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University of Ottawa

IMPACT OF ALPINE SKI TRAIL CORRIDORS
ON A BEECH-MAPLE FOREST COMMUNITY,
MONT-STE-MARIE, QUEBEC:
SPATIAL VARIATION OF EDGE EFFECTS

A thesis submitted to
The School of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of
Master of Arts in Geography

by

Diane Chapman
Ottawa, Canada
February, 1988

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UNIVERSITÉ D'OTTAWA
UNIVERSITY OF OTTAWA

ABSTRACT

The purpose of this study was to investigate the impact effects of alpine ski trail corridors on the adjacent beech-maple forest community at Mont-Sainte-Marie, Quebec, fourteen years after trail clearance. Specific objectives were to measure the spatial variation of structural and species compositional changes to the adjacent vegetation, and to consider implications of impact effects on future forest development.

A stratified approach to site selection was adopted to ensure that results would reflect trail impact effects rather than a response to natural abiotic variation. Sample plot design was systematic. Three replicate sample units of 10x30 metres and SSW orientation were outlined adjacent to the trail, and three more in a control area beyond the influence of trail impact; each unit was divided into six contiguous 10x5 metre plots aligned with the trail edge and extending into the forest interior.

Vegetation characteristics were recorded in six structural layers: ground (0-0.5 m), shrub (0.5-2 m; 2-5 m), and tree (>2.5 cm dbh: <10 m; 10-20 m; >20 m). Primary characteristics recorded were stem counts and cover estimates for all layers, and circumference at breast height for all trees. Secondary characteristics recorded for trees included orientation of

longest branches and stem inclination.

Preliminary analysis of the data involved the calculation of mean values and standard deviations for sample replicates, the derivation of basic indices, and the comparison of samples in terms of distance effects by statistical tabulation and graphic display. Data summarization was subsequently obtained by computer-assisted multivariate analyses which involved the calculation of similarity and distance measures (Gower coefficient, information analysis), and the ordination of sample data by correspondence analysis and principal component analysis. Graphic displays of the reduced data were examined for distance effects.

Results of the study indicate that the distance of impact effects, and the structural and species compositional characteristics that change, vary with structural layer. Findings indicate an overall impact distance of 10-15 metres; increases in species diversity (richness) in the ground, shrub, and lowest tree layers; community retrogression characterized by changes in species composition (a decline in the importance and the elimination of many 'interior' species; the appearance of and high relative abundance of a considerable number of shade-intolerant 'edge' species; an increase in the importance of shrub and herb species); a reduction in the average size of the dominant species as a result of increases in density and cover in the ground, shrub, and lowest tree layers; the development of two distinct buffer zones as a consequence of these increases in density and cover--the outer dominated by shade-intolerant

species and the inner dominated by Sugar Maple; increases in the variability of density, cover, and species richness in the ground, shrub, and lowest tree layers; and structural adaptation in all tree layers.

Future implications of an age (size) class analysis of these impact effects are a change in canopy dominance from Beech to Sugar Maple from 5-15 metres of the trail edge, and the maintenance of the outer edge-zone in a permanently altered state of arrested successional development.

Some unique findings of this study are: the appearance of a secondary buffer zone of Sugar Maple interior to the outer zone of predominantly shade-intolerant species; the transformation of continuous microclimatic gradients into discontinuous gradients by the vegetation response to impact; an indication that the recovery rate of impacted forest may be directly related to the intensity of the initial response to disturbance; and evidence that topography exerts an indirect influence on vegetation response to (and recovery from) disturbance through its effects on microclimate.

The response of the beech-maple forest community to corridor disturbance was considered in this investigation in relation to two components of relative stability: resistance and resilience. The principal findings of the study can be considered as measures of the resistance of the community (i.e. ability to resist displacement) to the stress imposed by the ski trail. The ability of the community to buffer corridor disturbance suggests considerable inherent resilience (i.e. ability to recover) even though the stress is sustained through corridor maintenance.

Nevertheless, the threshold of resilience is exceeded close to the trail edge where community characteristics will remain permanently altered as long as the edge is maintained. Moreover, a long-term shift in dominant species from Beech to Sugar Maple from 5-15 metres of the trail edge implies incomplete resilience to this type of stress.

It is apparent from the results of this study that fragmentation by open corridors could have long-term effects on the species composition of adjacent forests. The denser the network of corridors, the more widespread these impact effects are likely to be. On the basis of the study results, a minimum placement distance of 60 metres between trails is recommended in the Beech-Maple forest community at Mont-Ste-Marie.

ACKNOWLEDGEMENTS

The completion of this project was made possible by the contributions of a number of agencies and individuals. Firstly, without the support and authorization of educational leave by the Geographical Services Division of the Department of Energy, Mines, and Resources the project could not have been initiated. Thanks are also due to the Geodetic Survey of the same Department for the loan of field equipment.

I gratefully acknowledge the support and encouragement of my thesis advisor, Professor Michel Phipps, who sacrificed his wristwatch in a shared day of torrential rain climbing, chest-high in trail vegetation, in search of a suitable study site; who spent another day, along with fellow student Sylvain Parent, taking increment cores of virtually impenetrable beech trees; who helped me negotiate the transition to the computer era; and who, following long periods of project inactivity once I had returned to work, would, in one brief discussion, restore my motivation and belief in this project by his boundless interest, enthusiasm, energy, and sound advice.

I am also indebted to Gary Clark, then Chairman of the Board of Directors of Mont-Ste-Marie Limited who gave permission for the investigation to be carried out and who demonstrated interest

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INTRODUCTION

BACKGROUND AND PURPOSE

Ecosystems experience a wide variety of natural and man-made disturbances that vary in type, frequency, duration, magnitude, and spatial extent (Peterman 1980). As systems differ in their ability to withstand disturbance, there is a critical need for a greater understanding of the levels of manipulation that can be imposed on ecosystems without producing serious or harmful transformations (Hill 1975).

In the context of this general concern, this study was initiated to determine the response of a forest community to man-induced disturbance. More specifically, the purpose of the study was to investigate the impact effects of alpine ski trail corridors on adjacent vegetation at Mont-Ste-Marie, Quebec.

Defined objectives were:

1. To measure impact effects in terms of structural and species compositional changes to the adjacent vegetation;
2. To measure the spatial variation of impact effects in terms of distance from the trail edge; and
3. To consider the implications of impact effects for future forest development.

Vegetation structure can be defined as the arrangement in space of the components of vