of hickory was significantly higher on the southern aspect (P <.01, Welch's approximation; Table 10), and abundance was greatest in the edge positions of both aspects. Red-berried elder (Sambucus pubens Michx.) was confined to positions interior of 10 m on the northern aspect and 30 m on the southern aspect, whereas common elder (S. canadensis L.) was most abundant within the first 10 m of forest on the northern aspect. Choke-cherry (Prunus virginiana L.), blackberry, hawthorn and viburnum (Viburnum opulus L.) were found within the first 35 m of forest on the southern aspect only. White oak seedlings were found only within the first 15 m of forest on both aspects.

Site 2 (2.70 ha)

Although patterns of distribution and abundance for individual species which reflected edge and aspect influence were evident in this site, they were generally of a lesser magnitude than in Site 1. In the canopy, sugar maple showed no strong position or aspect differences but density was highest at position 0-5 m north (Figure 16). Total sapling density was significantly greater on the northern

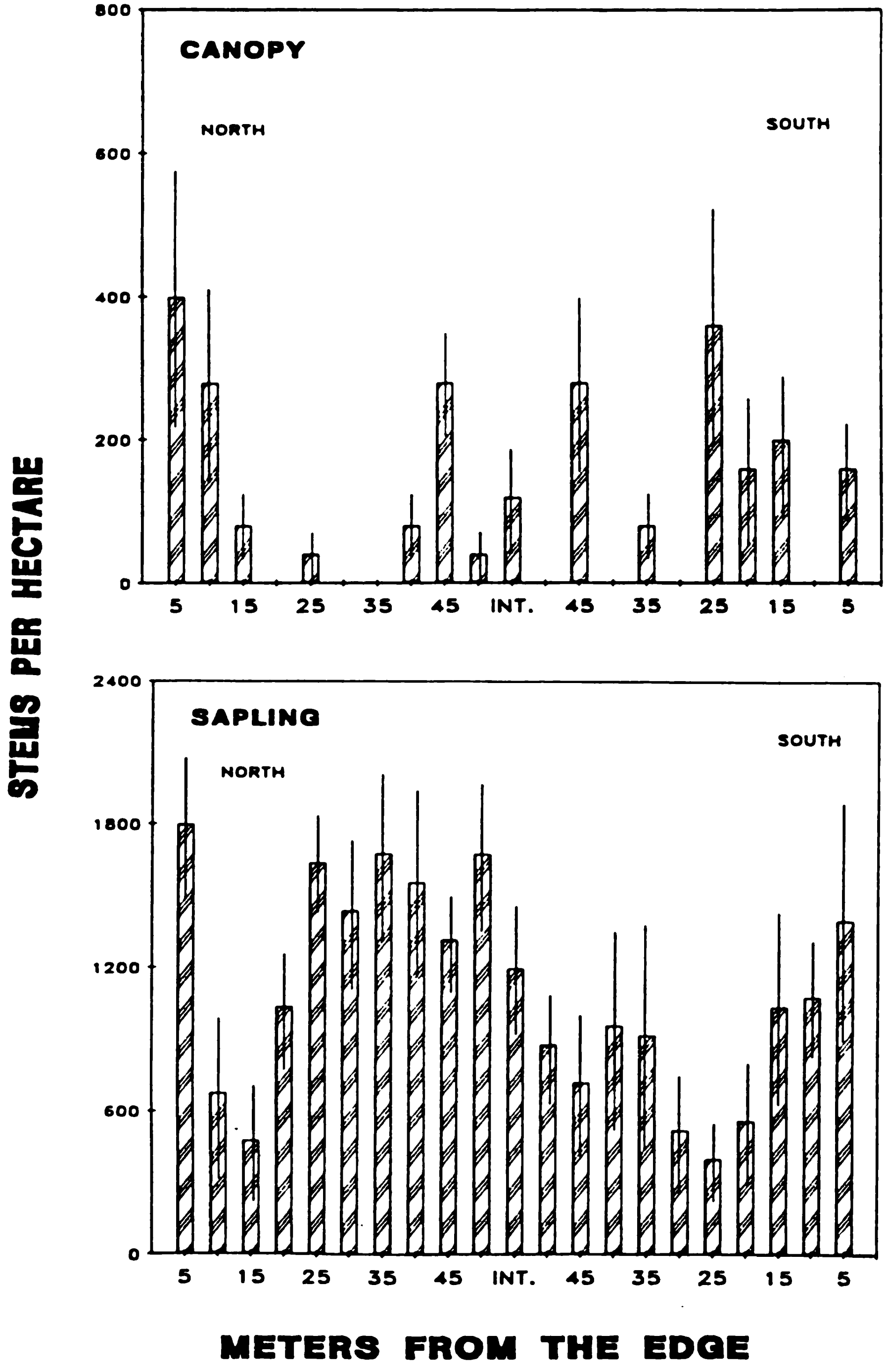


Figure 16. Sugar maple canopy and sapling density profiles from the edge to 50 m on the northern and southern aspects in Site 2. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=5.

aspect (P <.01, Welch's approximation; Table 10), but no position trends were clearly evident (Figure 16). In the shrub layer density was highest at or near the edge on both aspects (Figure 17). Densities of positions 0-5 m north, and 10-20 m south were significantly greater than in the remainder of plots interior to these on their respective aspects (P <.05, orthogonal contrasts). As in Site 1, total ground layer density of sugar maple was greatest on the northern aspect (P <.01, t-test; Table 10). The low densities on the southern aspect extended 45 m into the forest (Figure 17).

The distribution and abundance patterns of American beech were very similar in all strata (Figure 18). The species was not found in the extreme edge position on either aspect in the upper 3 strata. Abundance patterns were marked by an increase interior of 25 m on the southern aspect, while on the northern aspect abundances were low to 50 m. Total sapling density was significantly greater on the southern aspect (P <.05, Welch's approximation; Table 10).

Although not confined to the southern aspect, basswood did have highest abundance at or near the southern edge in all strata (Figure 18). Contrary to its canopy and sapling distribution in Site 1, white ash was found on both the northern and southern aspects (Figure 19). However abundance was highest in the first 20 m of the forest in all strata. In the upper 3 strata the species was not found interior of 35 m on either aspect, while the ground layer distribution extended 50 m into the forest on the northern aspect.

As in Site 1, the distribution of ironwood was reflective of edge and southern aspect affinities. Canopy abundance was highest at position 0-5 m south and in this stratum the species was not found

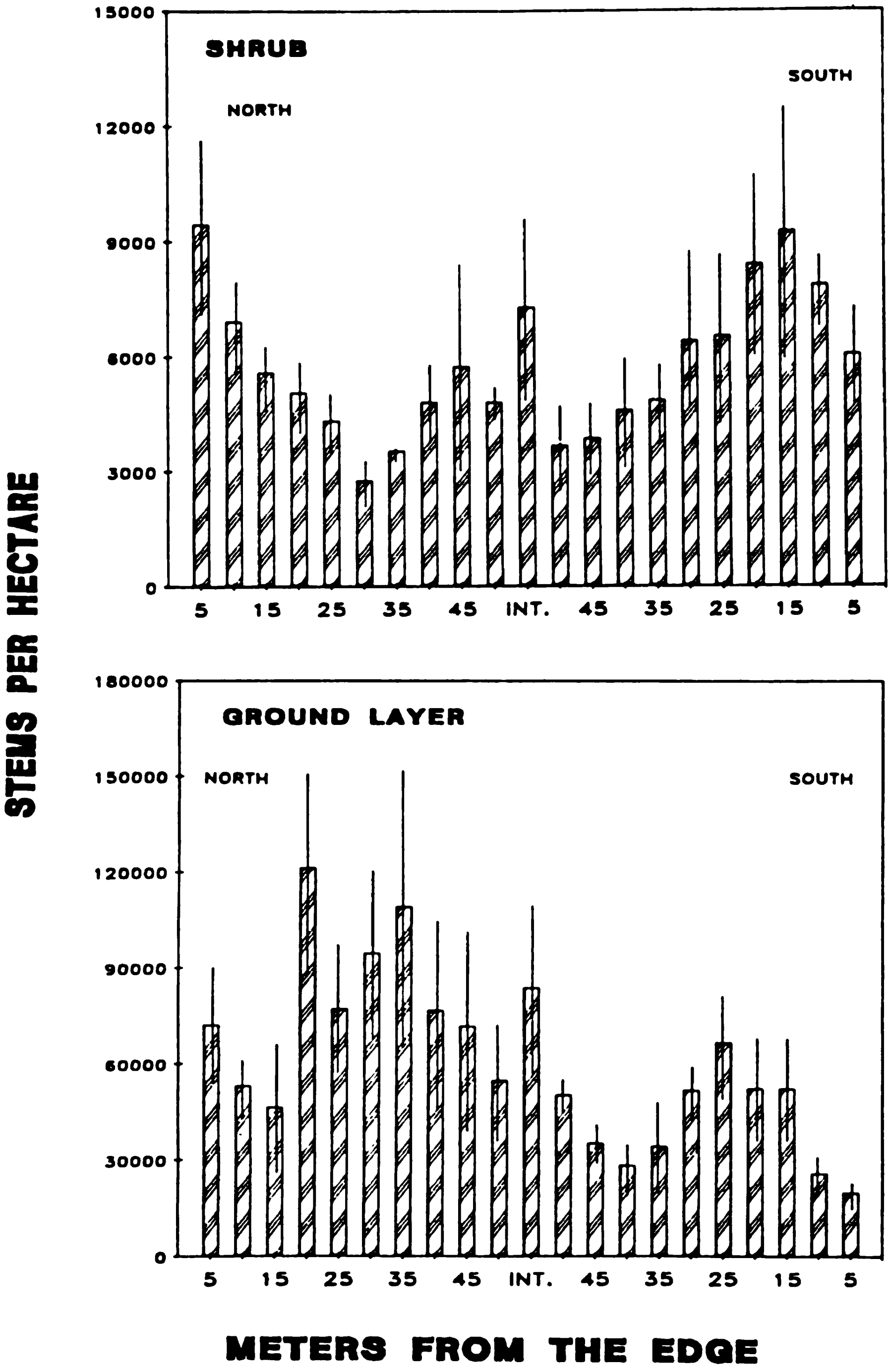


Figure 17. Sugar maple shrub and ground layer density profiles from the edge to 50 m on the northern and southern aspects in Site 2. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=5.

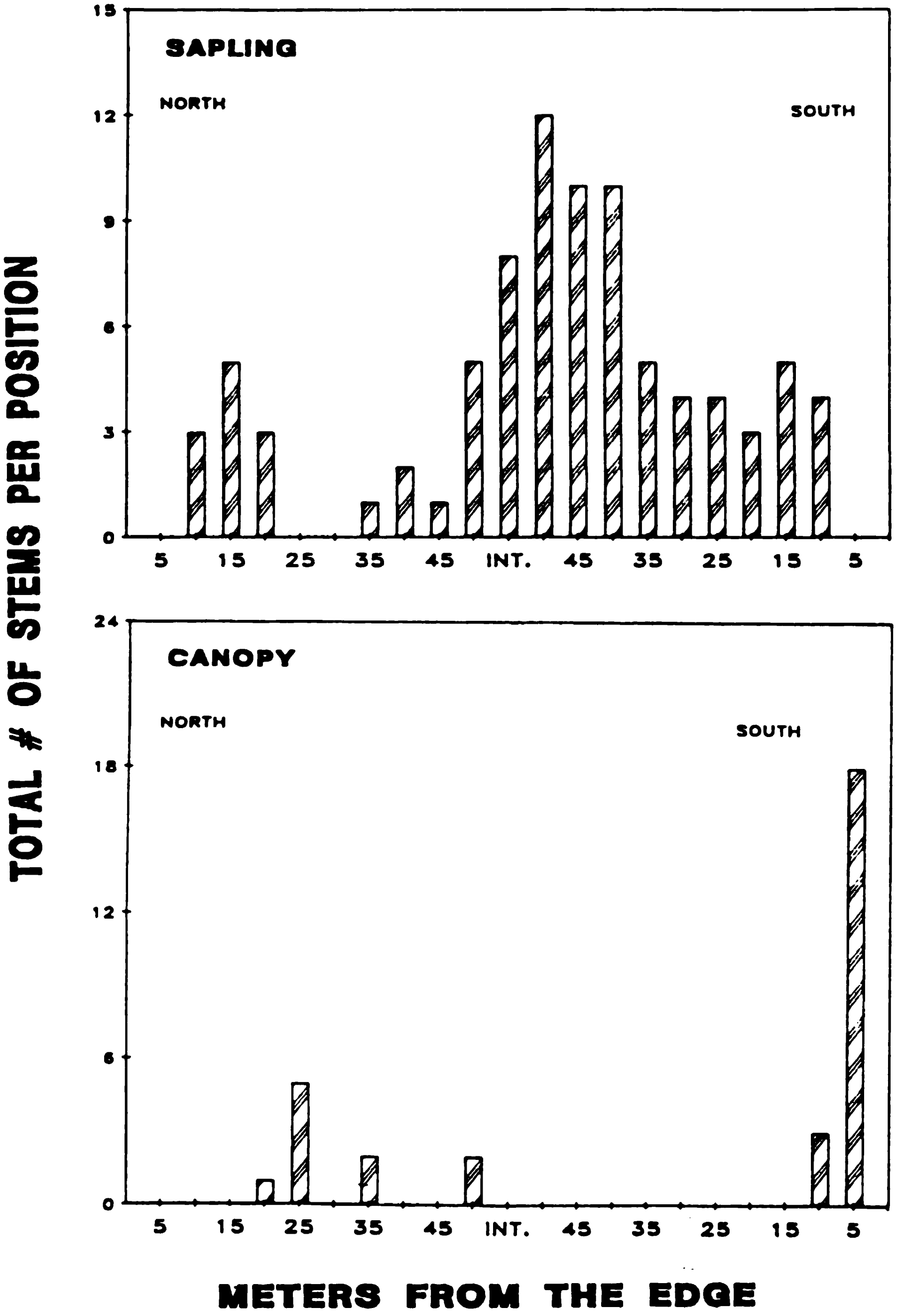


Figure 18. American beech sapling (top) and basswood canopy (bottom) abundance profiles from the edge to 50 m on the northern and southern aspects in Site 2. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number of stems encountered in each 5 m interval and in the interior. Beech canopy, shrub, and ground layer profiles were similar to the sapling profile; basswood sapling, shrub, and ground layer profiles were similar to the canopy profile.

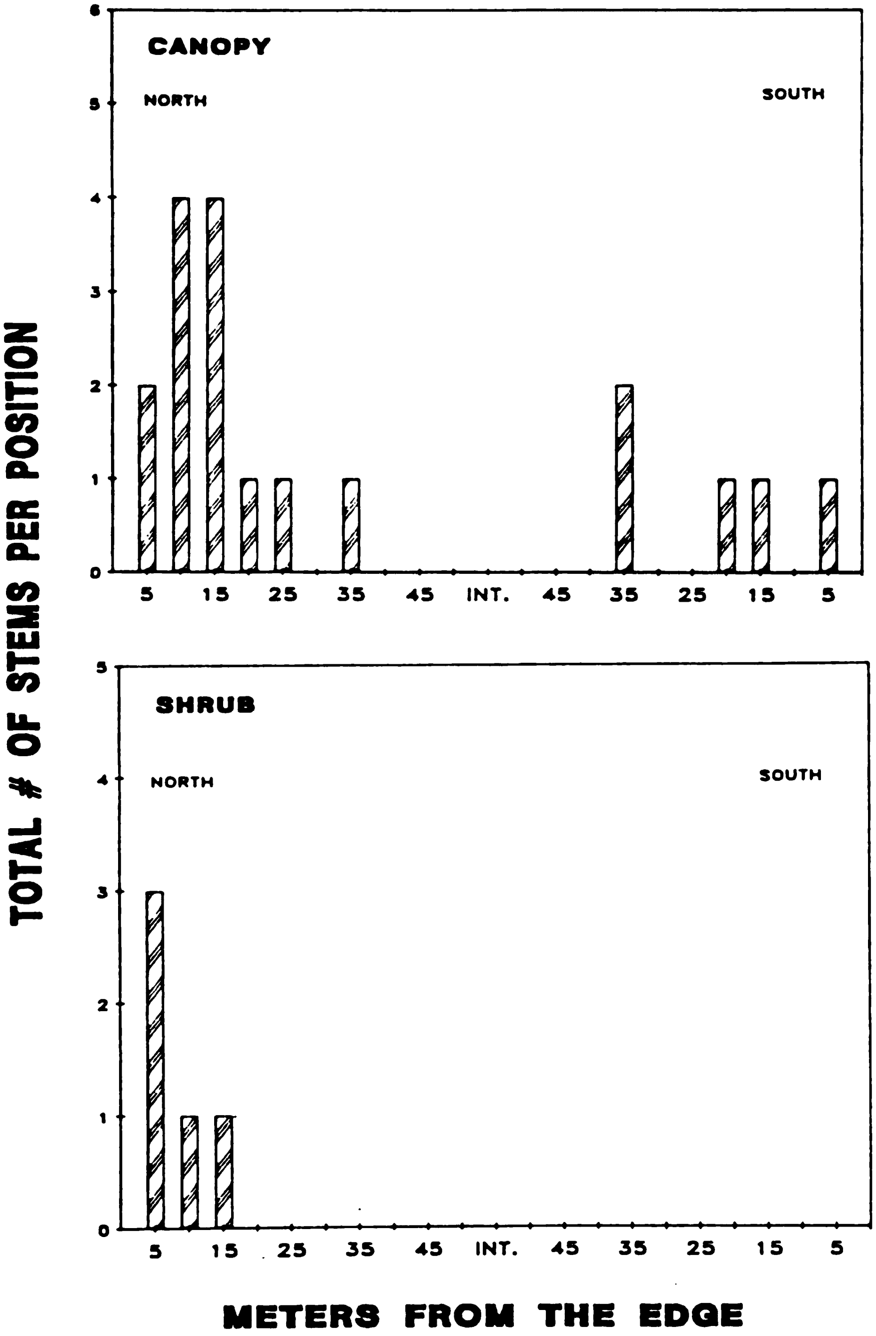


Figure 19. White ash canopy and shrub abundance profiles from the edge to 50 m on the northern and southern aspects in Site 2. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number is stems encountered in each 5 m interval and in the interior. The sapling profile was similar to the canopy profile.

interior of 35 m on either aspect (Figure 20). Ironwood was distributed throughout both aspects in the sapling strata (Figure 20) but total density was significantly greater on the southern aspect (P <.001, Welch's approximation; Table 10). High abundance extended 45 m into the forest. In the shrub layer the species was confined to positions exterior of 40 m on both aspects, while in the ground layer ironwood was found only exterior of 15 m on the southern aspect.

Slippery elm (not illustrated) was confined to positions exterior of 20 m in the canopy and 35 m in the sapling strata, on northern aspect. In the lower strata its distribution was somewhat wider on the northern aspect; however, abundance was still highest at the northern edge. Red oak (not illustrated) was confined to the first 15 m of forest on southern aspect in the canopy and sapling strata, and was found only in the extreme edge position on both aspects in the ground layer. Shrub-sized individuals were not found. In the canopy black cherry (not illustrated) was confined to the first 25 m of forest on the northern aspect. Sapling distribution extended 45 m into the forest on the northern aspect. In the shrub layer this species was found only at position 0-5 m south, while in the ground layer black cherry was distributed throughout the northern aspect and the most interior positions on the southern aspect. Total ground layer density was also significantly higher on the northern aspect (P <.01, Welch's approximation; Table 10).

Additional distributions of interest but not illustrated included: gooseberry, which was found throughout the southern aspect; hornbeam, which was found only in the first 25 m of forest on the northern aspect; gray dogwood (<u>Cornus racemosa</u> Lam.) which was

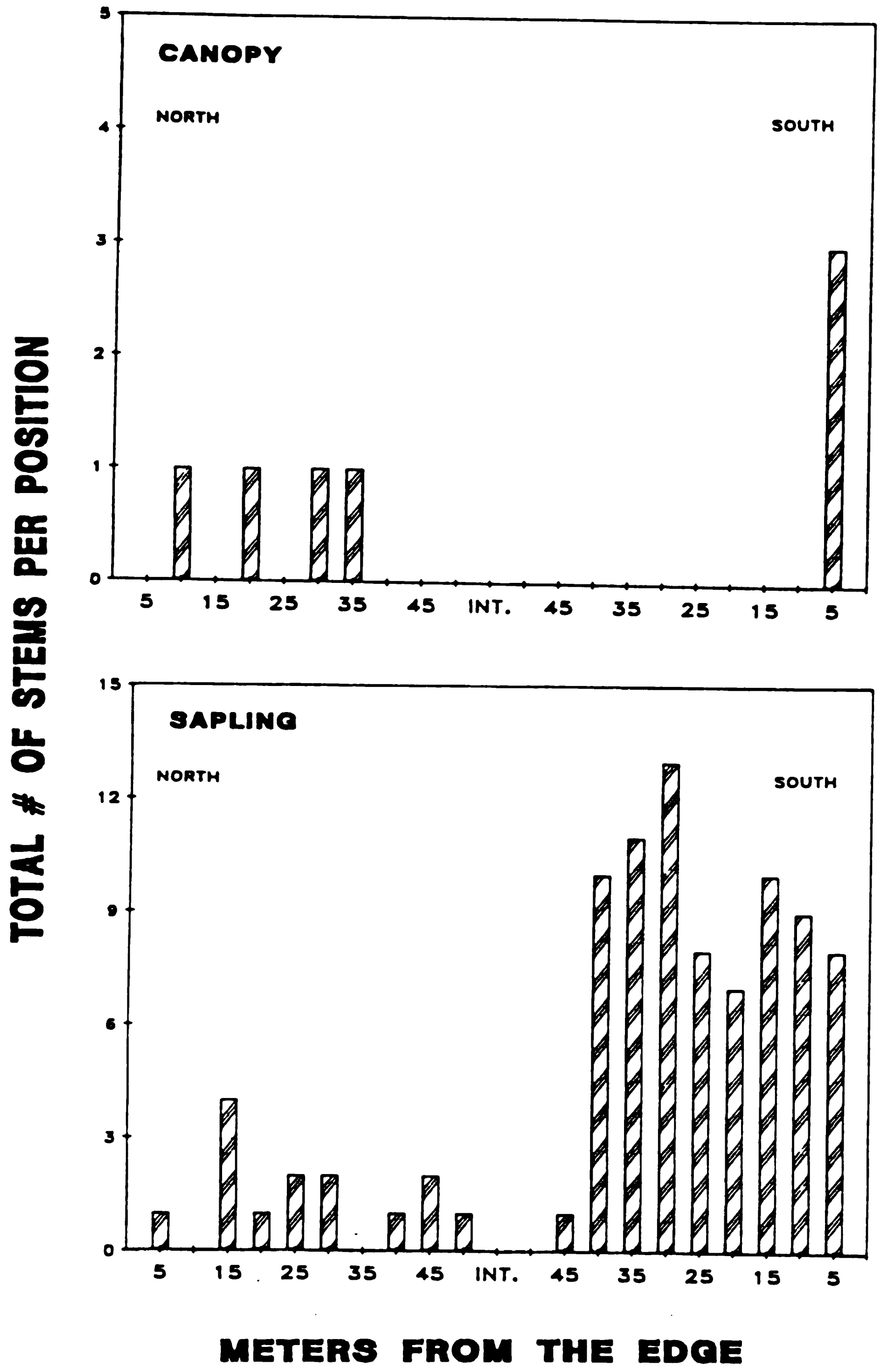


Figure 20. Ironwood canopy and sapling abundance profiles from the edge to 50 m on the northern and southern aspects in Site 2. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number of stems encountered in each 5 m interval and in the interior.

confined to the extreme edge on the northern aspect; and common elder which was confined to positions exterior of 5 m in the shrub layer and 25 m in the ground layer on the northern aspect.

Oak Fragments

Site 3 (3.60 ha)

Black oak was nearly ubiquitous in the canopy, showing no strong position or aspect trends (Figure 21). The species was not found in the sapling layer, and was of only minor importance in the first 10 m of forest on the southern edge in the shrub layer. Ground layer distribution was concentrated within the first 30 m of forest on the southern aspect (Figure 21). Although abundance was not exceptionally high, the pattern may be indicative of the environmental conditions necessary for the establishment of oak regeneration.

Canopy abundance of pignut hickory showed a strong decrease from the northern edge to the interior (Figure 22). Highest abundance on the southern aspect was also found near the edge. Total density was significantly higher on the northern aspect ($P < .001$, Welch's approximation; Table 11). In the sapling and shrub strata, pignut hickory was found throughout the southern aspect, with highest abundance at or near the edge (Figure 22). The species was distributed widely in the ground layer, with no strong position trend evident but abundance was highest in the mid-to-exterior positions on both aspects.

In the canopy, red maple abundance increased from the edge to the interior on the northern aspect (Figure 23). On the southern aspect,

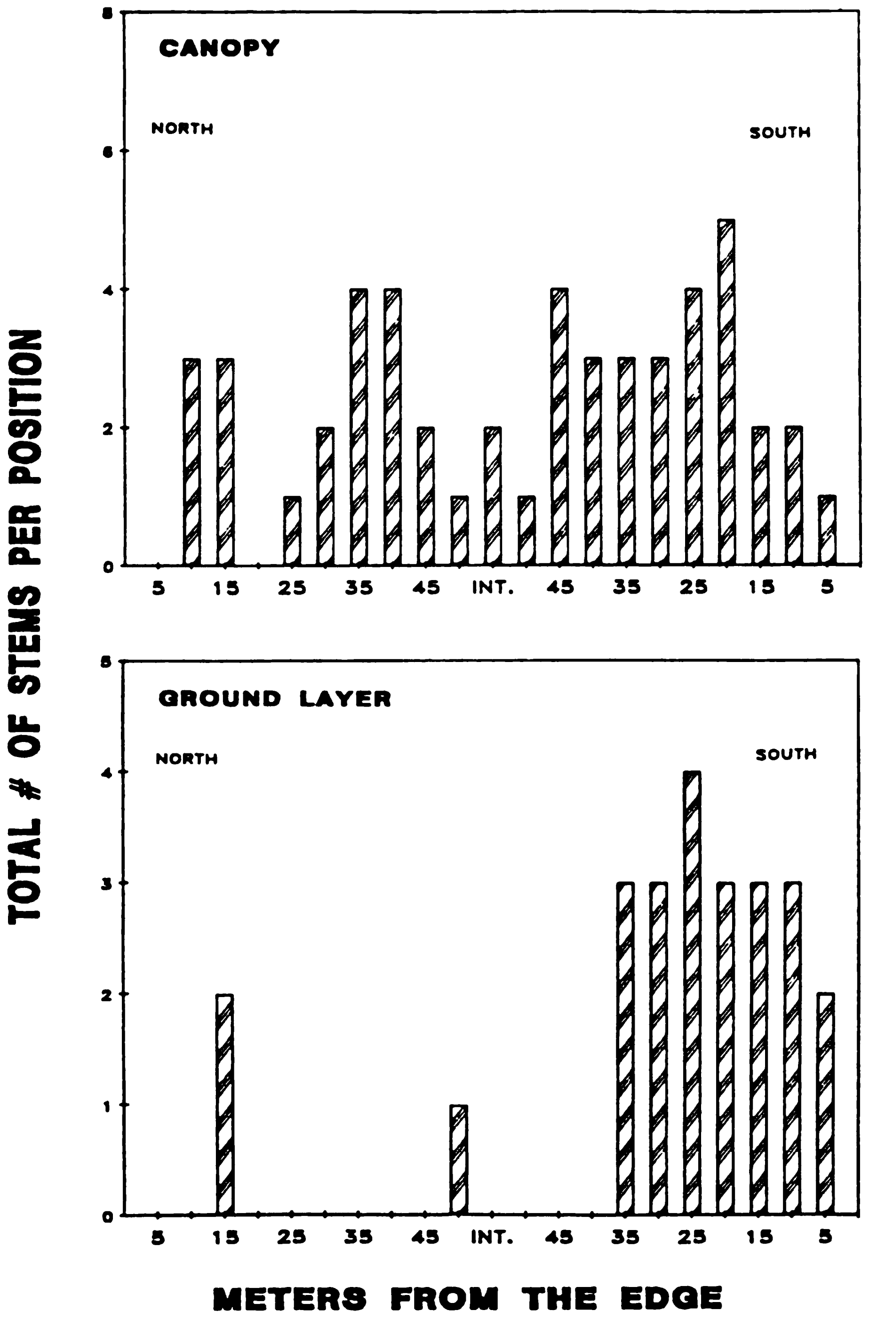


Figure 21. Black oak canopy and ground layer abundance profiles from the edge to 50 m on the northern and southern aspects in Site 3. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number of stems encountered in each 5 m interval and in the interior.

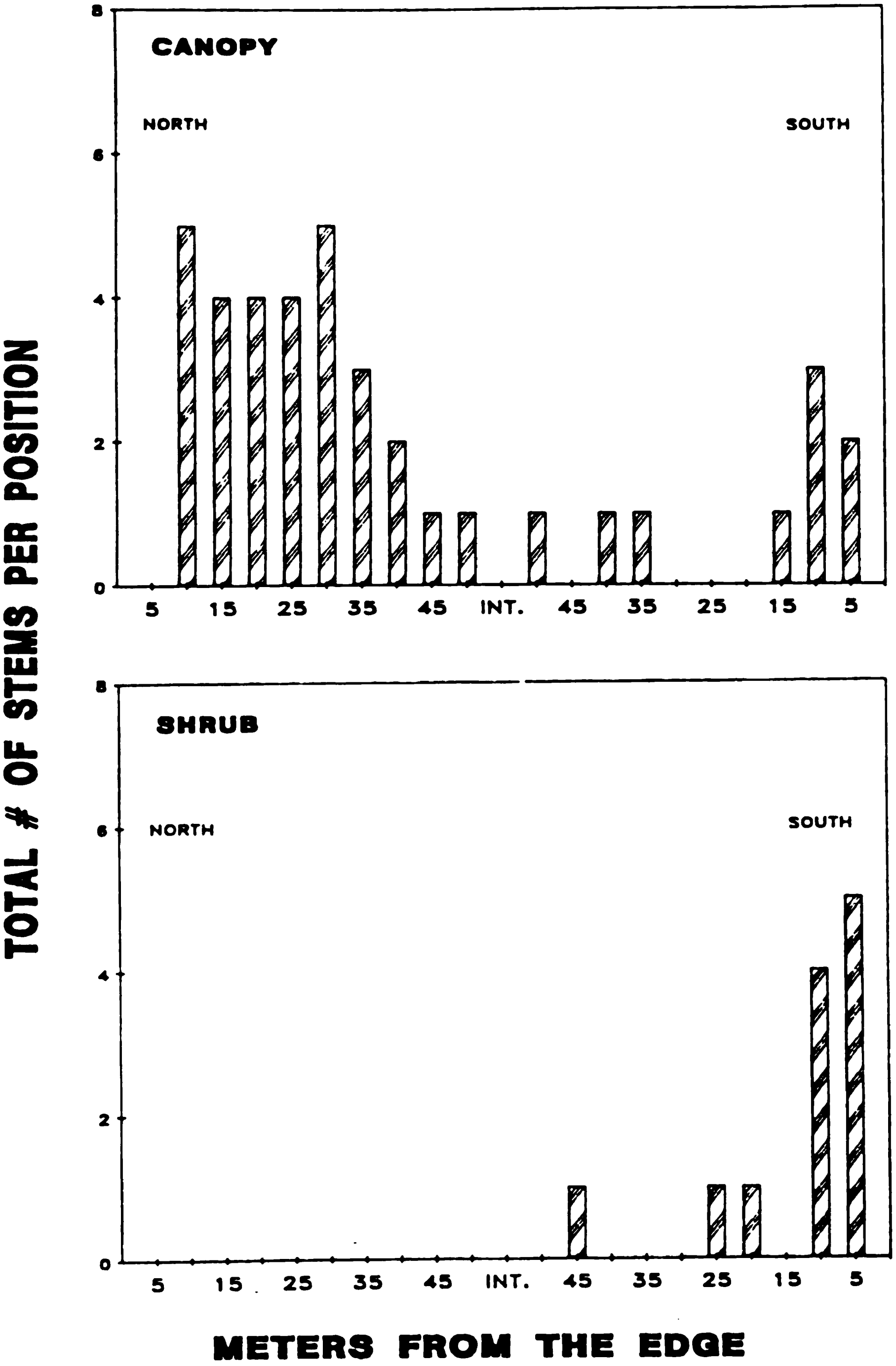


Figure 22. Pignut hickory canopy and shrub abundance profiles from the edge to 50 m on the northern and southern aspects in Site 3. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number of stems encountered in each 5 m interval and in the interior, The sapling profile was similar to the shrub profile.

Table 11. Density per hectare of selected species in the canopy, sapling, shrub, and ground layer (g.l.) strata on the northern and southern aspects (edge to 50 m) in oak fragments.

			Aspect	
Site	Species	Stratum	North	South
3	*Acer rubrum*	canopy	128 (27)*[a]	20 (9)
		sapling	338 (61)**	188 (42)
		g.l.	12100 (2182)**	6250 (904)
	Carya glabra	canopy	116 (20)**	36 (12)
	Prunus serotina	canopy	116 (20)	268 (34)**
		sapling	144 (24)	368 (47)**
		shrub	300 (93)	713 (129)**
		g.l.	800 (271)	3150 (851)**
	P. virginiana	shrub	573 (230)	2193 (366)**
		g.l.	5450 (917)	12650 (1945)**
	Ulmus rubra	shrub	80 (39)	213 (50)*
		g.l.	150 (85)	750 (192)*
	Amelanchier arborea	sapling	36 (12)	84 (18)*
		shrub	133 (51)	420 (100)*
4	*Acer rubrum*	shrub	544 (138)*[b]	156 (57)
		g.l.	2438 (719)*	688 (283)
	Prunus serotina	sapling	360 (137)	673 (92)*
		shrub	1189 (224)	2500 (267)**
		g.l.	3063 (735)	8500 (1437)**
	Fraxinus americana	sapling	80 (33)	393 (67)**
		shrub	1644 (351)*	722 (180)
		g.l.	22917 (2128)**	13000 (1628)
	Rubus allegheiensis	g.l.	12188 (2564)**	1813 (800)

[a] The mean of 50 plots +/- (se).
[b] The mean of 30 plots +/- (se).
* P <.05, ** P <.01 indicates significantly higher density than corresponding aspect.

the species was confined to positions interior of 25 m, with abundance low in all positions. Total canopy density was significantly greater on the northern aspect (P <.05, Welch's approximation; Table 11). Sapling density increased from the southern edge to about 45 m into the forest (Figure 23). Ground layer density was lowest within the first 10 m of forest on the southern aspect and highest from 15 to 25 m on the northern aspect (Figure 24). Total densities were significantly greater on the northern aspect in both the sapling and ground layers (P <.01, Welch's approximation; P <.01 ANOVA; Table 11). In the shrub layer no significant position or aspect differences were evident; however, highest densities were found in the middle positions on the southern aspect (Figure 24). Red maple density was low in the interior position in the subcanopy strata, while abundance was moderate in the canopy (Figures 23 & 24).

Black cherry abundance was highest on the southern aspect in all strata. In the canopy, high densities extended to 50 m, while in the subcanopy strata density was highest within the first 30 m of the forest (Figure 25). Total density was significantly higher on the southern aspect in all strata (P <.01, Welch's approximation; Table 11). Choke-cherry distribution was similar to black cherry, extending 50 m into the forest on the southern aspect, with highest abundance near the southern edge. Total shrub and ground layer densities were significantly greater on the southern aspect (P <.01, Welch's approximation; Table 11).

<u>Rosa</u> <u>multiflora</u> Thunb. was widely distributed on both aspects in the shrub layer but the patterns of abundance clearly illustrated an interaction of edge and aspect (Figure 26). Densities were highest

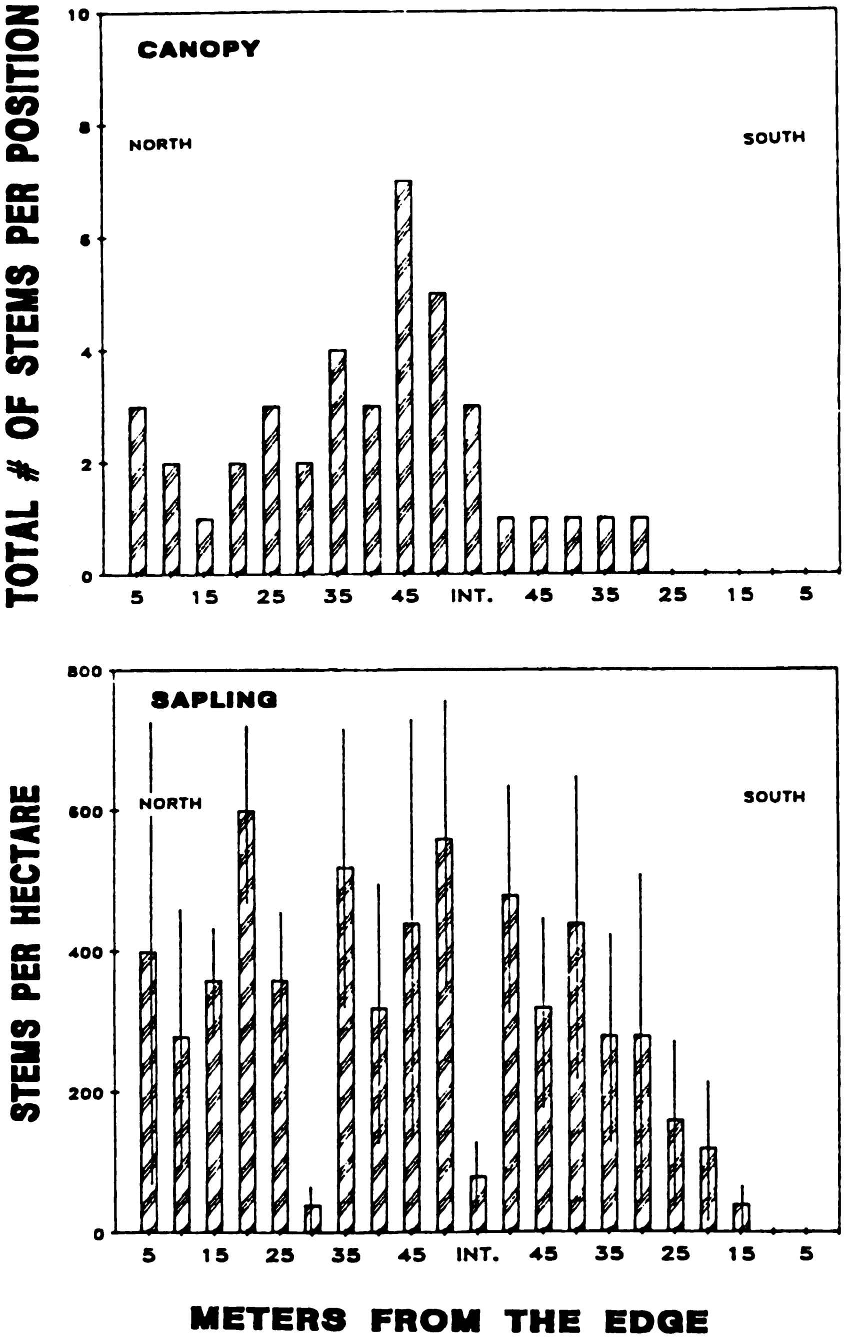


Figure 23. Red maple canopy abundance (top) and sapling density (bottom) profiles from the edge to 50 m on the northern and southern aspects in Site 3. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values in the top profile are the total number of stems encountered in each 5 m interval and in the interior. The y-axis values in the bottom profile are means +/- se; n=5.

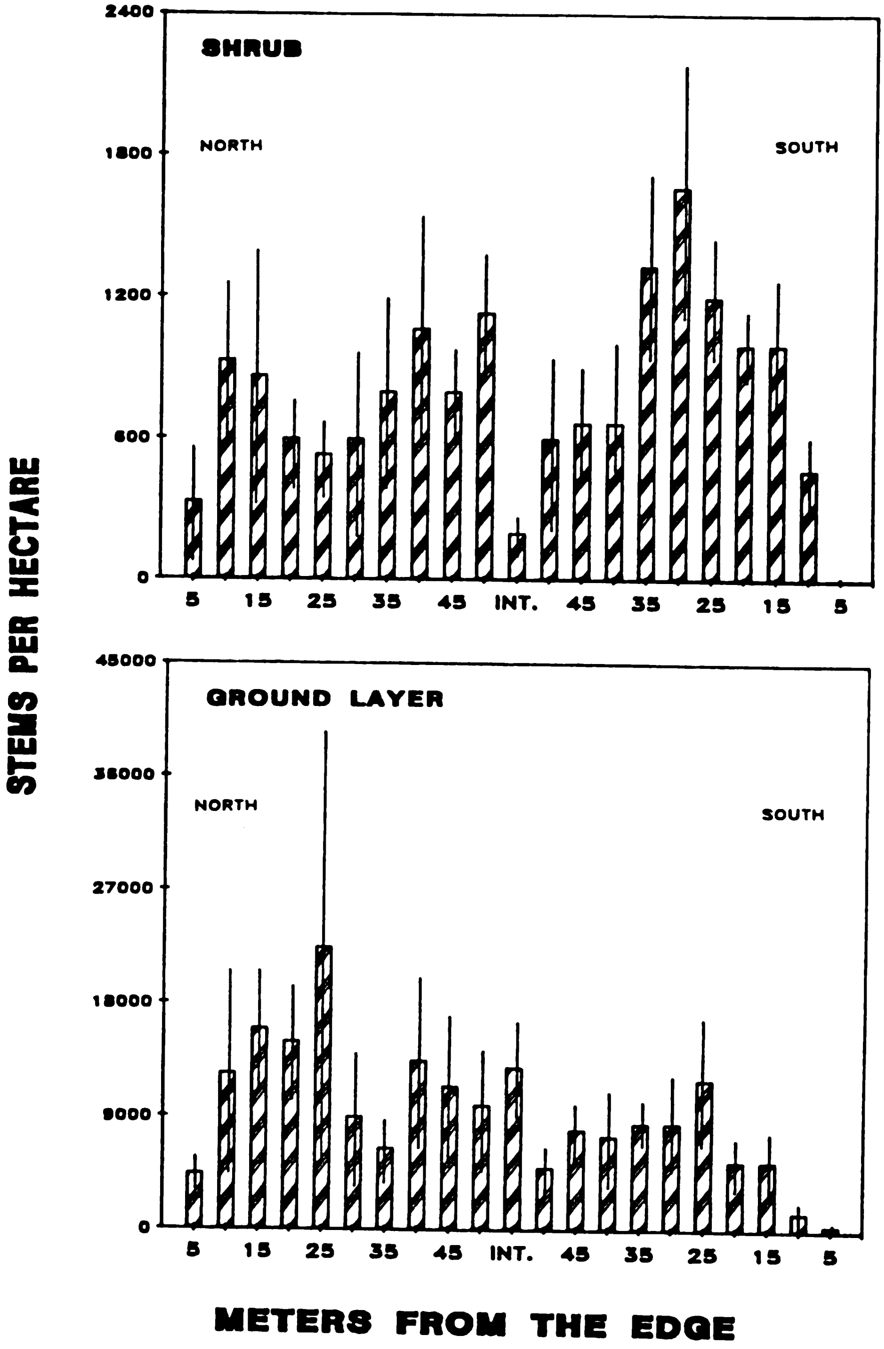


Figure 24. Red maple shrub and ground layer density profiles from the edge to 50 m on the northern and southern aspects in site 3. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=5.

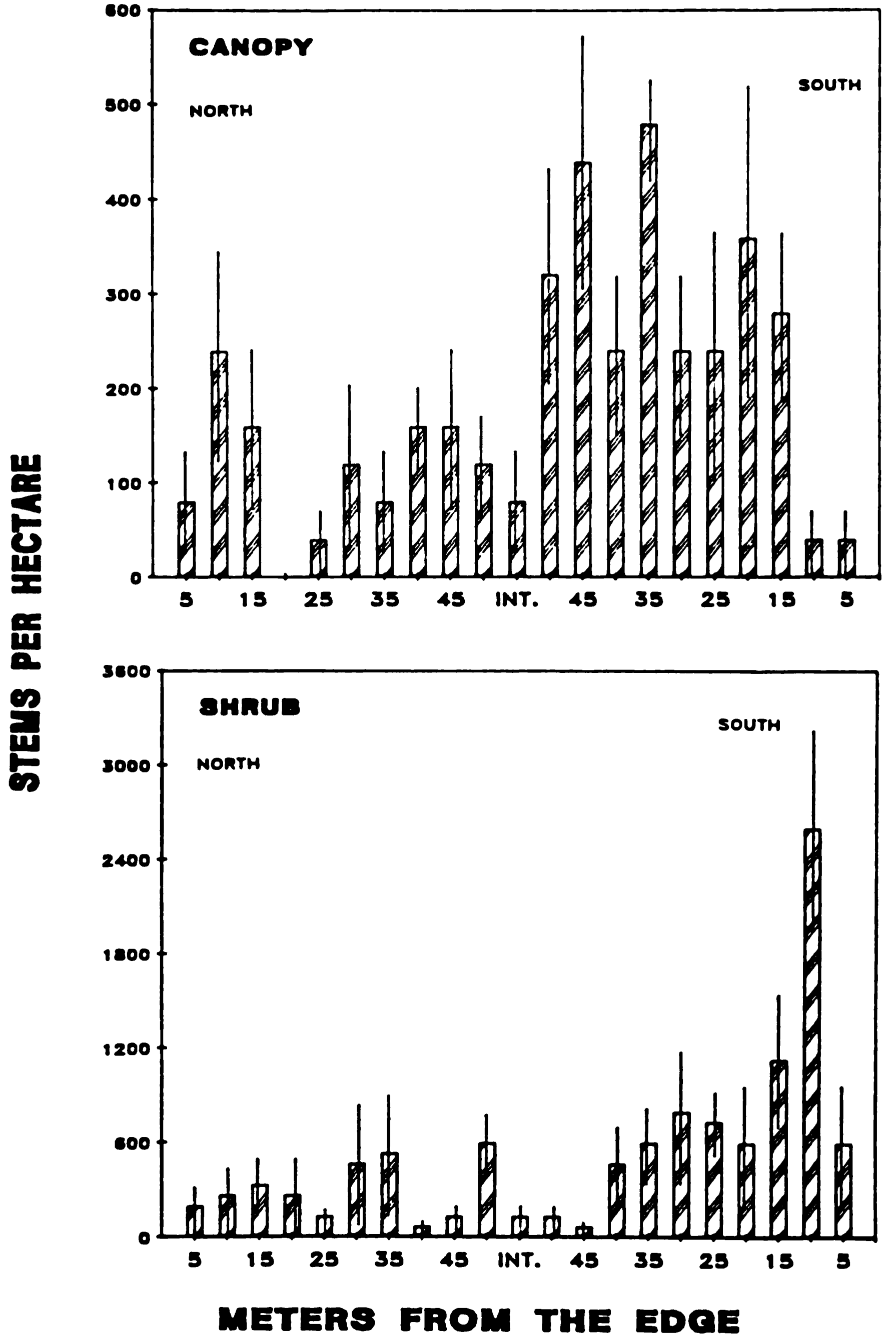


Figure 25. Black cherry canopy and shrub density profiles from the edge to 50 m on the northern and southern aspects in Site 3. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=5. The sapling and ground layer profiles were similar to the shrub profile.

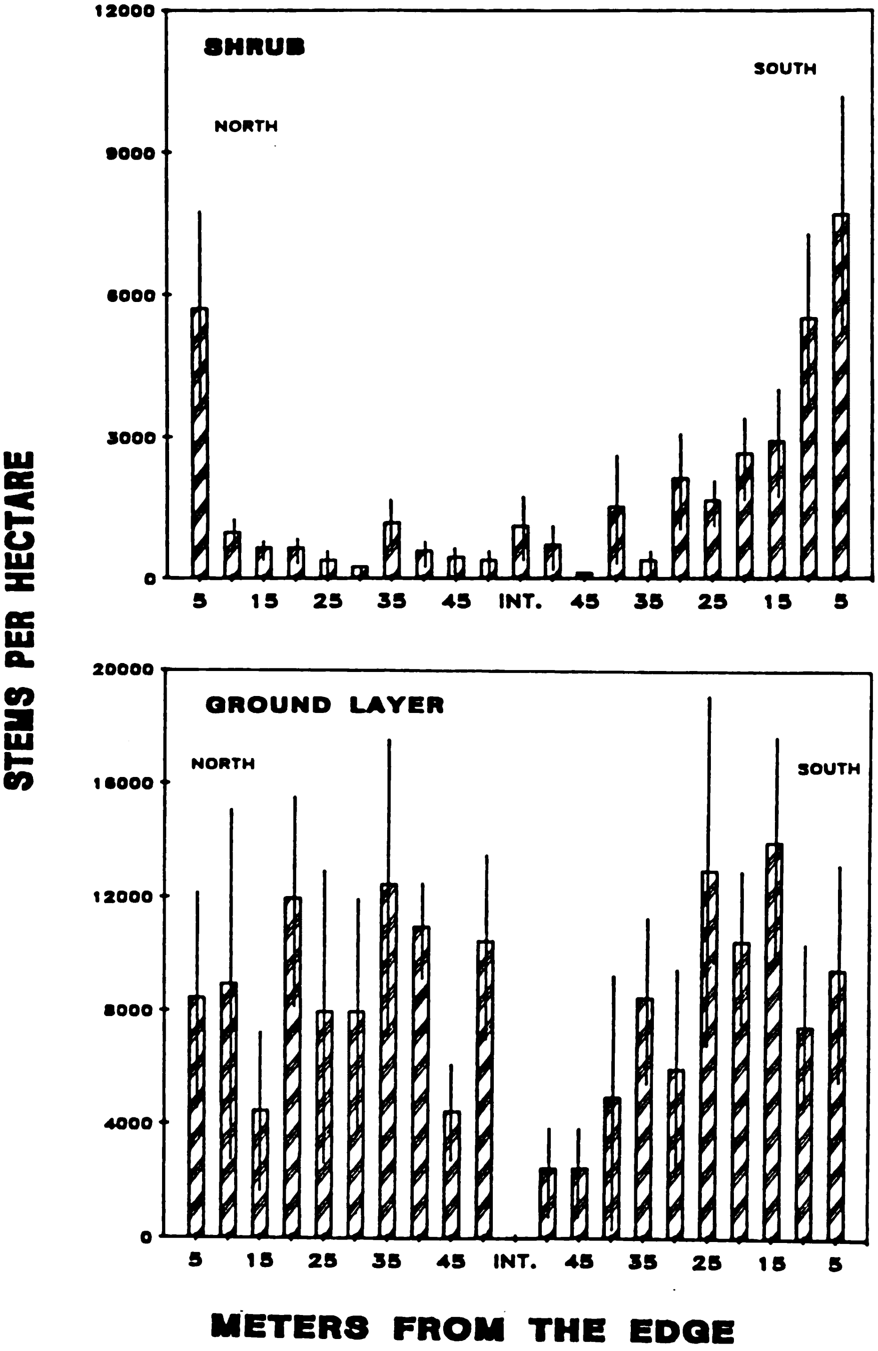


Figure 26. Rosa multiflora shrub and ground layer density profiles from the edge to 50 m on the northern and southern aspects in Site 3. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=5.

in the extreme edge positions on both aspects, decreasing into the interior. The higher densities extended farther into the forest on the southern aspect. In the ground layer the species was distributed to 50 m on both aspects but it was not found in the interior position (Figure 26).

Canopy individuals of slippery elm (not illustrated) were only found on the southern aspect, while in the subcanopy its distribution extended to 50 m on the southern aspect and 35 m on the northern aspect. Total shrub and ground layer densities were significantly higher on the southern aspect (P <.05, Welch's approximation; Table 11). Canopy individuals of basswood, white ash and boxelder (none illustrated) were found only in position 0-5 m north. In the sapling stratum, white ash distribution extended 45 m into the forest on the northern aspect and 15 m on the southern aspect.

Serviceberry (*Amelanchier arborea* (Michx. f.) Fern.; not illustrated) was found throughout the southern aspect and in the interior position; however, abundance was greatest within the first 30 m of forest. On the northern aspect the species was confined to the first 25 m of forest. Total sapling and shrub densities were significantly greater on the southern aspect (P <.05, Welch's approximation; Table 11).

Additional species whose distributions reflected edge and aspect affinities but are not illustrated included: hawthorn, tatarian honeysuckle, and Russian olive (*Elaeagnus umbellata* Thunb.), which were only found in the first 25 m of forest on the southern aspect; *Viburnum opulus*, which was confined to the first 40 m of forest on the northern aspect; and *Lonicera* sp. which was distributed to 45 m on the southern aspect. Wayfaring tree and gray dogwood were only found exterior of 35 m on both aspects, while gooseberry was confined to the first 20 m of forest on both aspects. Sassafras was confined to the first 5 m and 30 m of forest on the northern and southern aspects respectively. Wild crab apple (Malus coronaria L.) was found in the sapling and ground layers on both aspects, exterior of 15 m, while blackberry was distributed throughout both aspects and into the interior, with similar abundance in all positions.

White oak regeneration was confined to positions exterior of 10 m on the southern aspect and 5 m on the northern aspect. Although rare, sugar maple was found in all the subcanopy strata. Its distribution was confined to positions interior of 15 m on the northern aspect and 35 m on the southern aspect. Abundance was greatest at position 40-45 m north.

Site 4 (1.5 ha)

Canopy individuals of white oak were confined to positions interior of 10 m on the northern aspect and 15 m on the southern aspect (Figure 27). Highest abundance was found interior of 25 m on both aspects. In the sapling stratum the species was found throughout the southern aspect and into the interior, while in the shrub layer it was confined to the first 5 m of forest on the southern aspect.

Red oak was widely distributed in the ground layer but abundance was low throughout the sampled forest. In the sapling and shrub strata, distributions were limited to the more exterior positions on both aspects (Figure 28). In the canopy, red oak abundance was

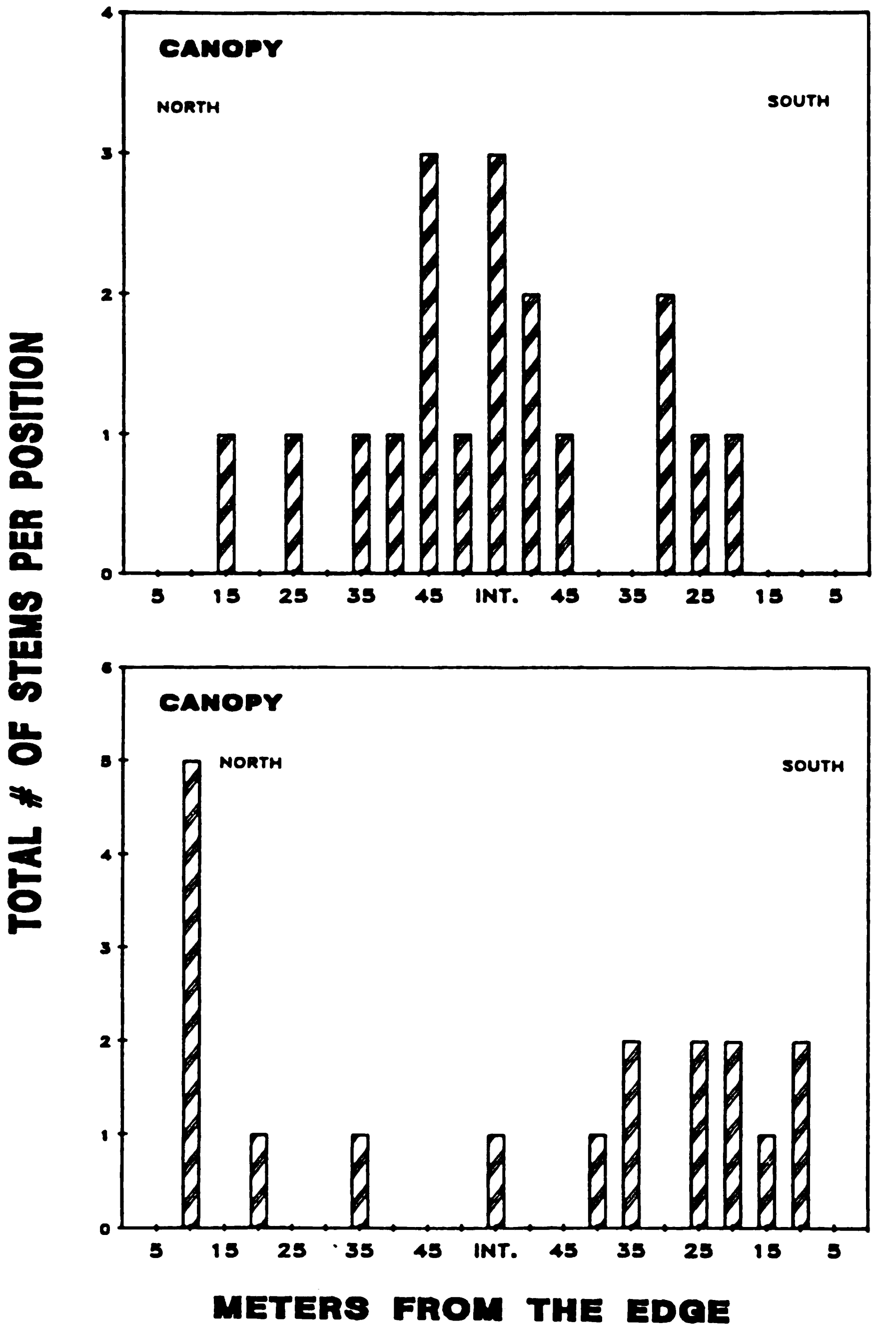


Figure 27. White oak (top) and red oak (bottom) canopy abundance profiles from the edge to 50 m on the northern and southern aspects in Site 4. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number of stems encountered in each 5m interval and in the interior.

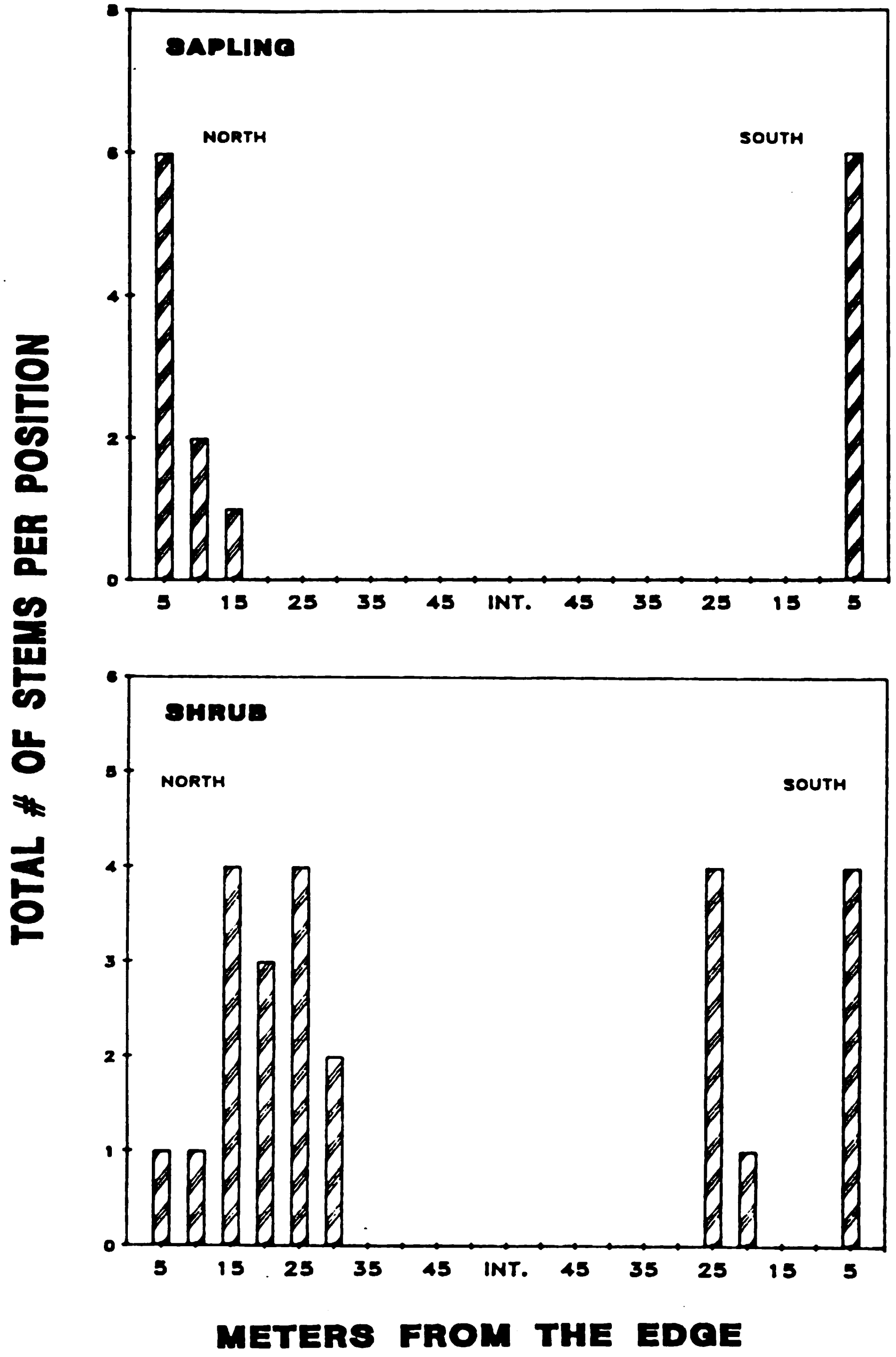


Figure 28. Red oak sapling and shrub abundance profiles from the edge to 50 m on the northern and southern aspects in Site 4. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number of stems encountered in each 5 m interval and in the interior.

highest near the northern edge (Figure 27).

Red maple was widely distributed in all strata but total densities in the shrub and ground layers were significantly greater on the northern aspects (P <.05, Welch's approximation; Table 11). Sapling abundance was greatest interior of 25 m on both aspects (Figure 29). In all subcanopy strata abundance was highest in the interior.

White ash was most abundant on the northern aspect in the canopy (Figures 30). Abundance was greatest in the first 25 m of forest from the edge. This species was distributed throughout the entire sampled forest in the shrub and ground layers (Figure 31) but total shrub and ground layer densities were significantly greater on the northern aspect (P <.05, ANOVA; P <.001, Welch,s approximation; Table 11). Conversely, total sapling density was greatest on the southern aspect (P <.001, Welch's approximation; Table 11), with high abundance extending 35 m into the forest on this aspect (Figure 30).

One canopy individual of black cherry was found in this site, however distributions in the subcanopy strata encompassed the entire sampled area (Figure 32). Total densities in the sapling, shrub, and ground layers were significantly greater on the southern aspect (P <.05, Welch's approximation; P <.001 ANOVA; P <.01, Welch's approximation; Table 11). Highest densities were found in the interior (Figure 32).

Hawthorn was distributed 35 m and 10 m into the forest on the northern and southern aspects, respectively, in the sapling layer, and was found scattered throughout the site in the two lower strata (Figure 33). Densities of gray dogwood decreased from the edge to the

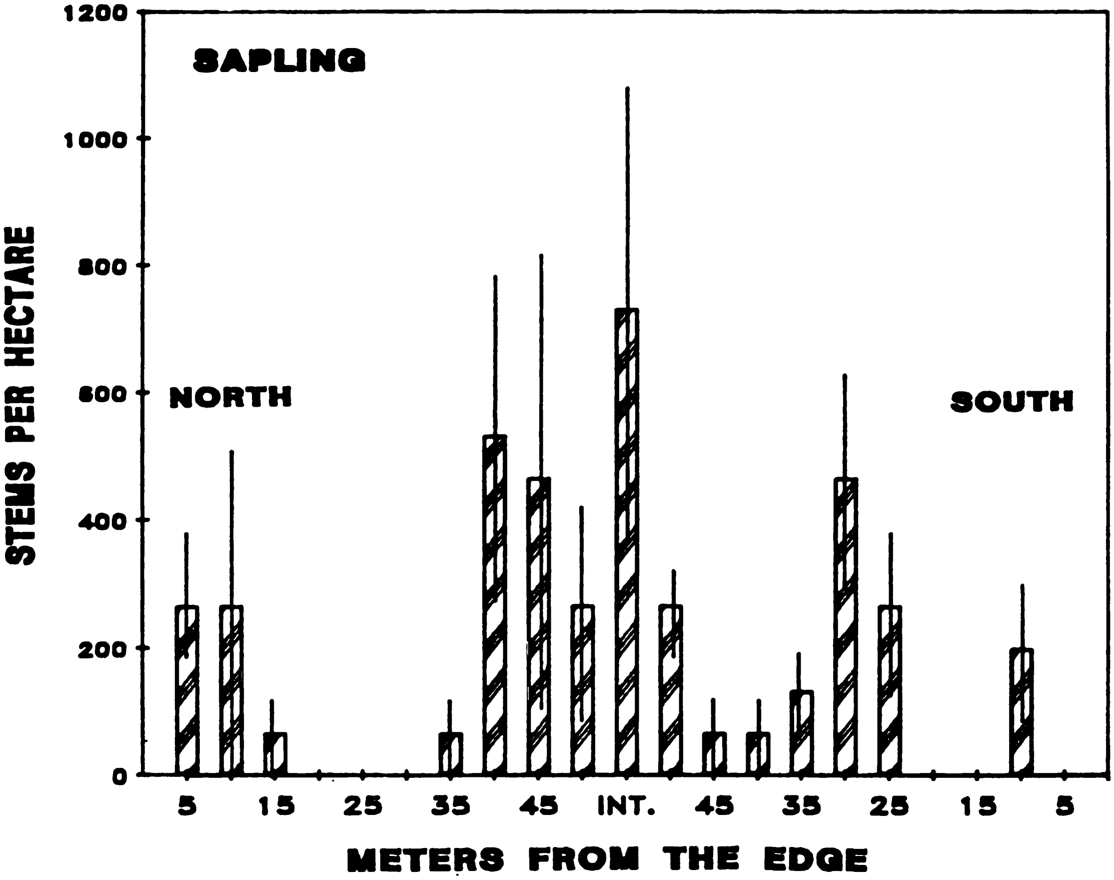


Figure 29. Red maple sapling density profile from the edge to 50 m on the northern and southern aspects in Site 4. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=3.

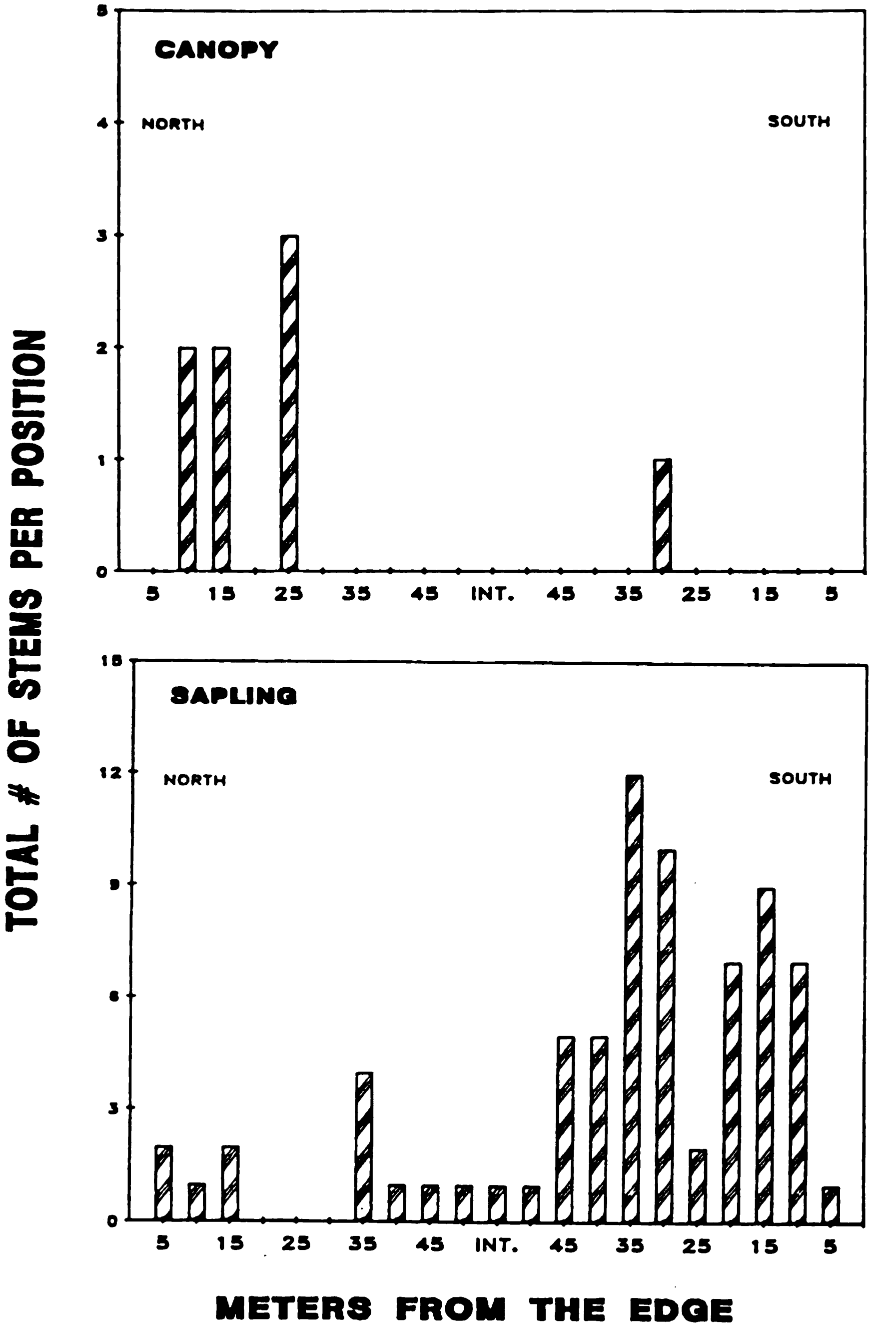


Figure 30. White ash canopy and sapling abundance profiles from the edge to 50 m on the northern and southern aspects in Site 4. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are the total number of stems encountered in each 5 m interval and in the interior.

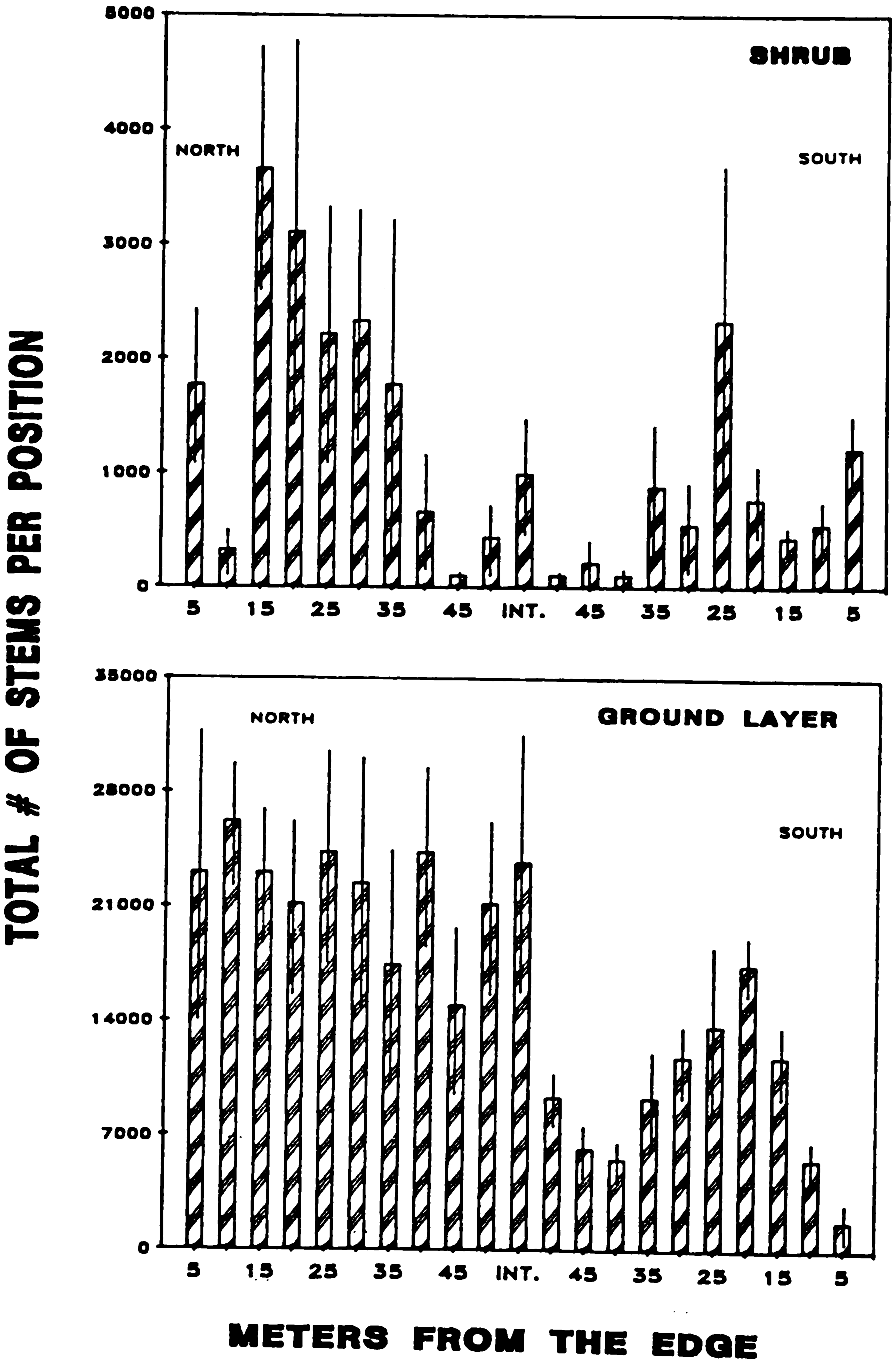


Figure 31. White ash shrub and ground layer density profiles from the edge to 50 m on the northern and southern aspects in Site 4. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all aspects. The y-axis values are means +/- se; n=3.

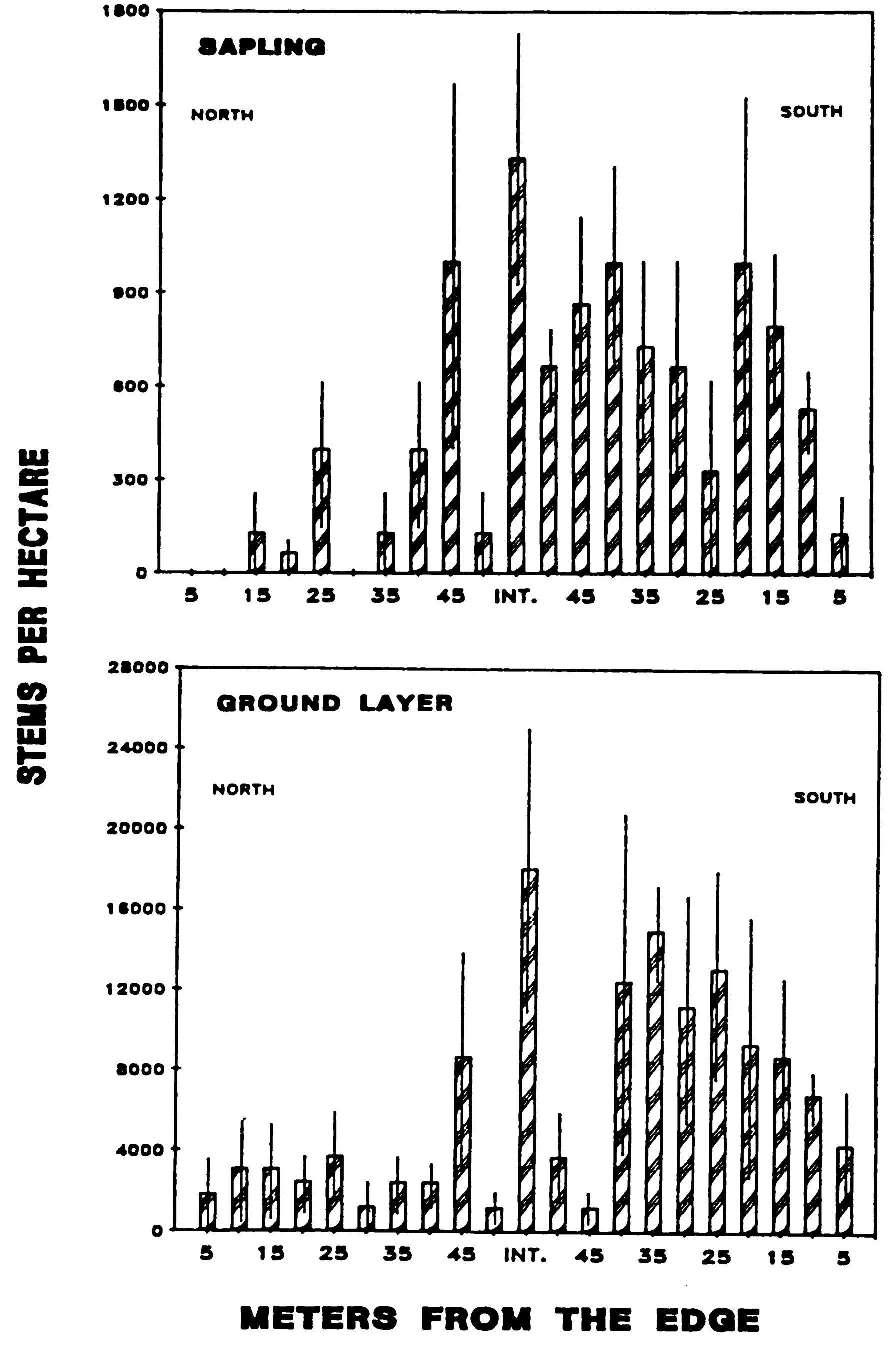


Figure 32. Black cherry sapling and ground layer density profiles from the edge to 50 m on the northern and southern aspects in Site 4. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m from all edges. The y-axis values are means +/- se; n=3. The shrub profile was similar to the ground layer profile.

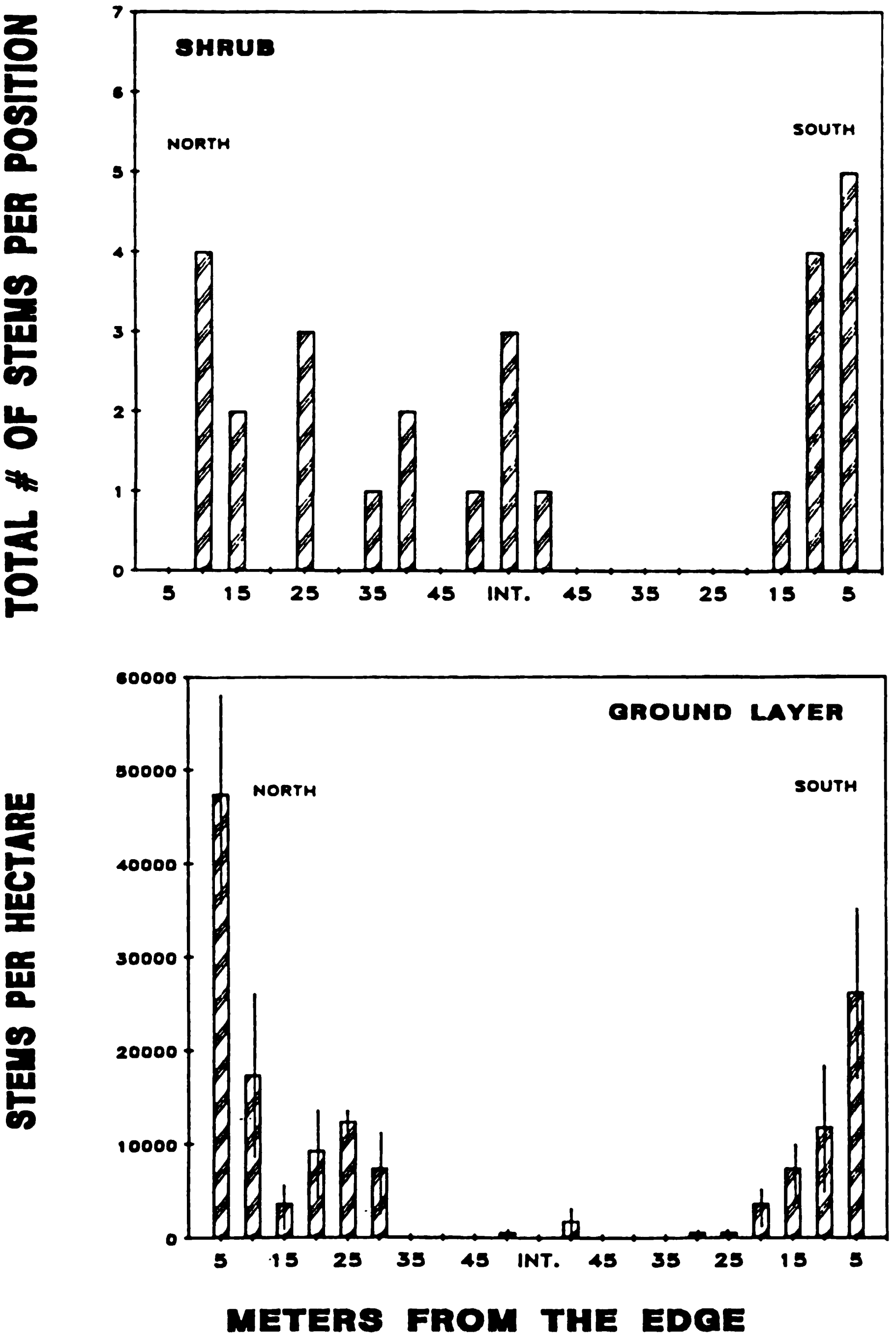


Figure 33. Hawthorn shrub abundance (top) and gray dogwood ground layer density (bottom) profiles from the edge to 50 m on the northern and southern aspects in Site 4. The x-axis values are the upper limits of 5 m distance intervals (positions). The interior (INT.) is 50 m interior of all edges. The y-axis values in the top profile are the total number of stems encountered in each 5 m interval and in the interior. The y-axis values in the bottom profile are means +/- se; n=3.

interior on both aspects (Figure 33). In the sapling stratum, slippery elm (not illustrated) was confined to the first 10 m of forest on the northern aspect, while on the southern aspect its distribution extended to 45 m. In the shrub and ground layers the species was found throughout both aspects and in the interior. Blackberry was widely distributed on the northern aspect and into the interior in the shrub and ground layers. Total ground layer density was also significantly greater on the northern aspect ($P < .001$, Welch's approximation; Table 11).

Additional distributions of interest but not illustrated included sassafras, which was most abundant exterior of 45 m on on the southern aspect and cottonwood (*Populus deltoides* Marsh.), which was found only within the first 25 m of forest on the northern aspect and had highest abundance near the edge. Staghorn-sumac (*Rhus typhina* L.) and willow (*Salix* sp.) were confined to position 0-5 m north. Prickly ash was confined to the first 10 m of forest on the southern aspect and the first 25 m on the northern aspect, while hazel-nut (*Corlylus americana* Walt.) was distributed throughout the northern aspect and in the interior.

Several species, which in Sites 1-3 had distributions limited to more extreme edge positions, had much wider distributions in this site. They included: gooseberry, which was distributed to 50 m on the northern aspect and 5 m on the southern aspect; hornbeam, which was found throughout the southern aspect and in the interior in the subcanopy strata; serviceberry, which was widely distributed throughout both aspects and in the interior in the sapling and shrub strata, and had highest abundance interior of 25 m; wild crab apple, which was distributed to 45 m on the northern aspect and 15 m on the southern aspect; and ironwood, which was found within the first 40 m of forest in the shrub layer on the southern aspect. As in the previous oak site, sugar maple was found in all subcanopy strata. Its distribution was confined to positions interior of 15 m on the northern aspect, and in the interior position. Abundance was greatest in the 45-50 m position on the northern aspect, and in the interior.

The Compositional Gradient

Species Richness

The total number of species by position for Site 1 is illustrated in Figure 34. Species richness was highest at position 0-5 m south. Further, the southern aspect as a whole had both a higher absolute number of species and a higher mean species richness per position (Table 12). In Site 2, species richness was highest at or near the edge on both aspects (Figure 34). Both the absolute number of species and the mean number per position were nearly equal on the two aspects (Table 12). In Site 3, species richness was highest near the edge (Figure 35), with little difference between aspects in absolute or mean species richness (Table 12). Site 4 species richness peaked at 23 about mid-way into the forest on the northern aspect (Figure 35). Higher absolute species richness, and mean richness per position, were also found on this aspect (Table 12).

The contribution to species richness is separated into canopy and non-canopy components in Figures 34 and 35 and Table 12. Non-canopy species are defined as those species that do not typically enter the

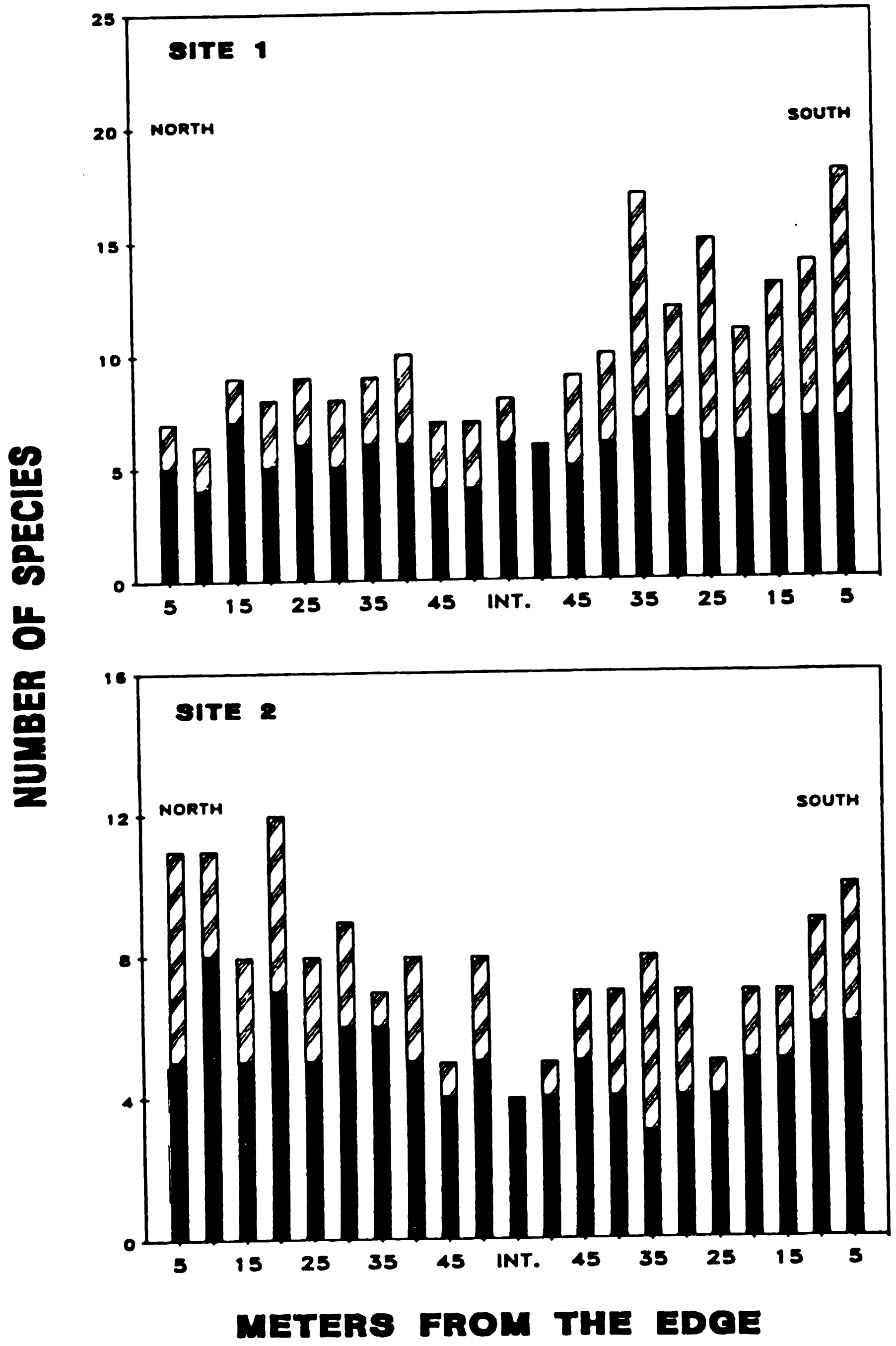


Figure 34. Species richness profiles from the edge to 50 m on the northern and southern aspects in beech-sugar maple fragments. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. Species richness is separated into canopy species ■ and non-canopy species ▨ .

Table 12. Species richness, separated into canopy and non-canopy components, on the northern and southern aspects (edge to 50 m) in Sites 1-4.

		Absolute number of species			Mean number of species per position[a]		
		Species			Species		
Site	Aspect	Canopy	Non-canopy	Sum	Canopy	Non-canopy	Sum
1	North	9	8	17	5.2	2.8	8.0
	South	9	19	28	6.4	6.1	12.5
2	North	9	8	17	5.6	3.1	8.7
	South	8	8	16	4.6	2.6	7.2
3	North	10	20	30	6.3	8.1	14.4
	South	9	23	32	5.2	9.0	14.9
4	North	10	24	34	6.7	11.5	18.2
	South	10	18	28	5.7	8.4	14.1

[a] The mean of 10 positions (5 m distance intervals from the edge to 50 m) on an aspect.

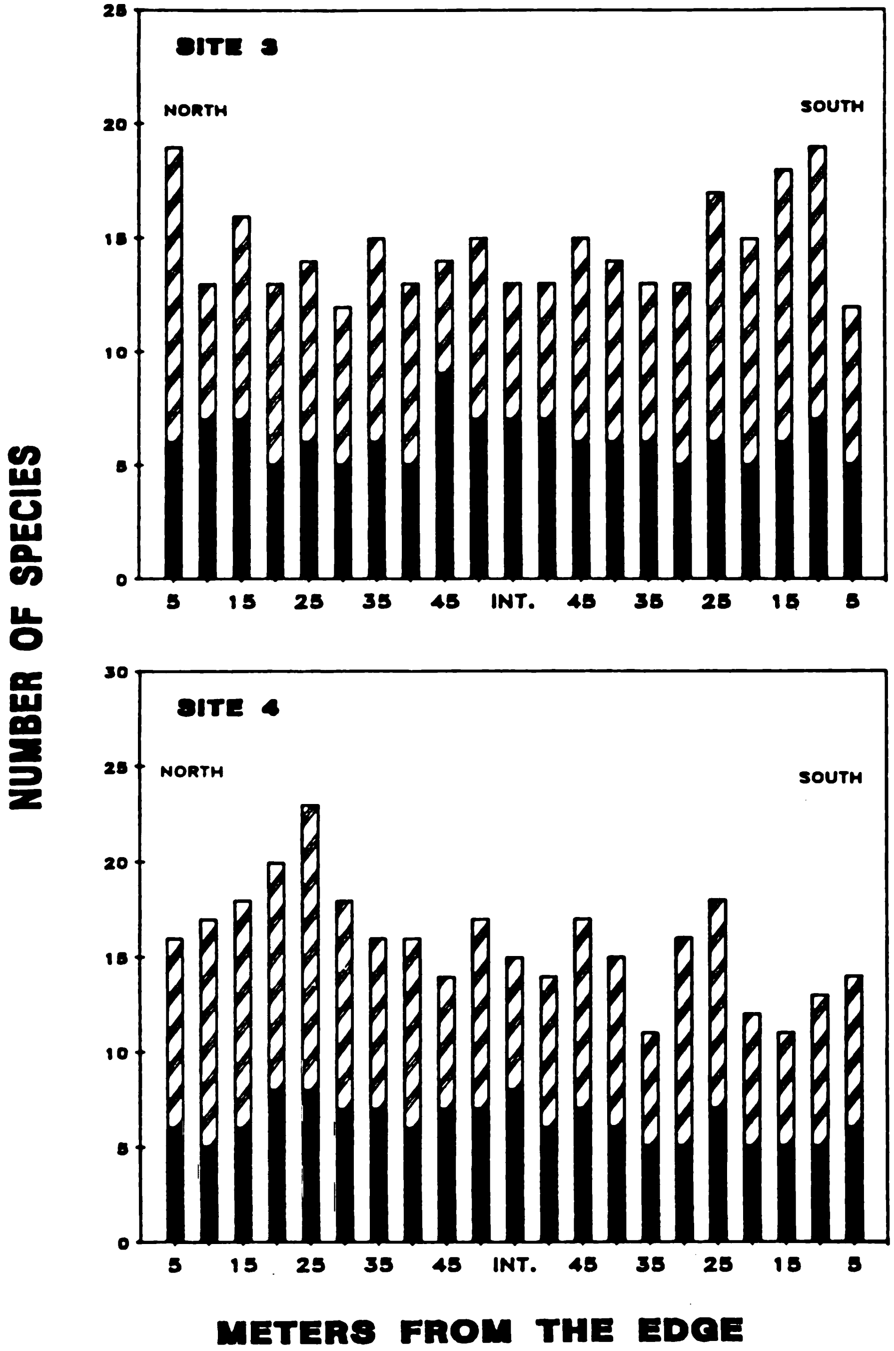


Figure 35. Species richness profiles from the edge to 50 m on the northern and southern aspects of oak fragments. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. Species richness is separated into canopy species ■ and non-canopy species ▨ .

canopy in forests of the study area (see Tables 6-9). In general the richness trends described above resulted from changes in the number of non-canopy species (Figures 34 & 35), whereas the number of canopy species tended to remain fairly constant. This trend is reflected in the lower standard deviations of the canopy component, relative to the non-canopy component, in all sites (Table 13). An exception is found in Site 2, in which richness patterns were similar for canopy and non-canopy species components. For all sites there were no great differences between aspects in the absolute number of canopy species, nor the mean number of canopy species per position. The difference between aspects, particularly evident in Sites 1 and 4, was a consequence of changes in the non-canopy species component, similar to the trend for positions.

Importance Percentages

An examination of the percent contribution by potential canopy dominant species to total importance, by position and stratum, was made in each site. Potential canopy dominant species were limited to those species that were most important in the canopy at the time of this study, or in the case of the oak sites, had the potential to increase in importance in the future given a minimal amount of disturbance. In Sites 1 and 2 potential canopy dominant species included sugar maple and beech. Potential canopy dominant species in Site 3 included black and white oak, and in Site 4, red and white oak. Additionally, red and sugar maple and American beech were included as potential canopy dominant species in Sites 3 and 4. The inclusion of

Table 13. Mean species richness in Sites 1 through 4 separated into canopy and non-canopy species.

Site	Canopy species	Non-canopy species
1	5.8 (1.0)	4.3 (2.8)
2	5.1 (1.2)	2.7 (1.5)
3	6.1 (1.0)	8.4 (2.2)
4	6.3 (1.1)	9.5 (2.3)

Values are means +/- (sd); n=21 (10 values each on the northern and southern aspects and one in the interior).

the latter three species in the oak forests was based on a substantial literature documenting an increase in importance of these species in more mesic oak sites with the suppression of fire (Ward 1956; Dix 1957; Monk 1961a, 1961b; McClain & Ebinger 1968; Lafer & Wistendahl 1970; Buell et al. 1966; Schmelz et al. 1975; Miceli et al. 1977; Nigh et al. 1985, 1986; Sherwood & Parker 1986 (for sugar maple and beech); Dodge 1987 for sugar maple, beech and red maple; Lorimer 1984 for red maple).

Pignut and shagbark hickory were not included as potential canopy dominant species in the analysis. Dodge (1987) proposed that these species may be increasing in importance in the oak forest of the study area, also because of fire suppression. However, their contribution to total importance in oak forests of the region has never been substantial, even in less fire prone sites (Braun 1950), and they are still of minor importance today (Dodge 1984, 1987), indicating that their potential to dominate the canopy is minimal.

In Site 1 importance percentages of beech and sugar maple in all strata increased from the edge-to-interior on the southern aspect. The trend was particularly pronounced in the subcanopy strata (Figure 36). On the northern aspect very high importance was generally maintained from the interior to just short of the edge. Although present, trends in Site 2 were not as pronounced as in Site 1 (Figure 37). Importance percentage of beech and sugar maple were generally lowest at or near the edge, increasing into the interior. The trend was most evident in the canopy and sapling strata. In the canopy of Site 3, importance of potential canopy dominant species on the northern aspect showed a moderate increase

Figure 36. Importance percentage of potential canopy dominant species from the edge to 50 m on the northern and southern aspects in Site 1. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. Potential canopy dominant species include American beech and sugar maple. Each percentage is of a total importance value (IV) of 300 in the canopy and sapling layers, or 200 in the shrub and ground layers. Total IV is the sum of individual species IV's (relative density + relative frequency + relative basal area in the canopy and sapling layers; relative density + relative frequency in the shrub and ground layers) in each interval.

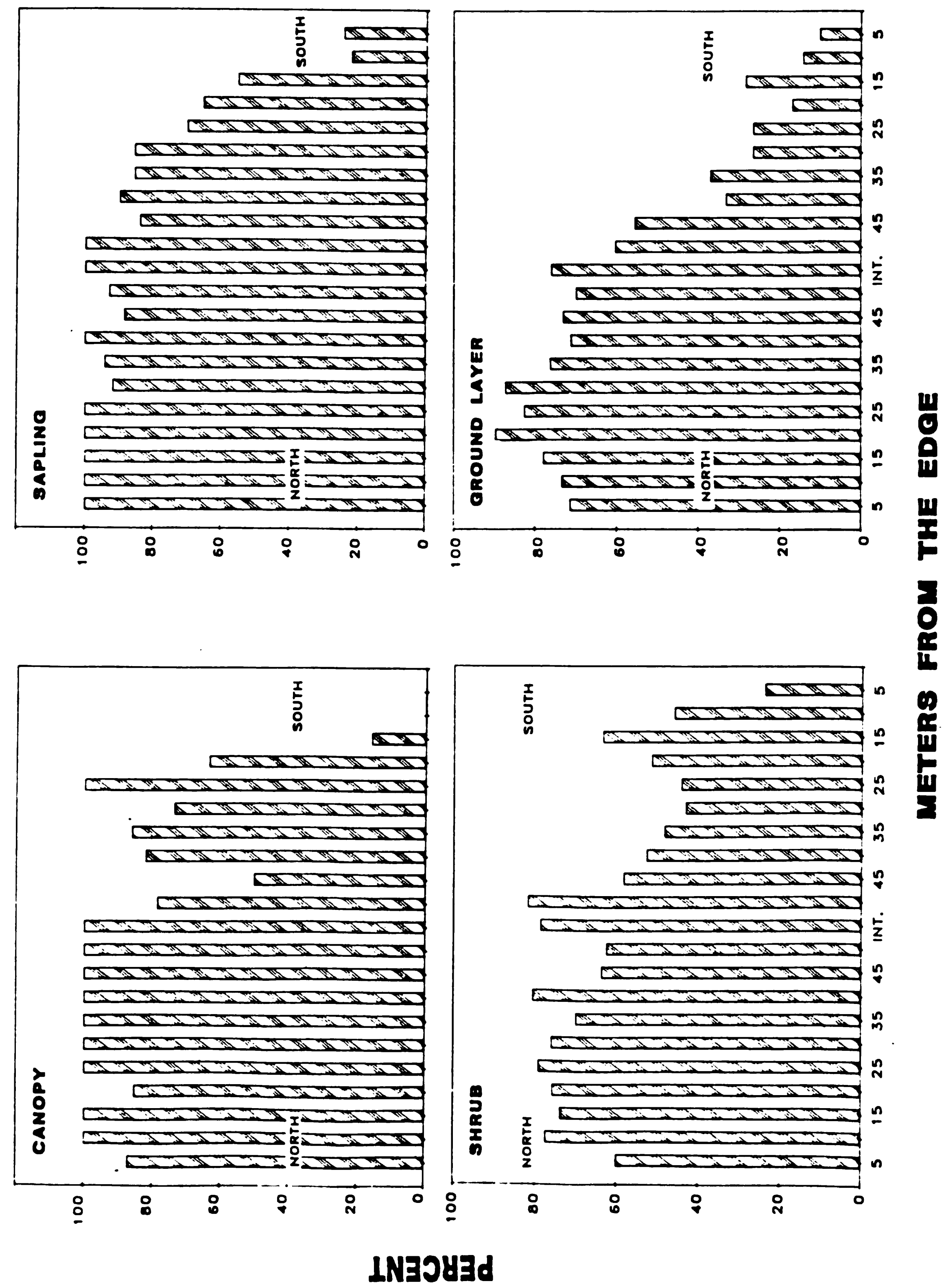
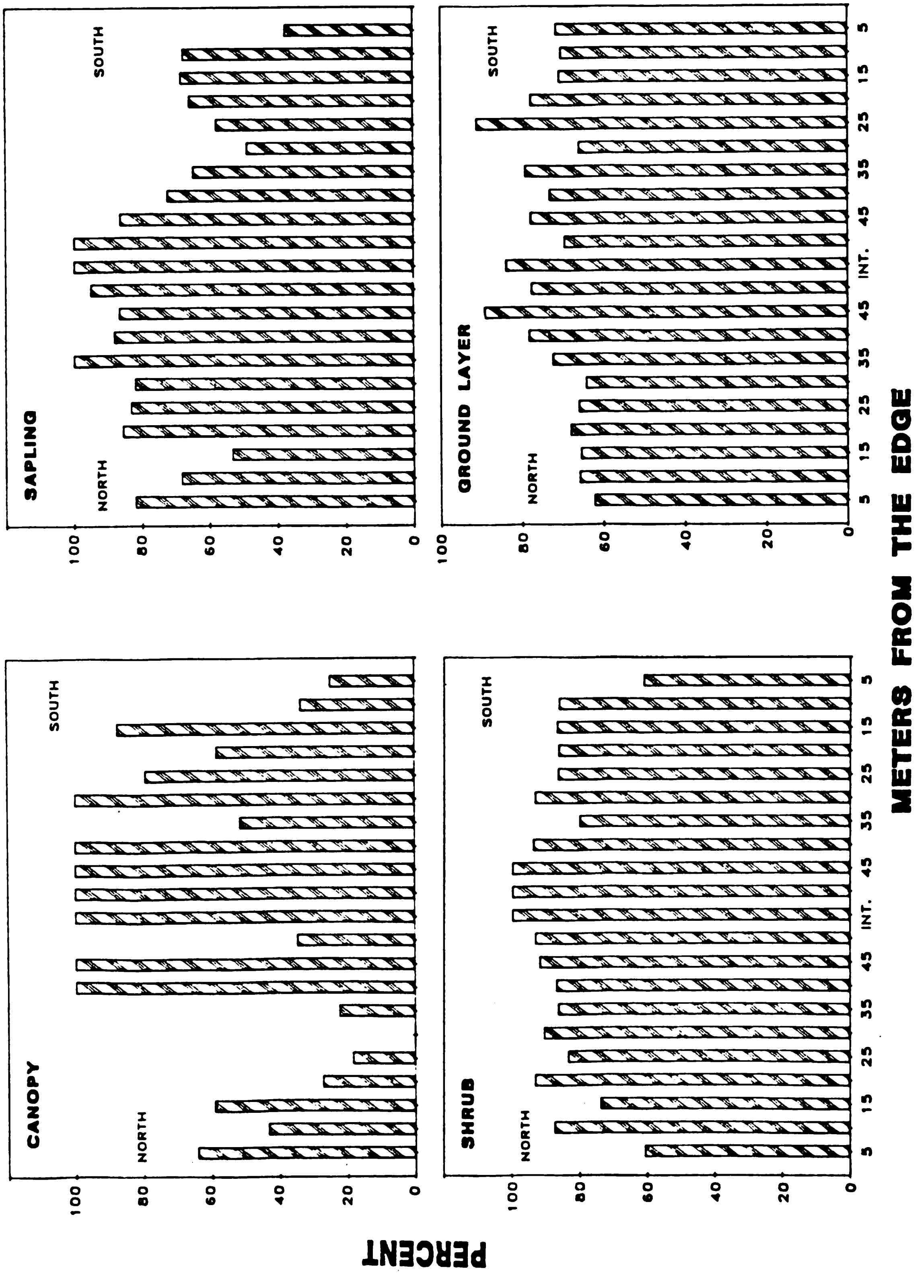

CANOPY
SAPLING
SHRUB
GROUND LAYER
NORTH
SOUTH
PERCENT
METERS FROM THE EDGE
0
20
40
60
80
100
5
15
25
35
45
INT.

Figure 37. Importance percentage of potential canopy dominant species from the edge to 50 m on the northern and southern aspects in Site 2. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. Potential canopy dominant species include American beech and sugar maple. Each percentage is of a total importance value (IV) of 300 in the canopy and sapling layers, or 200 in the shrub and ground layers. Total IV is the sum of individual species IV's (relative density + relative frequency + relative basal area in the canopy and sapling layers; relative density + relative frequency in the shrub and ground layers) in each interval.


CANOPY
SAPLING
SHRUB
GROUND LAYER
NORTH
SOUTH
0
20
40
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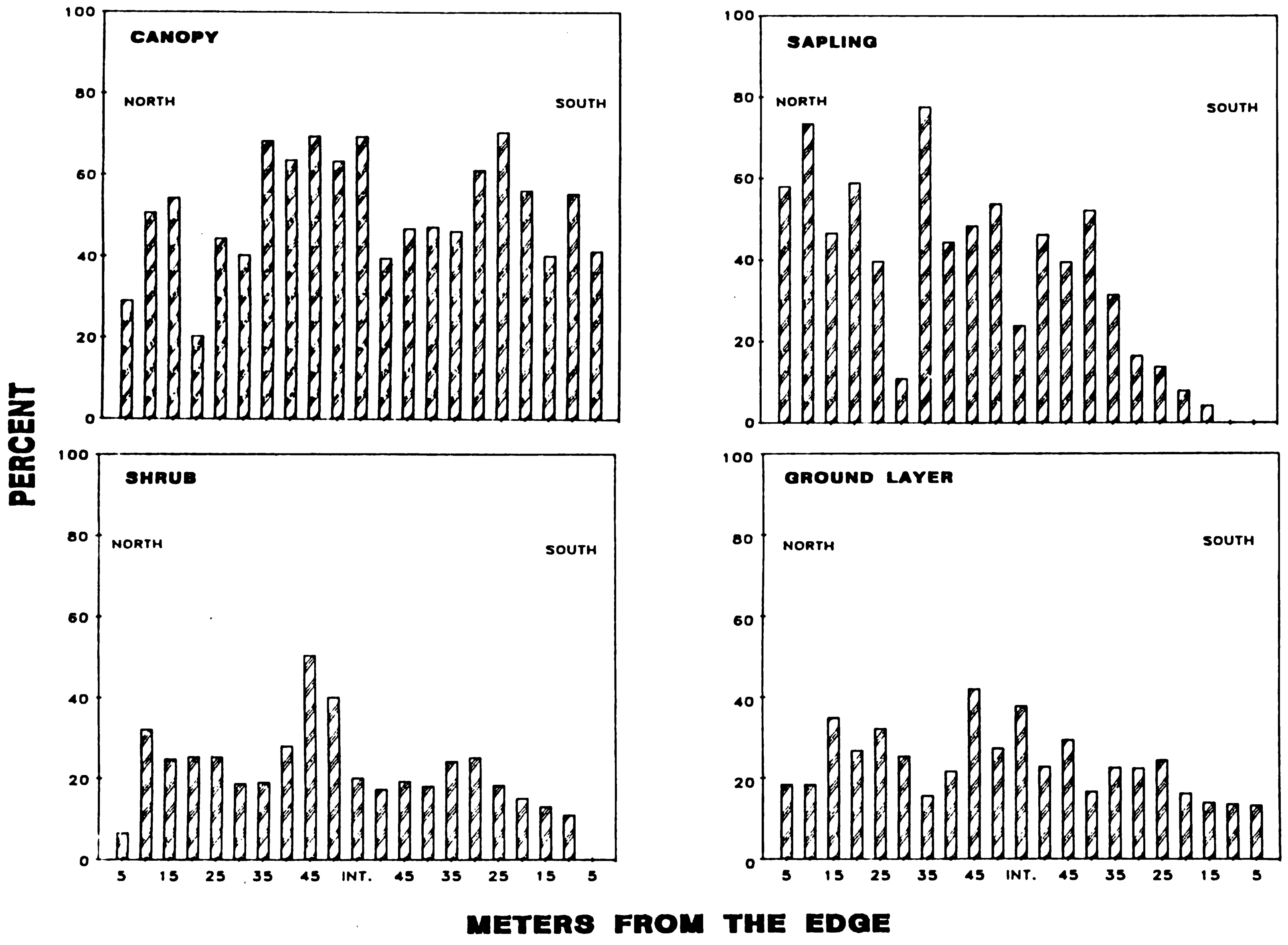
5
15
25
35
45
INT.
45
35
25
15
5
METERS FROM THE EDGE
PERCENT

from edge to interior, while percentages in most of the southern aspect positions were generally lower than northern interior positions (Figure 38). In the subcanopy strata a gradient of increasing importance percentages of potential canopy dominant species from the southern edge position to the northern aspect was evident, particularly in the sapling stratum (Figure 38). Importance percentages in Site 4 were quite variable throughout the forest in the canopy stratum. Percentages were lowest in the exterior portion of the northern aspect, and the interior portion of the southern aspect (Figure 39). In all subcanopy strata, importance percentage of potential canopy dominant species was highest in the interior position, although the increase over other positions was minimal (Figures 39). Contribution by this ecological group to total importance in both oak sites was quite low in the subcanopy strata, relative to the beech-sugar maple sites, throughout the sampled forest. The difference was most evident in Site 4.

Figure 38. Importance percentage of potential canopy dominant species from the edge to 50 m on the northern and southern aspects in Site 3. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. Potential canopy dominant species include: black oak; white oak; red maple; sugar maple; and American beech. Each percentage is of a total importance value (IV) of 300 in the canopy and sapling layers, or 200 in the shrub and ground layers. Total IV is the sum of individual species IV's (relative density + relative frequency + relative basal area in the canopy and sapling layers; relative density + relative frequency in the shrub and ground layers) in each interval.


PERCENT
CANOPY
SAPLING
SHRUB
GROUND LAYER
NORTH
SOUTH
100
80
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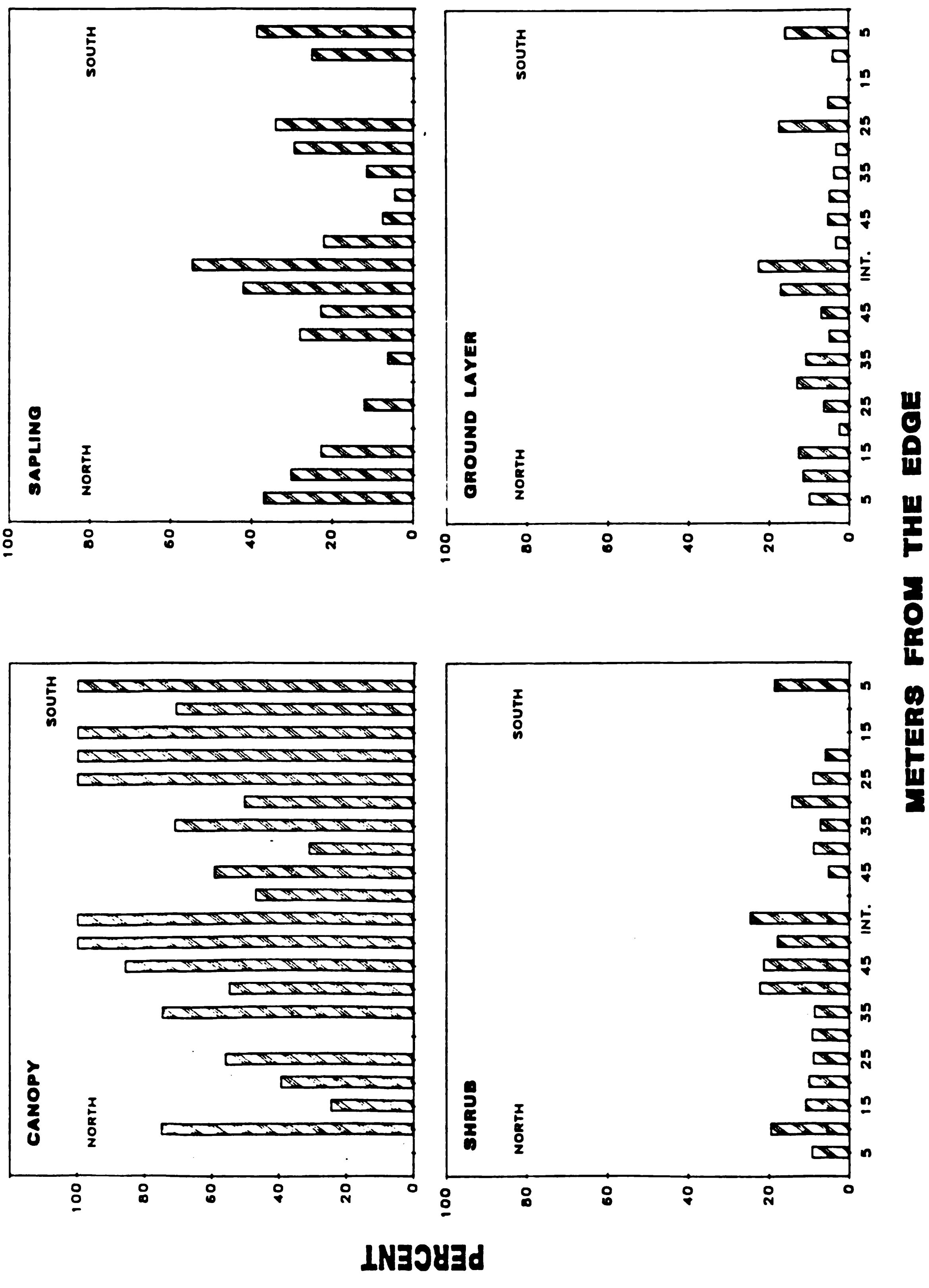
5
15
25
35
45
INT.
45
35
25
15
5
METERS FROM THE EDGE

Figure 39. Importance percentage of potential canopy dominant species from the edge to 50 m on the northern and southern aspects in Site 4. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. Potential canopy dominant species include: white oak; red oak; red maple; sugar maple; and American beech. Each percentage is of a total importance value (IV) of 300 in the canopy and sapling layers, or 200 in the shrub and ground layers. Total IV is the sum of individual species IV's (relative density + relative frequency + relative basal area in the canopy and sapling layers; relative density + relative frequency in the shrub and ground layers) in each interval.


CANOPY
SAPLING
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0
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DISCUSSION

The Effects of Edge and Aspect

An examination of the data for each site reveals differences between edge and interior forest for many of the attributes measured. Often an edge-to-interior gradient of change in the value of an attribute was evident. Differences between aspects for many measured attributes were also evident.

The edge-to-interior trends were not always without variability. Further, the existence of edge and/or aspect effects were not supported by all data sets. A hypothesized edge-to-interior gradient of forest structure and composition can be idealized as a continuous increase or decrease in some parameter of interest, e.g. decreasing stem densities from edge-to-interior. Such a idealized situation assumes: 1) a decrease in the influence of the edge microclimate as interior positions are reached; and 2) the influence of other factors acting on the composition and structure of the gradient is minimal.

Realization of the latter assumption is unlikely. Many temperate forests are dependent upon small scale disturbance, in the form of treefalls, to promote regeneration of dominant species and maintain populations of less tolerant species that may establish in larger treefall gaps (Forcier 1975; Runkle 1981, 1982; Donnelly 1986). Additionally, "internal edges" such as south slopes or saturated soils may increase light availability and serve to maintain less tolerant "edge" species in the forest interior (Donnelly 1986).

Anthropogenic disturbance may also influence forest structure. Selective tree removal may function similar to treefalls, freeing large amounts of resources which can be utilized by pioneer species. Grazing alters forest structure by promoting the development of an even aged regenerative layer after it is discontinued, and by allowing the establishment of resistant, opportunistic species (Auclair & Cottam 1971).

When examining an edge-interior forest gradient, the variability within it, induced by internal edges, may mask any edge-interior forest differences, or introduce variability that may obscure potential gradient structure. For example, consider Figure 40, a profile of black cherry ground layer density in Site 1. The figure implies a positive response of black cherry seedlings to northern interior positions. However, a physical reexamination of this area of the site showed that one sample transect bisected a recovering gap, formed by a black cherry individual, that contained a very high density of black cherry seedlings. It is unlikely that in small fragments, recovering gaps or other internal edges can be avoided and still adhere to the constraints of random sampling. It is therefore necessary to either: 1) treat such instances when recognized as outliers, as was done in the the case of the example by adjusting black cherry seedling densities in the affected portion of the transect to levels consistent with the analogous portions on the other transects; or 2) examine how the interaction of internal edges with lateral edge effect may influence the spatial extent of edge forest.

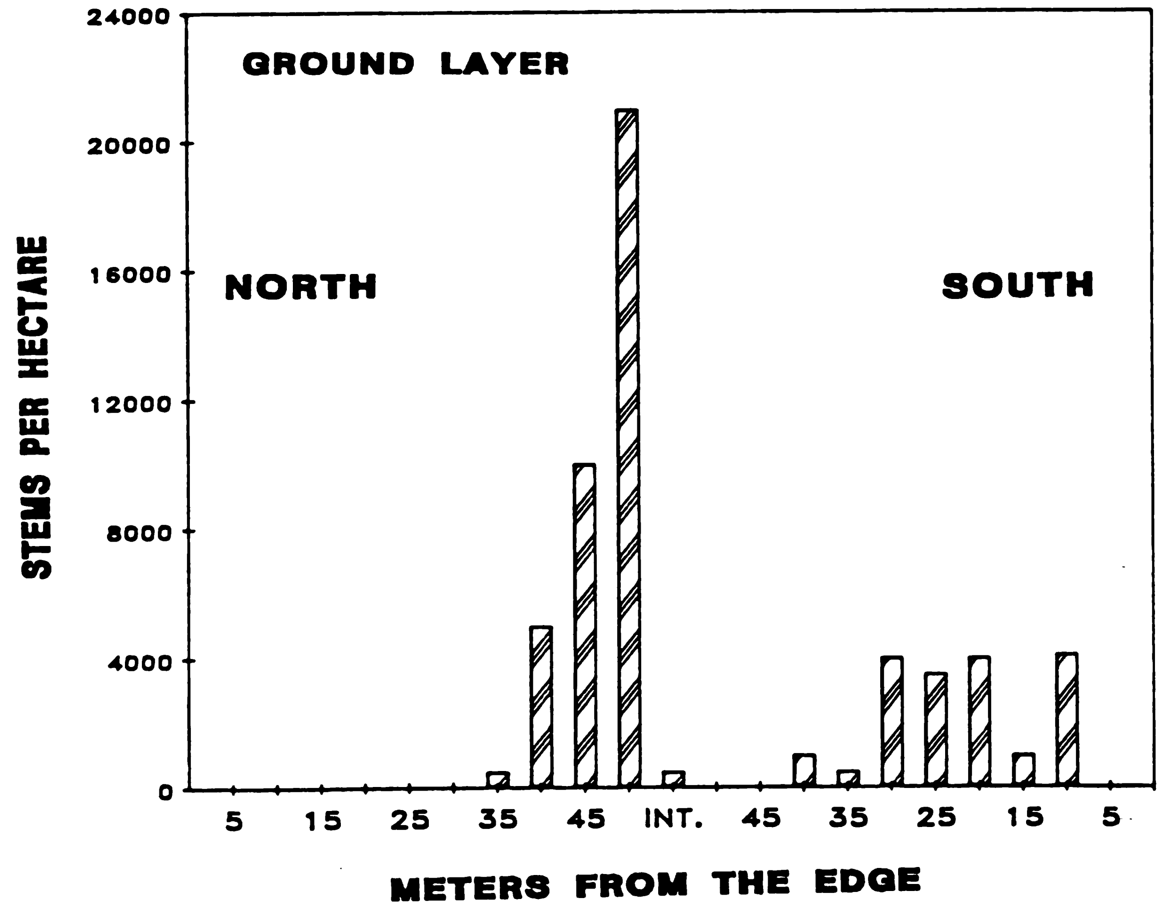


Figure 40. Black cherry ground layer density profile from the edge to 50 m on the northern and southern aspects in Site 1. The x-axis values are the upper limits of 5 m distance intervals. The interior (INT.) is 50 m from all edges. The y-axis values are means; n=5.

The second alternative may be most appropriate in small fragments, in which no area is far removed from edge forest.

Soil Moisture and Light

Some cautionary remarks concerning soil moisture measurements are necessary. Soil moisture content and availability are not always synonymous. Textural differences between soil samples with similar moisture content may translate into differences in the amount of moisture available for plant use (Oosting & Kramer 1946). In this study no major differences in soil texture were apparent, except for samples collected exterior of the forest boundaries. These samples appeared sandier than those of the interior. This may reflect a decrease in organic matter input at the forest border, or an actual increase in the percentage of sand in the soil. The significantly lower moisture content of soil from these exterior positions may be caused by compositional differences as much as, or more than, the drying influence of the microclimate. The assessment of relatively uniform textural composition of interior samples was qualitative only, and therefore any discussion of soil moisture differences should be viewed with caution, keeping in mind possible differences in moisture availability.

The soil moisture and light profiles illustrated the influence of edge and aspect on these two microclimatic variables. The surface soil was dryer during July and there was more diffuse light penetrating into the forest nearer the edge than in the interior. Drier, lighter conditions extended farther into the forest from the edge on the southern aspect than on the northern aspect. There were no consistent position trends in soil moisture for April and September but the significantly lower moisture on the southern aspect for both dates exemplified the influence of exposure on microclimate.

The significant soil moisture differences along the gradient strengthen the findings of Oosting & Kramer (1946), who found an increase in soil moisture, although not statistically significant, from the edge-to-interior on the northern aspect of their site. The significant decrease in diffuse light availability, from 0.8 and 8 percent of full sunlight at the northern and southern edges respectively, to 0.2 percent by 50 m into the forest on both aspects, was contrary to the results of Wales (1969) who found no differences in diffuse light from edge-to-interior using a similar procedure.

Differences in light should have a greater influence on subcanopy vegetation, relative to canopy individuals, since these strata do not normally receive lateral exposure. Additionally, the canopy in Site 2 may have been of insufficient age to have been affected by current edge conditions when many of the individuals established. Differences in surface soil moisture should also affect subcanopy vegetation to a greater degree, since a larger percentage of the rooting zone of the understory strata is likely to to be found within the soil depth sampled (Oosting & Kramer 1946).

There is some evidence to support the above contention in that importance percentages of canopy dominant species by position were positively correlated with soil moisture and negatively correlated with light, consistently on both aspects, in the shrub and sapling strata only (Table 14). This suggests that increased light and/or decreased soil moisture may favor less tolerant species. There were

Table 14. Correlations between importance percentage of potential canopy dominant species and A) July soil moisture, B) light along the edge to interior gradients (0-50 m) on the northern and southern aspects in Site 2.

	A) Soil Moisture		B) Light	
	Aspect		Aspect	
	North	South	North	South
Canopy	-.644**	.771***	.180	-.801
Sapling	.634**	.269	-.269	-.584*
Shrub	.679**	.589*	-.841***	-.809***
Ground layer	.054	-.132	-.534	-.235

* P <.10, ** P <.05, *** P <.01 indicates a significant Pearson product-moment correlation.

significant correlations in other strata but not consistently for both variables on both aspects. There were no significant correlations between soil moisture and light and any component of species richness.

It is reasonable to attribute higher light levels nearer the edge to lateral light penetration alone, given the significant regressions of light on distance from the edge. Alternatively, more light may have been available if foliar cover near the edge was less than in the interior. Cover was not measured but stem densities in the canopy, sapling, and shrub layers were positively correlated with light levels on both aspects (Table 15), which may mean there was increased foliar cover at the edge. Thus, supporting the existence of lateral light penetration effects.

An explanation for the soil moisture pattern is more complicated. Certainly it is reasonable to assume that if more light is available temperature may be increased and surface soil may dry out to a greater degree, and in fact July soil moisture and light were negatively correlated on both aspects (Table 15). However, higher stem densities, particularly in the shrub and ground layer where a high percentage of roots may be concentrated in the surface soil, may deplete soil moisture reserves to a greater degree than in the interior forest. Significant negative correlations between shrub densities and soil moisture on both aspects existed (Table 16). The high stem densities in turn may be in response to increased light levels.

In general, the microclimatic parameters measured and the current vegetative structure of Site 2 were not as well synchronized as might be predicted if a lateral gradient in microclimate has indeed been the

Table 15. Correlations between light and A) canopy, sapling, and shrub densities, B) July soil moisture along the edge to interior gradients (0 to 50 m) on the northern and southern aspects in Site 2.

		Aspect	
		North	South
A)	Canopy	.672**	.694**
	Sapling	-.012	.648**
	Shrub	.825***	.634**
B)		-.594*	-.696**

* P <.10, ** P <.05, *** P <.01 indicates a significant Pearson product-moment correlation.

Table 16. Correlations between July soil moisture and stem densities along the edge to interior gradients (0-50m) on the northern and southern aspects in Site 2.

	Aspect	
Stratum	North	South
Canopy	-.564*	-.498
Sapling	.247	-.112
Shrub	-.844***	-.736**
Ground layer	.613*	.294

* P <.10, ** P <.05, *** P <.01 indicates a significant Pearson product-moment correlation.

major factor controlling the development of the vegetation along the edge-to-interior gradient. However, given the history of grazing in the site this may not be surprising since subcanopy vegetation would have been suppressed for some time after grazing was discontinued. The correlation of microclimate with density and importance percentage of canopy dominant species in the shrub layer may reflect a greater influence of edge microclimate on a specific size class of vegetation. The lack of correlation in the ground layer may reflect a greater ability of early tree regeneration to tolerate a variety of microclimatic conditions, or it may reflect an independent response of this stratum to the physical environment, relative to the upper strata.

General Characteristics of Edge Forest

Although edge forest structure and composition can be quite site specific, as will be examined in a subsequent section, some generalizations can be made. Edge forest was characterized by higher stem densities in the canopy stratum. Basal area showed little or no position trend. A similar trend was found in the sapling stratum of the beech-sugar maple sites. Conversely, in the oak sites sapling density was lower in the edge forest. This may reflect specific differences between forest types, i.e., age of the edge, microclimate, canopy structure, etc.

Shrub layer stem density was higher in the edge forest, with the exception of Site 1, where there was no clear distinction between edge and interior forest. Finally, in the ground layer there were no strong differences in total stem density between edge and interior forest along the gradient. The lack of distinction between edge and interior forest in the ground layer may be an expression of the independent response of different vegetative layers to the physical environment. Rogers (1981), McCune and Antos (1981), and Dunn and Stearns (1988) have presented results that illustrate this type of independent response among strata in various forest types. Higher stem densities in the upper strata of the edge forest is consistent with the results of past studies (Gysel 1951; Wales 1972; Bruner 1977; Ranney et al. 1981). The lack of a consistent trend in basal area was in contrast to the results of Ranney et al. (1981) who found higher tree basal area in the edge forest.

Although time constraints prevented a quantitative examination of forest height along edge-to-interior gradients, personal observation suggested that edge forest stature was generally less than that of interior forest. This difference is expressed in the convex profile often evident in forest fragments. Smaller stature may be a reflection of the younger age of an edge that was allowed to advance from its original position into the surrounding matrix. Alternatively, or perhaps in addition to an age factor, the smaller stature of edge forest may be a result of the reduced height growth of edge trees, relative to those of the interior. Jacobs (1954) and Neel and Harris (1971) found that trees allowed to naturally sway in the wind, and those that were mechanically shaken, had reduced height growth and greater radial increment, relative to trees prevented from moving. The higher wind velocities incident on the forest edge may increase movement of edge trees, relative to those of the interior, resulting in smaller statured trees in the edge forest. This in turn may influence diffuse light penetration into the forest, since smaller statured trees, coupled with the low growing horizontal limbs characteristic of edge trees (Gysel 1951), may increase shade just interior to the edge, relative to this area in a newly established edge.

Species composition of edge forest will of course depend on forest type, age of a site, and its history (Whitney & Runkle 1981). Nevertheless, general trends encompassing all sites were evident. Edge forest was characterized by a greater contribution to total richness by species that do not typically reach the canopy in the light-limited interior forest. Additionally, edge forest contained a greater percentage of species common to disturbed habitats, and species that were not characteristic of the forest type of each particular site.

Table 17 summarizes this trend, showing that in general a higher percentage of species found between 0 and 10 m were species characteristic of disturbed or early successional habitats, relative to those between 40 and 50 m (Barnes and Wagner 1986; Voss 1985). The contrast was even more striking between edge forest and positions interior to 50 m (Table 17) but the interior species' totals were derived from 75% less sampling area than the 0-10 m and 40-50 m totals and should be interpreted with caution. The distinction was even more pronounced when in addition to disturbance species, non-characteristic species were included (Table 17).

Although species richness and composition were influenced by edge conditions, these attributes say nothing about the influence of

Table 17. The contribution (percent) to total species richness in three areas of each fragment by either 1) species indicative of disturbed habitats or 2) species characteristic of a non-disturbed habitat other than beech-sugar maple forest (in Sites 1 and 2) or oak forest (in Sites 3 and 4).

Site	Area	Disturbance Species	Percent	Non-characteristic Species	Percent	Sum
1	0-10 m[a]	*Prunus serotina* *P. virginiana* *Crataegus* sp. *Rosa multiflora* *Lonicera tatarica* *Zanthoxylum americanum* *Rubus allegheniensis*	33[c]	*Viburnum opulus* *Sambucus canadensis*	10	43
	40-50 m[a]	*Prunus serotina* *P. virginiana*	17	*Sambucus canadensis*	8	25
	Interior[b]	*Prunus serotina*	13		---	13
2	0-10 m	*Prunus serotina* *P. virginiana* *Rubus allegheniensis* *Cornus racemosa*	24	*Sambucus canadensis* *Fraxinus quadrangulata*	11	35
	40-50 m	*Prunus serotina* *P. virginiana* *Cornus racemosa*	33		---	33
	Interior		---		---	---

Table 17. (cont'd.)

3	0-10 m	*Rosa multiflora* *Cornus racemosa* *Prunus serotina* *P. virginiana* *Rubus allegheniensis* *Eleagnus umbellata* *Sassafras albidum* *Acer negundo* *Crataegus* sp. *Malus coronaria* *Lonicera tatarica* *Rosa* sp.	43	*Viburnum opulus* *Sambucus canadensis*	7	50
	40-50 m	*Prunus serotina* *P. virginana* *Rosa multiflora* *Rubus allegheniensis* *Crataegus* sp. *Rosa* sp.	27	*Viburnum opulus*	5	32
	Interior	*Rosa multiflora* *Prunus serotina* *P. virginiana* *Rubus allegheniensis*	31		---	31

Table 17. (cont'd.)

4	0-10 m	*Prunus serotina*	41	---	41
		P. virginiana			
		Cornus racemosa			
		Crataegus sp.			
		Rubus allegheniensis			
		Zanthoxylum americanum			
		Populus deltoides			
		Rhus typhina			
		Malus coronaria			
		Salix sp.			
		Rosa multiflora			
	40-50 m	*Prunus serotina*	33	---	33
		P. virginiana			
		Cornus racemosa			
		Malus coronaria			
		Crataegus sp.			
		Corylus americana			
		Rubus allegheniensis			
		Sassafras albidum			
	Interior	*Prunus serotina*	33	---	33
		P. virginiana			
		Crataegus sp.			
		Corylus americana			
		Rubus allegheniensis			

[a] Meters from the edge; both aspects combined.

[b] Fifty meters from all edges.

[c] Percent of the total number of species in that area of the fragment.

different species on forest structure. On the other hand, a synthetic species importance value is a weighted measure indicative of the influence of a particular species on forest structure. Consequently, the stratal profiles of importance percentages of potential canopy dominant species gives insight into the structure of the forest. The decreased importance of potential canopy dominant species at or near the edge is suggestive of an earlier successional status of the edge forest, relative to interior. A categorization of edge forest in the sites of this study as successional, relative to interior forest, supports the conclusions of Wales (1972), Ranney _et al_ (1981) and Whiney and Runkle (1981), who noted similarities between edge forest and earlier seral stages in the regions of their studies. In the context of this analysis an "edge species" can be defined as one that has greater importance in the edge forest than it typically does in the interior forest.

General Effects of Aspect

Examples of differences in community structure and composition induced by extremes in microclimate on a local scale include: different exposures on a mountain; exposed ridges and sheltered valleys; and slopes within a forest (Cantlon 1953; Niering 1953; Zager & Pippen 1977). As in the above examples, the northern and southern aspects of small temperate forest fragments may be subject to microclimatic extremes, caused by differences in intensity of solar radiation, wind velocities and amounts of precipitation (Wales 1967, 1972; Ranney 1978; Ranney _et al_. 1981). Intuitively, any distinctions in community composition and structure resulting from microclimatic differences would be most extreme on these aspects. The predicted result of this assumption is a greater influence of edge effects in southern aspect forest, since the edge microclimate presumably penetrates farther into the forest on this aspect.

The influence of aspect on total stem density was variable among sites. Often high densities at or near the edge extended 5 to 10 m farther into the forest on the southern aspect. Beyond this point responses were variable. This variability resulted in higher total densities on the southern aspect in some instances and on the northern aspect in others (Table 5). The variability in density trends by aspect between strata and forest type may be reflective of an independent response of structural layers and different species to environmental conditions. Alternatively, the differences may have resulted from site specific disturbance events or management practices.

Differences in species richness between aspects did not show any consistent trend among sites for either total number of species or for non-canopy species (Table 12). The only consistent trend in species richness was a similar number of canopy species on both aspects of all sites. Differences between aspects in the number of successional and disturbance oriented species was also variable among sites (Table 18). The number of non-characteristic species was low in all sites and did not vary much between aspects (Table 18).

The contribution to total importance by potential canopy dominant species did reflect an aspect distinction. In general, percent importance (mean of all positions on an aspect) contributed by canopy

Table 18. The number of species on the northern and southern aspects in each site that were either 1) species indicative of disturbed habitats, or 2) species characteristic of a non-disturbed habitat other than beech-sugar maple forest (for Sites 1 and 2) or oak forest (for Sites 3 and 4).

Site	Aspect	Disturbance Species	Non-characteristic Species
1	North	2	1
	South	7	1
2	North	3	2
	South	3	1
3	North	11	2
	South	11	2
4	North	13	1
	South	9	0

dominants was higher on the northern aspect in all strata (Table 19). Exceptions to this trend were found in the canopy of Sites 2-4 and the shrub and ground layers in Site 2. The exceptions in the canopy may be reflective of the original composition of the forest when size reduction to the present fragment size occurred.

One of the hypotheses of this research was that secondary forest fragments are too young for the canopy to demonstrate strong edge or aspect effects, and that trends would be most evident in the subcanopy strata. The exceptions noted in the canopies of Sites 2-4 lend support to this hypothesis. The lower importance of canopy dominants on the southern aspect in Site 1, an old-growth site in which adequate time for edge development has elapsed, further supports the hypothesis. The additional exceptions noted for Site 2 are most likely related to the management history of the site (see site comparisons below).

The compositional differences between aspects based on importance of potential canopy dominant species parallels the edge-to-interior trends noted previously. In the southern aspect forest, as in edge forest in general, less tolerant species contribute more to forest structure than do potential canopy dominants. The recognition of some aspect distinctions points out the loss of refinement in an analysis that is restricted to edge effects alone. For example, Whitney & Runkle (1981) demonstrated marked edge-interior forest differences on a western aspect; however, their findings would have been much more informative if differences between aspects were also addressed. The same criticism applies to Gysel (1951), who combined northern and southern aspects in his analysis.

Table 19. Importance percentages of potential canopy dominant species by stratum on the northern and southern aspects in Sites 1 through 4.

		Aspect	
Site	Stratum	North	South
1	Canopy	97.28 (1.82)	55.08 (11.81)
	Sapling	96.73 (1.41)	68.01 (8.53)
	Shrub	71.97 (2.34)	51.40 (4.77)
	Ground layer	77.34 (2.21)	30.88 (5.23)
2	Canopy	47.06 (10.66)	73.59 (9.24)
	Sapling	82.50 (4.17)	67.11 (5.54)
	Shrub	84.77 (3.23)	87.44 (3.55)
	Ground layer	71.15 (2.66)	74.98 (2.25)
3	Canopy	50.49 (5.31)	50.61 (3.21)
	Sapling	51.27 (5.91)	21.29 (6.22)
	Shrub	27.15 (3.81)	16.31 (2.29)
	Ground layer	26.35 (2.62)	19.53 (1.75)
4	Canopy	51.11 (10.97)	72.99 (8.19)
	Sapling	20.27 (4.74)	17.46 (4.56)
	Shrub	13.90 (1.80)	7.00 (1.98)
	Ground layer	9.69 (1.38)	6.33 (1.79)

Each value is a mean of the importance percentages in 10 positions (5 m distance intervals from the edge to 50 m) on an aspect +/- (se).

Potential canopy dominant species include: American beech, sugar maple, red maple, and red oak (Sites 1-4); black oak (Site 3); and white oak (Site 4).

Importance percentage is of 300 (total importance value) in the canopy and sapling layers or 200 in the shrub and ground layers. Total importance value is the sum of individual species importance values [relative density + relative frequency (shrub and ground layers) + relative basal area (canopy and sapling layers)] on an aspect.

Site Specific Distinctions

Beech-Sugar Maple Fragments

Site 1

This site best exemplified edge and aspect distinctions. In the upper strata stem densities were generally higher near the edge and on the southern aspect. The stark contrast between edge and interior sapling densities on both aspects was particularly demonstrative of the lateral penetration of edge effects. Highest species richness was found in the first 30 m of forest on the southern aspect and the increase in richness was due primarily to non-canopy species.

The low contribution to total importance by sugar maple and beech in the edge for all strata stresses the compositional distinction between edge and interior forest. Other striking examples of this difference were reflected in the distributions of slippery elm, red oak, and white ash, species which had greatest abundance in the southern edge positions. The lack of a strong species response on the northern aspect reflects the narrower breadth of edge forest in response to the more interior-like microclimatic conditions on the northern aspect.

The restriction of beech to more interior positions on both aspects in all strata suggests that for this species edge conditions may act to limit its distribution to more mesic interior forest, a result consistent with the findings of Gysel (1951) and Ranney et al. (1981). Beech has the ability to produce vigorous root sprouts (Curtis 1959; Ward 1956, 1961; Forcier 1975). Since the canopy distribution of beech in this site was restricted to interior positions, vegetative stems in the lower strata would be restricted to locations occupied by the root system of the canopy individuals. This suggests that the absence of beech in the understory of the exterior positions may be caused by a lack of parent roots. This is of course a circular argument; if there are no parent roots there can be no sprouts to produce parent trees. However, it seems unlikely that the current canopy distribution of the species is a result of stochastic events alone. Even if parent roots extended into the exterior positions the importance of vegetative sprouting may be minimal (Ward 1961). In a beech-sugar maple forest in southwestern Michigan Donnelly (1986) found that a very low percentage of beech stems were of sprout origin. Seedling regeneration was evident in the interior forest of Site 1, indicating that regeneration was not solely dependent on vegetative propagation. Given the old-growth status of the site, adequate time has elapsed for beech establishment by seed throughout the entire forest, yet this has failed to happen on the forest margins.

Although beech is a shade-tolerant species (Baker 1949) it is dependent on the liberation of resources by treefall gaps for recruitment into larger size classes (Forcier 1975; Donnelly 1986). If recruitment and increased growth in the gap is in response to increased light availability, one might suspect that conditions at the edge might be favorable for beech. However potential competition from very high densities of sugar maple stems on the northern aspect and the extreme edge conditions on the southern aspect, and/or competition from the less tolerant species on the southern aspect, may inhibit beech establishment in these areas.

Sugar maple, which is also dependent on light gaps for recruitment (Forcier 1975; Runkle 1981; Donnelly 1986), may be inhibited by the same conditions as beech on the southern aspect. Although present in the subcanopy strata, density was very low in the ground layer relative to the northern aspect. Individuals may fail to recruit into the canopy, perpetuating the exclusion of the species from this stratum on the southern edge. The high stem densities in the canopy and sapling strata on the northern edge suggest a response to the increased light availability. In general there was a strong trend of species sorting along the edge-to-interior gradient and/or aspect in this site, reflecting the development of extensive edge conditions as would be expected in an old-growth forest fragment.

Site 2

The general structural patterns in this site were similar to Site 1: highest canopy and sapling densities at the edge; highest total density in the shrub and ground layer on the southern and northern aspects respectively, with no trends along the edge to interior gradient evident.

However, exceptions reflective of the site's past history were evident. The increased canopy density characteristic of edge forest (Site 1 this study; Ranney et al. 1981; Bruner 1977) did not extend as far into the forest as in the previous site. This may be a consequence of past management practices which included selective tree removal from the edge forest, or it may reflect a lack of sufficient time, since reduction of fragment size, for the development of strong edge-interior differences. Although sapling density was highest at the edge, densities were generally very high throughout the sampled forest, with no significant difference between aspect positions and the interior, as in Site 1. Additionally, total sapling density in this site was significantly higher than Site 1 ($P < .001$, t-test). The high sapling densities likely resulted from the establishment of a cohort of seedlings and sprouts after grazing was discontinued. The compositional patterns in this site were also reflective of its past history. Total species richness was lower than in Site 1. In a forest that had been actively grazed, excluding all but the most resistant or unpalatable species, richness would be expected to be low for some time after release from grazing.

In general, species were not as strongly sorted along the edge-to-interior gradient. For example, basswood, slippery elm, red oak and black cherry, which showed strong edge responses in Site 1, did so only moderately in this site. This reflects the undeveloped nature of edge vegetational conditions.

As in Site 1, percent importance of sugar maple and beech were generally lower in the exterior positions in all strata, reflecting the decreased ability of the interior canopy dominant species to sustain themselves in edge forest, or under the previous management conditions of this site (i.e., grazing). However, beech was found closer to the edge on both aspects, and sugar maple on the southern aspect, than in Site 1. In the canopy this distribution may be remnant from a time when the site was larger, such that the current edges were once interior forest, while in the subcanopy strata it may reflect the lack of strong competition from edge species. Beech distribution in this site may suggest a more recent isolation, relative to Site 1.

Highest species richness was found in the extreme edge positions on both aspects, where extrafragment diaspore input would be most intense (Ranney 1978; Ranney _et al_ 1981; Levenson 1981). This, plus higher total species richness on the northern aspect and the higher importance percentage of potential canopy dominant species on the southern aspect in the subcanopy strata, suggest that post grazing species sorting by aspect has been minimal.

Oak Fragments

Site 3

Moderate structural trends delineating edge and aspect differences in the canopy and sapling strata were present in this site. These included high canopy densities near the northern edge and higher total sapling density on the southern aspect. Density profiles in the shrub layer best exemplified edge and aspect effects in this site. Densities were highest between 0 and 5 m on the northern aspect and 0 and 20 m on the southern aspect. This supports the hypothesis that subcanopy strata in secondary forests are more likely to reflect edge and aspect effects than is the canopy. A lack of position response in the ground layer was consistent with patterns in the previous sites.

The distribution of individual species indicated sorting in response to edge and aspect differences. Pignut hickory regeneration was confined to positions near the southern edge, even though canopy individuals were most abundant on the northern aspect. The optimal requirements for establishment of this species include mesic soil conditions (Fowells 1965). However, its subcanopy distribution in this site may suggest a requirement for a less light-limited condition than that of interior or northern aspect forest.

The distribution of red maple reflected differential response to edge and interior conditions. Highest abundance in the canopy, sapling and ground layers were found in the northern interior positions. On the southern aspect the distribution was restricted to the interior portion of the gradient. Subcanopy abundance in the interior was low relative to the northern aspect positions. This could be interpreted as a positive response by the species to extensive edge conditions on the northern aspect. However, the restricted distribution of the species on the southern aspect, and the successful recruitment into the canopy, as evidenced by moderately high interior abundance, suggest that the optimal distribution of the species is in interior forest. The increased importance of red maple in mesic oak forests, presumably in response to fire suppression, has been reported by several workers (Lorimer 1984; Dodge 1987). The distribution in this site suggests that the potential for this happening in the southern edge forest may be limited, a situation which in time may serve to strengthen edge-interior forest distinctions in the site.

The distributions of species such as black cherry, serviceberry, hawthorn, dogwood and blackberry in this site supported their designation as edge indicators (Gysel 1951; Wales 1972; Ranney <u>et</u> <u>al</u>.

1981; Whitney & Runkle 1981). The confinement of sugar maple to the northern aspect and the interior of this site may parallel the location of mesic microsites. Auclair and Cottam (1971) have said that these microsites may be required for successful establishment of sugar maple in oak forests.

Black oak was the dominant canopy species in this site but regeneration was minimal. This may be the result of an increase in oak wilt disease or possibly an increase in competition from additional species which establish after the suppression of fire (Auclair & Cottam 1971). In the southern edge forest of Site 3, competition may preclude the recruitment into larger size classes, but it may not preclude the initial establishment of oak regeneration, as suggested by the concentration of oak in the ground layer in this area. Initial establishment may be favored by a xeric microclimate or the increased availability of light on the southern edge. Such a situation may have some similarity to post-fire seedbeds with warmer, drier soil and more light incident on the forest floor, conditions often required for successful oak reproduction (Monk 1961; Nigh et al 1985).

Site 4

The high canopy density in the exterior positions of the forest was characteristic of edge conditions. However in the subcanopy strata there was a lack of strong trends along the edge-to-interior gradient. Additionally, total shrub density was higher on the northern aspect, in contrast to Sites 1-3. Total canopy density and basal area were significantly lower in this site than that of Site 3

(P <.01 and P <.05, t-test). Further, subcanopy densities were higher than in Site 3 (Table 20). The lower canopy density and basal area may have resulted in an increase in light availability to the lower strata, possibly explaining the high densities in the subcanopy strata (a situation analogous to lateral edge conditions). This may have been particularly true on the northern aspect, hence the high shrub density relative to the southern aspect.

Individual species distributions in the site reflected the deep penetration of edge conditions into the forest on both aspects. Red maple stem density in the subcanopy strata was generally low, relative to Site 3, and its distribtion was sporadic. This suggests that conditions favorable for red maple survival may be limited, similar to the situation in the edge forest of the previous site. The distribution in the canopy layer does not reflect any inhibition of the species by edge conditions as in the previous site. However, the present distribution may coincide with establishment at a time when the forest was larger, such that the present locations of canopy individuals were once in interior forest.

The widespread abundance of black cherry, with high subcanopy densities on both aspects, further illustrates the great extent of edge conditions in the forest. This species is rare in the canopy, but may be expected to increase in importance in the future given the current situation in the understory. The high position abundance and wide distribution of white ash, particularly in the subcanopy strata, not only serves to illustrate the extent of edge conditions in the forest, but also points to a potential shift in canopy dominance to this species. Other characteristic edge species found throughout the

Table 20. Density (stems per hectare) in subcanopy strata in Sites 3 and 4.

Stratum	Site 3	Site 4
Sapling	743 (55)	1400 (208)**
Shrub	5438 (795)	8037 (687)*
Ground layer	42752 (2390)	52024 (3162)*

Values are means +/- (se); n=21 (10 values on each aspect and 1 in the interior).
* P <.05, ** P <.01 indicates the mean is significantly greater than the corresponding stratum in site 3 (Welch's approximation).

site included blackberry, wild crab apple, slippery elm, red oak, gray dogwood and hawthorn (this study; Gysel 1951; Wales 1971; Ranney et al. 1981).

Although evidence for extensive edge effects on both aspects were evident, conditions on the northern aspect appeared to be of greater magnitude, possibly indicating disturbance beyond that caused by lateral edge effects alone. The open nature of the canopy in and around the bracken fern patch was indicative of a past disturbance such as fire or multiple tree blow down. Whatever the cause, the creation of an "internal edge" in such a small forest patch has contributed to serious degradation of original forest structure.

Although this is a small forest fragment with evidence of extensive edge conditions, it did contain a small population of sugar maple in the understory. However, its distribution may be indicative of limited availability of suitable sugar maple habitat in the forest. Seedlings were only found interior to 50 m on both aspects. In the shrub layer individuals were found between 15 and 50 m on the northern aspect and in the interior, but with highest abundance between 45 and 50 m and in the interior. Saplings were found only between 45 and 50 m on the northern aspect, and in the interior where abundance was highest.

There was one canopy individual of sugar maple in the north central interior area of the forest. The center of greatest abundance in the subcanopy strata was not far from what is most likely the parent tree; this was, therefore, an area of potentially high diaspore input. Samaras of other species in the genus have been found to be dispersed 50-100 m in a 10 km per hour wind (Matlack 1987).

Presumably, the potential dispersal distance for sugar maple is similar. This suggests that the potential for site-wide distribution exists.

In the context of this study, the area of concentrated sugar maple regeneration, the northern interior portion of the forest may be least affected by edge microclimate, relative to the remainder of the forest. The decreased influence of edge conditions may provide sugar maple with an advantage in this part of the forest. It is tempting to speculate on the potential of this population to drive the succession of this oak site to a sugar maple-dominated forest. However, the extensive edge conditions and small size (limited interior conditions) may prevent this from happening.

Depth of Edge

Some indication of the depth of edge penetration in each site was evident from the site-specific discussion. A more quantitative measure can be garnered by determining where along the edge to interior gradients the greatest number of transition events occurred. I have attempted to attach a degree of significance to as many of these events as possible. However, given the small sample sizes associated with many of the individual species, and the high amount of variability of many attributes examined, this was not always possible. Further, the presence of a species in a particular area of the forest and its total absence in all other areas precludes the assignment of an alpha value to the difference. Additionally, not all events may lead to the same conclusion. For example, profiles of total density in the canopy, sapling, and ground layers of a site may lead to one conclusion concerning edge depth, whereas the pattern in the shrub layer may lead to a very different conclusion. This was certainly true for some of the data in this study.

Rather than taking the exceptions to indicate negation of any edge effects it may be best to treat them as outliers. As discussed earlier, stochastic and deterministic processes will act on the forest at different times and in different fashions, such that an expectation of strict concordance between all data sets is not realistic. Rather, it is the trends that emerge from the data en masse that should be considered as most relevant to a correct interpretation. The four fragments examined in this study represented four very different conditions and histories. The depth of edge forest penetration was dependent on age and history of a particular site.

Site 1 (4.68 ha)

The number of transition events in all strata summed by position indicated that edge conditions penetrated at least 50 m into the forest on the southern aspect and 10 m on the northern aspect (Table 21). The extent of edge on the southern aspect was 20-30 m greater than has been reported in the literature to date by: Gysel 1951; Wales 1971; Bruner 1977; Ranney 1978; and Ranney et al. 1981, who examined similar forest attributes along edge-to-interior gradients of 30 m or less. The extensive penetration of edge conditions on the southern aspect in Site 1 might reflect the old-growth, undisturbed status of the site; a condition which may have provided sufficient time for

Table 21. The number of transitional events, summed over the canopy, sapling, shrub, and ground layers, along the edge to interior gradients on the northern and southern aspects in Sites 1 through 4.

	Meters From the Edge																				
	North																				South
Site	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	INT[a]	45-50	40-45	35-40	30-35	25-30	20-25	15-20	10-15	5-10	0-5
1	5[b]	7	3	1	1	0	0	0	0	0	4[c]	11	6	4	3	5	3	4	6	3	1
2	7	2	6	1	4	4	5	0	1	5	1	1	4	2	3	2	2	3	3	3	9
3	13	2	3	0	3	2	2	7	1	4	4	13	2	3	4	5	4	4	6	4	0
4	4	5	2	0	7	4	5	3	5	16[d]	22	16	6	1	2	2	3	3	2	4	5

[a] The interior (INT) is 50 m from all edges.

[b] A transitional event is defined as a change in: total density; an individual species distribution, density or abundance; species richness; importance percentage of potential canopy dominant species; or percent soil moisture or light, which indicates a change from edge to interior forest within that distance interval. The number of transitional events in distance 45-50 m were determined by comparing the value of a measured attribute to the value in the interior.

[c] The number of edge indicator events present within the interior including: high total stem density; high density or abundance of individual edge species; and low importance percentage of potential canopy dominant species.

[d] Transitional events in position 45-50 m were determined relative to values for measured attributes in the interior.

extensive edge development. Alternatively, it may simply reflect the greater extent of sampling along the edge-to-interior gradient in the current research, relative to previous studies. If the assumption is made that the extent of edge forest on the eastern and western aspects is intermediate to the two extremes (approximately 30 m) then the amount of potential edge forest in this site, assuming a fragment the size of the sampled upland portion, was 2.25 ha or 48.07% of the total area.

Site 2 (2.70 ha)

In this site the number of transition events indicate that edge conditions penetrated to about 5 m on both the northern aspect and the southern aspects (Table 21). The disturbance history of the site, and the young age of the edges, has prevented the development of much distinction between edge and interior forest, or between the two aspects in depth of edge. Assuming intermediatepenetration of edge conditions on the eastern and western aspects, approximately .32 ha or 11.85% of the site is edge forest.

Site 3 (3.60 ha)

In Site 3 edge conditions penetrated to 5 m on the northern aspect and approximately 50 m on the southern aspect (Table 21). A spatial estimate of edge forest in this site, assuming an intermediate edge extent on the eastern and western aspects of 22.5 m, is 1.66 ha or 46.04% of total area.

Site 4 (1.5 ha)

In this site edge conditions extended to at least 50 m on both aspects (Table 21). An assumption of 50 m edge penetration on all aspects suggests that the entire site is edge forest since linear dimensions were only 150 x 100 m. This conclusion is supported by the high number of edge species and the low importance of potential canopy dominant species in the interior. (Table 21).

Within and Between Site Comparisons

Two of the objectives of this research, investigated through between-site comparisons, were to ascertain what influence, if any, site history and forest composition had on the development of edge forest. An additional objective was to determine, through within-site comparisons, the effect of aspect on edge forest development. The results show that the extent of edge differed by aspect, but the magnitude of the difference and the aspect of greatest edge development were dependent upon site history. Site composition appeared to be less of a factor influencing edge characteristics.

The analogy between edge forest and recovering treefall gaps for certain structural features is not new (Gysel 1951; Wales 1972) but it has not been extended to include the similarity between southern and northern edge, and large and small gaps. The manner in which structure and composition differed between aspects of Site 1 illustrated this well. On the northern aspect there was high a density of sugar maple regeneration, with only a minimal contribution from more shade intolerant species. This shows some similarity to a small canopy gap which is filled primarily by recruitment of the dominant canopy species surrounding it. In the southern aspect edge forest, stem density was also high, but here the importance of less tolerant species was much greater. This is similar to a large canopy gap in which light demanding species are able to establish and successfully compete with the dominant canopy species of the interior forest (Runkle 1982). The development of these conditions was dependent on the relatively undisturbed nature of the site, which has allowed the vegetative differences resulting from microclimatic variation on the northern and southern aspects to be expressed.

In contrast, the current edge conditions in Site 2 are a result of past disturbance which resulted in minimized edge-interior distinctions in the tree and shrub communities. The current canopy species distributions suggest establishment in more interior conditions when the site was larger. The patterns in the understory are a result of grazing which would have suppressed all but the most unpalatable or resistant species. The establishment of vegetation subsequent to the release from grazing would be through the most readily available means, i.e. sexual reproduction and vegetative propagation of the resident canopy species. Not until adequate time had elapsed for dispersal of species from the local source pool into the site would the remnant vegetation face any competitive pressures from species better adapted to edge conditions. Additional consequences of grazing that may influence the development of edge-interior vegetational distinctions include soil compaction and root damage. Presumably this site is in the early stages of edge development as evidenced by low species richness, the minimal extent of edge conditions, and the current distribution of sugar maple and beech on the southern aspect, relative to Site 1.

In Site 3 the depth of edge conditions was similar to that of Site 1. However, canopy distinctions were not strong, which suggests that the time elapsed since the cessation of grazing (40-45 years) has been adequate to allow the development of recognizable edge conditions and aspect differences in the understory strata only.

Site 4 was perhaps the most interesting in terms of the development of edge conditions. The greater extent of edge forest on the northern aspect, relative to Sites 1-3, may be a consequence of the ready access of edge species propagules to the naturally occurring disturbance on the northern aspect in this site, essentially creating internal edge conditions that have coalesced to create an all-edge forest.

The characteristics that serve to distinguish edge forest from interior forest, i.e. higher stem densities, higher species richness, a greater number of non-canopy species, and increased importance of less tolerant species were important in both the beech-sugar maple and the oak sites. In addition to compositional differences inherent in the two forest types, there were also some differences in edge forest composition. For example, red and white oak served to distinguish edge conditions in the beech-sugar maple sites. The presence of these species in the canopy of the oak sites obviously could not be interpreted in a similar manner. However, the wide distribution of red oak in the ground layer of Site 4, which may have been in response to more xeric conditions, or a greater availability of light throughout the site, was used to illustrate the extent of edge in the site. An important edge indicator in both forest types was the restricted distribution of more shade tolerant species to more light-limited and/or mesic microsites in the forests. Many edge species were common to both forest types. For example, black cherry and choke-cherry, white ash, and slippery elm were characteristic edge species in all sites. The similarity of edge composition noted in forest types of this study parallels the similarity of edge composition in oak-hickory and maple-basswood forests studied by Wales (1972) and Ranney (1978) respectively.

Minimum Critical Fragment Size

Strict interpretation of the results of this study suggests that fragments below 1.5 ha in size will eventually become all-edge forest. This figure is consistent with that generated by a computer simulation of edge effects in forest fragments (Ranney 1978). Levenson (1981) suggested that for maple-basswood forests of southeastern Wisconsin fragments larger than 4 ha may be necessary to absorb random disturbance and still maintain their characteristic structure and function. Given the extent of edge reported in Sites 1 and 3 of this study I suggest that this may not be large enough.

Although edge species were found in all strata, their presence was particularly evident in the subcanopy strata. These species included less tolerant canopy trees that may senesce and die before ever reaching the canopy, and shrub species that will never be very abundant under a closed canopy. In a small forest fragment these edge species are never very far from any portion of the forest, including the interior. In a large, contiguous tract of forest, the effects of disturbances large enough to open up the canopy (e.g. multiple treefalls) and allow the establishment and success of edge species are dampened by the sheer expanse of closed canopy forest. However, in a small forest fragment such disturbance would occupy a greater percentage of total area. The accessibility of these "internal edges" to opportunistic species of the true edge may promote the coalescing of edge conditions throughout the fragment. On the basis of this hypothetical situation it may be desirable to identify two categories of critical fragment size; absolute and ecologically sound minimum critical size. The former describes a size large enough to potentially contain some interior forest, the latter, a size large enough to sustain interior forest in the face of random disturbance. Ecologically sound minimum critical size is obviously the more desirable attribute in a fragmented landscape. An examination of the frequency and distribution of disturbance in small forest fragments may prove useful for determining ecologically sound minimum critical size. Such information could be used to assess the stability of interior forest in Sites 1 (5.85 ha) and 3 (3.6 ha), both of which contained a large spatial extent of edge forest.

CONCLUSION

Summary

This study examined edge effects in the tree and shrub strata of four small forest fragments. The sites differed in disturbance history, size, and composition. In general, total stem densities in the canopy stratum were highest at or near the edge, decreasing into the interior. Sapling density followed a pattern similar to the canopy layer in the beech-sugar maple sites, while in the oak sites sapling density generally increased from the edge to the interior. In the shrub and ground layers densities differed more by aspect than distance from the edge. Abundance and distribution patterns of individual species may have been in response to microclimatic differences between edge and interior forest. Species richness decreased from the edge to the interior, primarily as a consequence of the reduction in the number of non-canopy species. The importance of less tolerant and disturbance oriented species was greater in edge forest, relative to interior forest. An "edge species" was defined as one that has greater importance in the edge than it typically does in the interior.

The depth of edge forest penetration varied with aspect, disturbance history, and size of a fragment. In Site 1, an old-growth, undisturbed beech-sugar maple fragment, edge conditions penetrated 10 and 50 m into the forest on the northern and southern aspects respectively. The depth of edge on the southern aspect was 30 m greater than previous literature reports for similar forests. This may reflect the greater linear extent of sampling from the edge that was done in the current study. Alternatively, it may be a consequence of the old-growth condition of the site, in which adequate time had elapsed for the development of strong edge-interior differences. In Site 2, a beech-sugar maple site released from grazing approximately 18 years prior to this study, the development of edge conditions was minimal on both aspects. This may reflect a lack of adequate time for edge species dispersal into the site and sorting along the edge-to-interior gradient or by aspect or both. A microclimatic gradient of decreasing diffuse light and increasing soil moisture from the edge-to-interior was present in this site; however, community attributes and the microclimatic gradient were not well correlated. The lack of strong coupling between microclimate and vegetation was attributed to the disturbance history of the site.

In Site 3, a second-growth oak fragment released from grazing approximately 40 years ago, edge depth was similar to Site 1. The greatest expression of edge conditions was in the sapling and shrub layers. The time elapsed since grazing was discontinued apparently has been adequate for the development of strong edge-to-interior distinctions in the understory, and presumably distinctions in the canopy will become stronger in the future.

An all-edge condition was present in Site 4, a very small (1.5 ha) oak fragment. This resulted from an interaction between size (which allowed edge species easy access to all areas of the forest, and limited the amount of interior forest present) and disturbance, which created a large area of "internal" edge on the northern aspect.

The general characteristics of edge forest, i.e. high stem densities, increased species richness, and increased importance of less tolerant and disturbance-oriented species, were represented in all sites regardless of forest type. Although there were compositional differences between edge and interior forest of beech-sugar maple and oak sites, many characteristic edge indicator species were shared by both forest types.

The results of this study have shown that size and disturbance interact to determine the amount of edge forest present in a particular fragment. The potential for extensive penetration of edge conditions into the forest as found in this study, coupled with the accessibility of disturbances in interior forest to edge species, suggest the need to differentiate between absolute and ecologically sound minimum critical fragment size when estimating long-term availability of interior forest in a fragmented landscape.

Future Work

Long term monitoring of the sites in this study would add to the understanding of forest edge dynamics. Questions to be addressed include: how stable is the well developed edge forest on the southern aspect of Site 1; will the development of the edge-to-interior gradient in Site 2 proceed as predicted; in what direction will forest development proceed given the all-edge conditions of Site 4? An examination of edge-interior differences in the herbaceous flora of these fragments may indicate different dimensions to edge forest than those which were derived by examining trees and shrubs. The monitoring of sugar maple populations in isolated oak fragments may help to assess the potential for successional development to sugar maple forests in a fragmented landscape. Finally, a detailed examination of the microclimatic gradient including potential evapotranspiration, relative humidity, wind velocity, and air and soil temperature in addition to soil moisture and light would help to solidify our understanding of the abiotic factors influencing the vegetational gradient.

APPENDICES

APPENDIX A

TOWNSHIP AND RANGE COORDINATES OF STUDY SITES

Site 1 (Toumey Forest):

NE 1/4, SE 1/4, Sec. 30, T.4N., R.1W.

Site 2 (Clever Woodland):

SW 1/8, NW 1/4, Sec. 31, T.4N., R.1W.

Site 3:

NE 1/8, SW 1/4, Sec. 23, T.5N., R.1W.

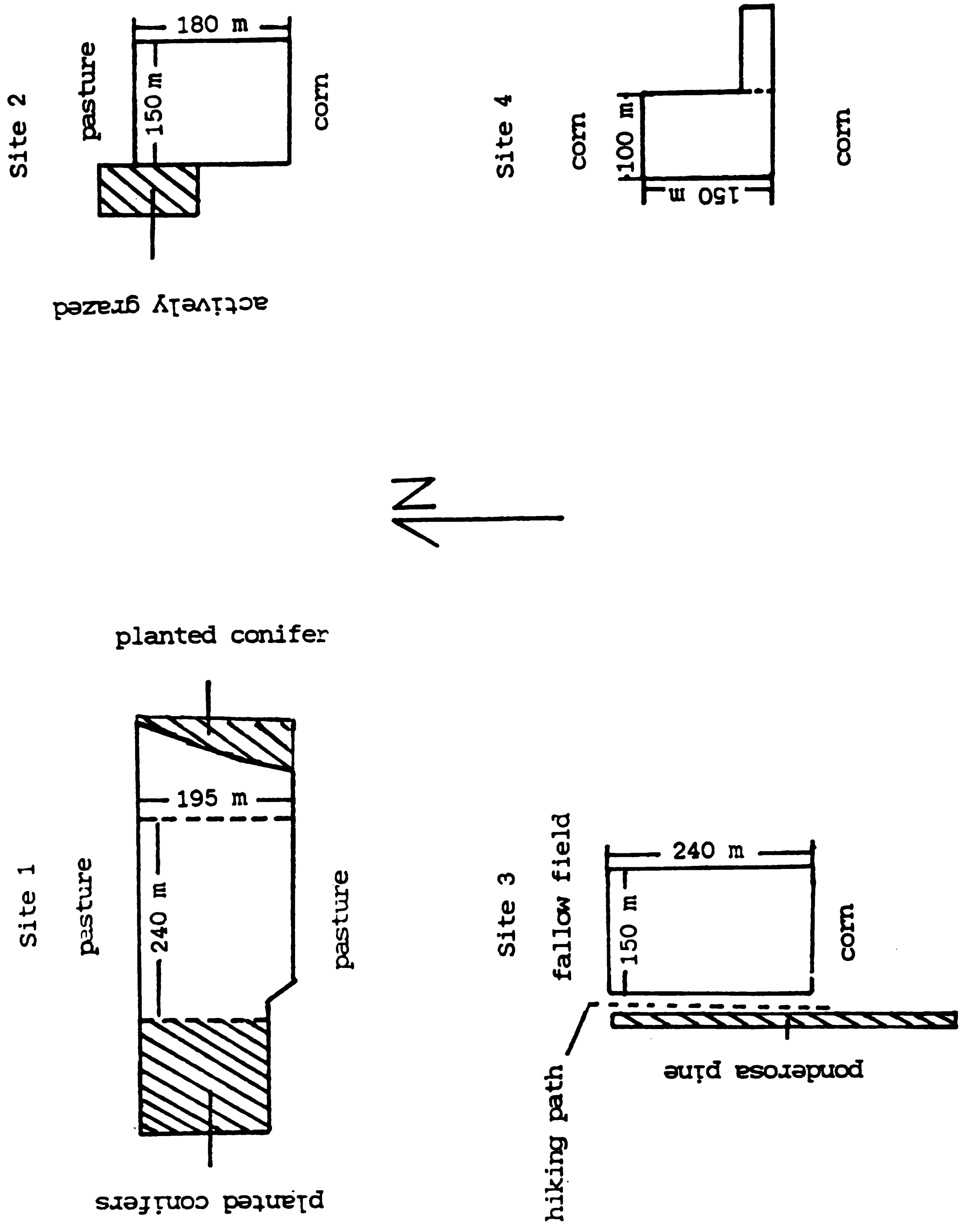
Site 4:

SW 1/8, SW 1/4, Sec. 19, T.4N., R.2E.

Figure 41. Site diagrams.

APPENDIX B

SITE DIAGRAMS



APPENDIX C

THE UTILITY OF DETRENDED CORRESPONDENCE ANALYSIS IN AN EXAMINATION OF EDGE AND ASPECT EFFECTS

Microclimatic differences resulting from the interaction of position (distance from the edge) and aspect influence forest structure at a particular point in a fragemnt. If the influence of other variables such as tree-fall gaps, or topographic and edaphic differences, can be minimized, point- distinctive vegetative structure may be ordered along an assumed edge-to-interior microclimatic gradient. The vegetative changes associated with this microclimatic gradient can be thought of as a community continuum in the sense of Curtis (1959), but on a microscale of variation.

Patterns of spatial variation in community structure can be examined objectively, without direct reference to an environmental gradient, using indirect gradient analysis by comparative ordination (Barbour _et_ _al_. 1980; Whittaker 1967). Ordination is used to simplify multivariate data, and mathematically express ecological differences between species or sites, through an examination of the covariance of some measurable attribute (e.g. abundance, frequency, importance value). The ordination can then be used to delineate the environmental gradients that are influencing community structure. When used in conjunction with a direct examination of structural and compositional changes along assumed environmental gradients, ordination can provide corroborative evidence for testing a hypothesized ecocline.

In the present study direct gradient analysis was used to measure the linear extent of vegetative edge effects on northern and southern aspects in four different forest fragments. Ordination was used not so much as corroborative evidence in this study, but to assess its applicability to an examination of changes in alpha diversity along edge-to-interior gradients.

Detrended Correspondence Analysis

Detrended correspondence analysis (DCA) is an eigenvector ordination technique based on reciprocal averaging (Hill 1973; Hill & Gauch 1980). I will not attempt to present a detailed description of the algorithm of DCA, but only a brief summary of the method (see Hill 1973, 1979; Hill & Gauch 1980; Gauch 1982 for details). Data sets to be analyzed using DCA consist of records of abundance for a set of species (i.e. species scores) in a set of samples. Sample scores are defined as the mean score of all the species found in that sample. New species scores are then defined as the mean of the scores of the samples in which a species occurs. This "reciprocal averaging" is repeated until species and sample scores stabilize to a solution that is independent of the original species scores. The final sample scores are scaled so that the lowest sample score is zero. This vector of sample scores defines the first solution of the ordination, i.e. the first ordination axis. Additional solutions exist, which are derived with the use of matrix algebra as detailed by Hill (1973), and correspond to subsequent axes of the ordinations. The ultimate goal of the analysis is to delineate actual environmental gradients based on the arrangement and separation of samples on the ordination axes. For each axis an eigenvalue is generated, which is a measure of the amount of variation explained by that axis. Eigenvalues decrease with each subsequent axis. Axes whose eigenvalues are much less than the highest eigenvalue are not likely to be of much significance. It is generally the first two axes of a DCA ordination that are most interpretable in terms of environmental gradients. The length of an ordination axis is a measure of species turnover along the gradient (Hill & Gauch 1980). Its value is the mean standard deviation of species scores in the data set. The longer the axis the greater the dissimilarity of samples. Samples on a gradient longer than 4 sd will generally have no species in common (Hill & Gauch 1980).

Methods

DECORANA, a microcomputer version of DCA (Hill 1979) was used to ordinate positions (i.e. 0-5 m north ... 45-50 m north, interior, etc.) by stratum in each site. Initial species scores consisted of square root-transformed importance values. The use of a transformation that serves to reduce large disparities between species in the measured attribute often helps to avoid a swamping out effect as a result of dominance by one or two species (Hill & Gauch 1980). In some cases not all species present in a particular position were included in the ordination. Rare species that have little real significance in community structure can often influence the ordination by their presence, particularly when the range of species scores is minimized with a transformation. Rare species can be downweighted, an option of DECORANA, or omitted. Hill & Gauch (1980) suggest that species with frequencies less than 20% in the entire data set should be omitted from the ordination. This criterion was adopted for this study.

Results and Discussion

Site 1

Ordination plots for each stratum are illustrated in Figures 42 and 43 and first and second axis eigenvalues are listed in Table 22. The predominant trend of the ordinations in all strata was the same. Positions were ordered along the assumed microclimatic gradient on the first axis, from the extreme southern edge positions to a combined grouping of southern interior and the bulk of the northern aspect positions. In the canopy, shrub and ground layers the extreme northern edge position was associated with the interior to mid positions on the southern aspect. From the canopy to the ground layer, this axis accounted for 70, 51, 30, and 31% of the variation in the data, respectively. The second axis separated positions by aspect in the upper two strata, however eigenvalues were low. Although some variation is evident, in general the ordinations indicate that a gradient of edge effects extends approximately 45 m into the forest on the southern aspect, and 5 m on the northern aspect. Further, the intermediacy of position 0-5 m north between the extreme southern edge

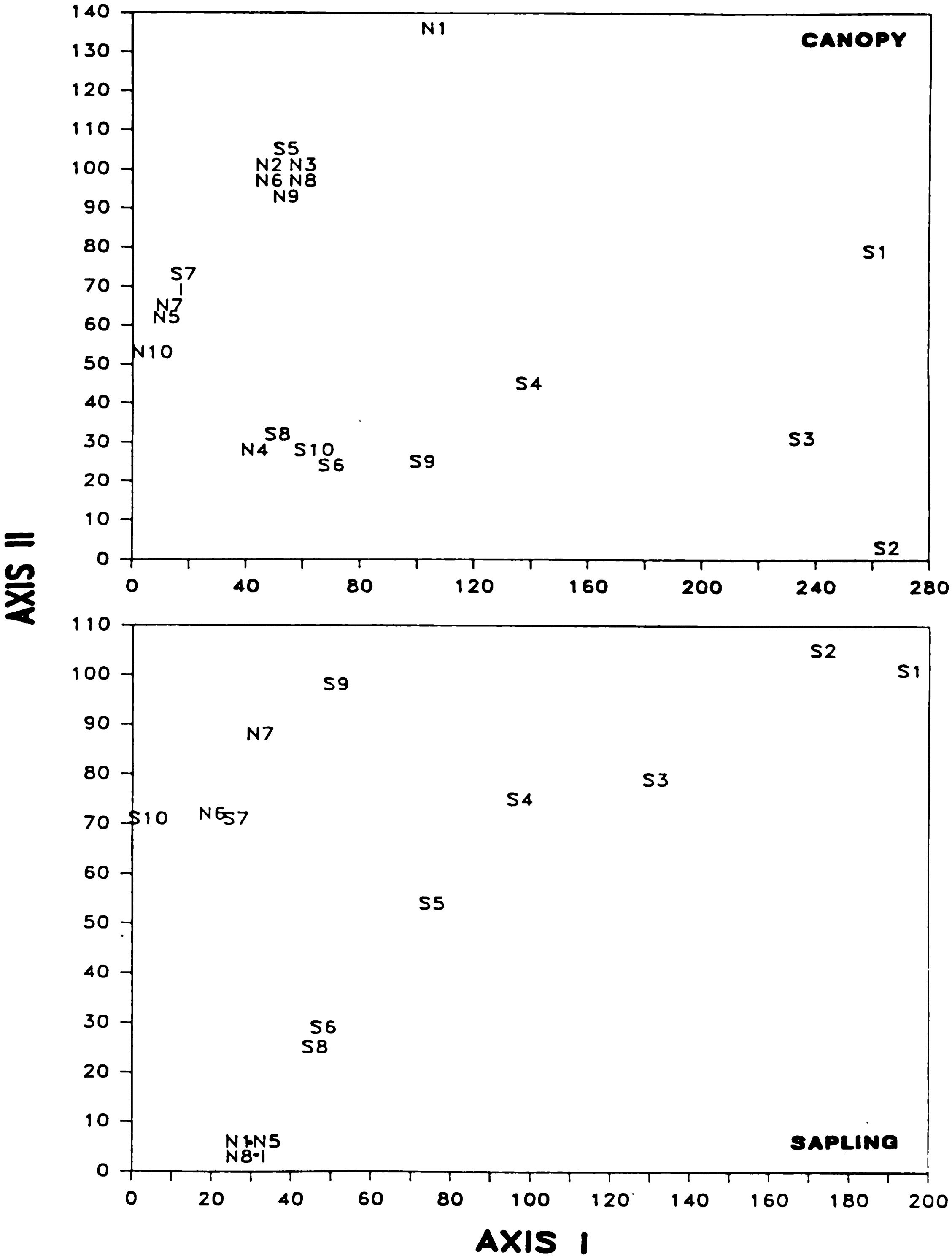


Figure 42. DCA ordinations of positions along the edge to interior gradients in Site 1. Symbols correspond to 5 m distance intervals from the edge to 50 m on the northern and southern aspects, (e.g. S1= 0-5 m from the southern edge and N10= 45-50 m from the northern edge). The interior (I) is 50 m from of all edges. Note that positions N1-N5, N8-N10 and I have equal scores in the sapling ordination.

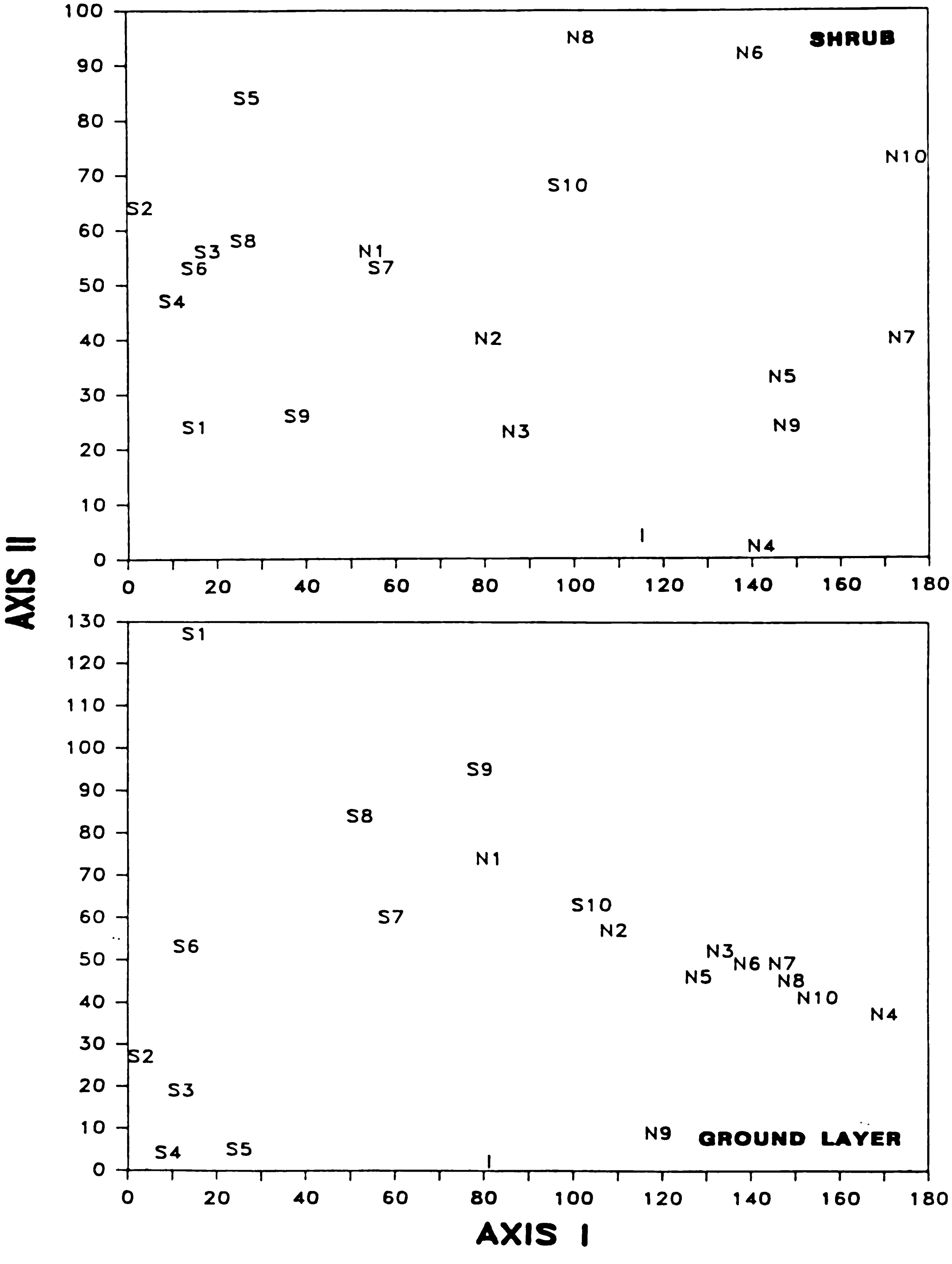


Figure 43. DCA ordinations of positions along the edge to interior gradients in Site 1. Symbols correspond to 5 m distance intervals from the edge to 50 m on the northern and southern aspects, (e.g. S1= 0-5 m from the southern edge and N10= 45-50 m from the northern edge). The interior (I) is 50 m from all edges.

Table 22. Eigenvalues by stratum in Sites 1-4.

		Eigenvalues	
Site	Stratum	1st axis	2nd axis
1	Canopy	.695	.209
	Sapling	.514	.133
	Shrub	.301	.062
	Ground Layer	.306	.106
2	Canopy	.546	.179
	Sapling	.186	.060
	Shrub	.278	.095
	Ground Layer	.205	.113
3	Canopy	.192	.095
	Sapling	.214	.059
	Shrub	.196	.124
	Ground Layer	.112	.067
4	Canopy	.433	.314
	Sapling	.445	.124
	Shrub	.241	.142
	Ground Layer	.202	.090

Eigenvalues of the 3rd and 4th axes were less than 2nd axis values in all cases.

and the interior is evident. These results are similar to those derived through direct gradient analysis.

Site 2

Eigenvalues were low for all but the first canopy axis (Table 22). The ordinations plots for this site (not illus.) failed to separate positions into an interpretable edge-to-interior gradient in any of the strata. The extreme edge positions on both aspects were generally separated from the remainder of the positions in the subcanopy strata. This is exactly the interpretation that was derived from direct gradient analysis, i.e. 5-10 m of edge forest on both aspects.

Site 3

Sapling and shrub ordination plots are illustrated in Figure 44. Eigenvalues were low for all axes (Table 22), however an examination of the figure shows slight separation of the first six southern aspect positions in the sapling layer and the first five in the shrub layer. Further, the two extreme edge positions on the northern aspect were widely separated from the remainder of the positions in the shrub layer. These examples illustrate that although low eigenvalues may result from an ordination with no interpretable gradient as in the previous site, they do not negate the existence of a partial gradient. The expression of the edge-to-interior gradient in the sapling and shrub strata is consistent with the finding of direct gradient analysis. The failure of the ordination to detect edge effects on the southern aspect to the extent that direct gradient analysis did was

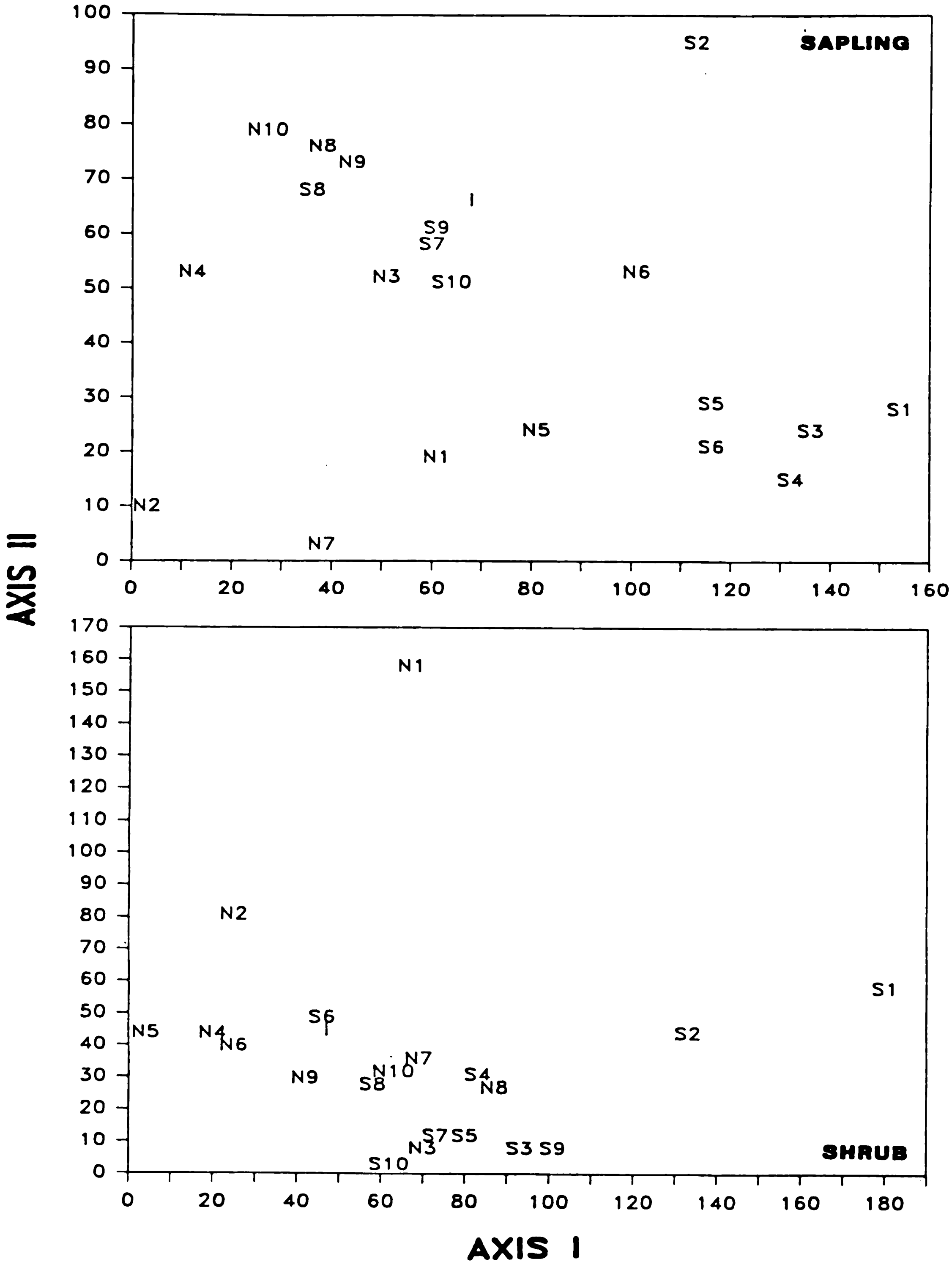


Figure 44. DCA ordinations of positions along the edge to interior gradients in Site 3. Symbols correspond to 5 m distance intervals from the edge to 50 m on the northern and southern aspects, (e.g. S1= 0-5 m from the southern edge and N10= 45-50 m from the northern edge). The interior (I) is 50 m from of all edges.

likely caused by the exclusion of species with frequencies below 20%. In the direct analysis these species were included in the tabulation of transitional events, since their distributions were obviously associated with edge and aspect effects.

Site 4

The canopy and sapling ordination plots for Site 4 are illustrated in Figure 45. The first canopy and sapling axes account for 43 and 45% of the variance respectively (Table 22), however no interpretable trend was evident on this or the second axis. The positions are widely separated along the gradient, indicative of a high amount of dissimilarity between them. There was also a lack of any interpretable trends in the shrub and ground layers (not illus.). Positions were again widely separated from one another. The lack of any easily interpretable gradient trends and the dissimilarity between positions can be interpreted as an indication of an all-edge condition of the forest, as was determined using direct gradient analysis.

Conclusion

The interpretability of the DCA ordinations was dependent on the condition of each particular site. In Site 1 the edge-to-interior gradient was developed to such extent in all strata that the ordination was able to extract nearly the same trends as did the direct analysis. In Site 3 the ordination only partially extracted the gradient to the extent of the alternative method. However, the expression of the gradients in the subcanopy strata was consistent

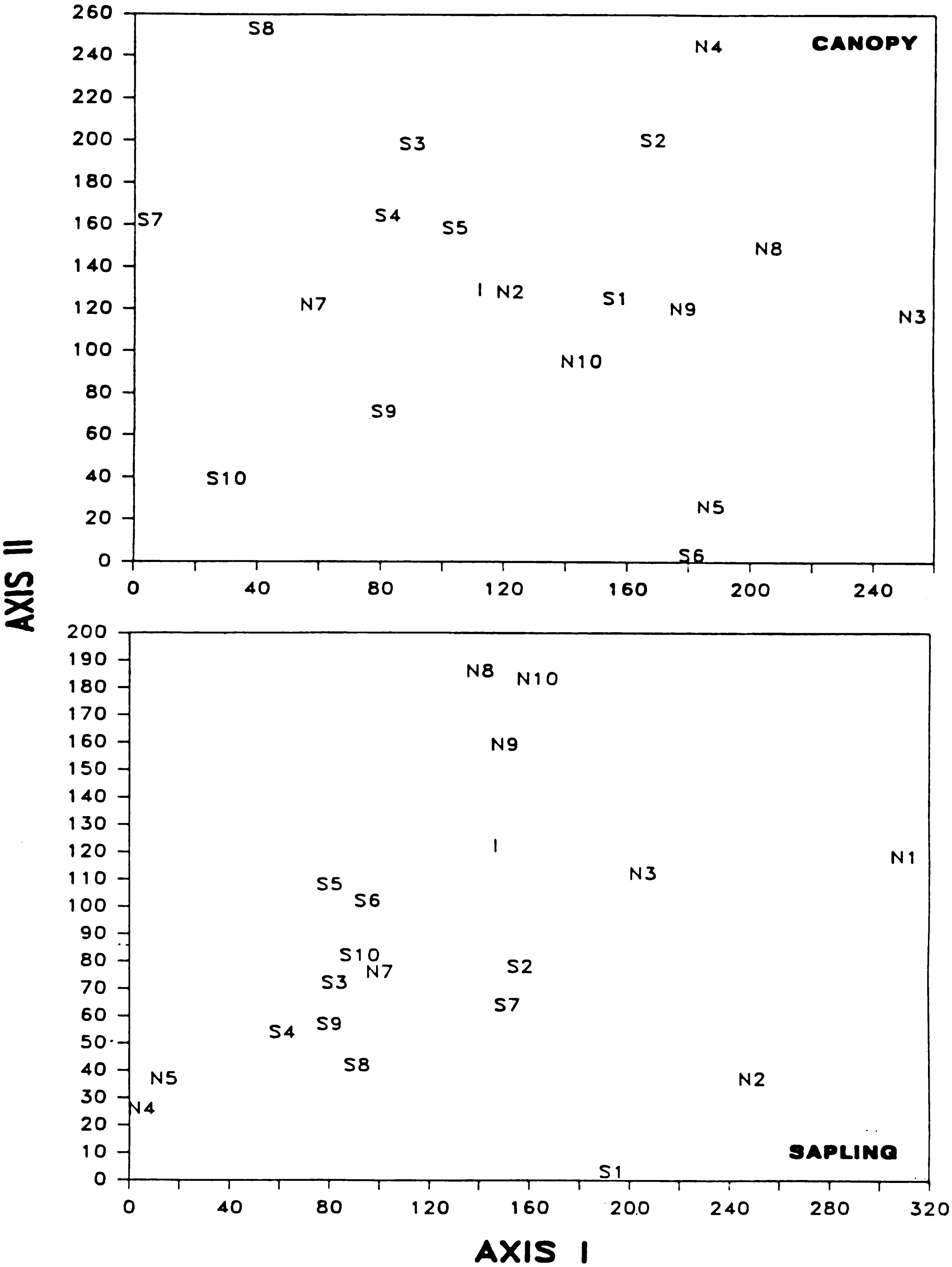


Figure 45. DCA ordinations of positions along the edge to interior gradients in Site 4. Symbols correspond to 5 m distance intervals from the edge to 50 m on the northern and southern aspects, (e.g. S1= 0-5 m from the southern edge and N10= 45-50 m from the northern edge). The interior (I) is 50 m from all edges. Note that N1 and N6 were omitted from the canopy ordination and N6 was omitted from the sapling ordination.

between methods. Gauch (1982) suggests the use of principle component analysis for the ordination of sites with low dissimilarity. This method may have been more appropriate for Site 3 and perhaps all situations in which trends in alpha diversity across short environmental gradients are being examined. The ordination results for Sites 2 and 4 exemplified the necessity for first evaluating an analytical technique against a known data set before applying it to a new situation. There was no a priori basis for interpreting the results as representative of little vegetative edge development in Site 2 and of extensive edge conditions in Site 4. However, the patterns observed, i.e., no easily interpretable gradients, low eigenvalues and correspondingly low and high dissimilarity between positions in Site 2 and 4, may now be used as base line comparative information in future studies.

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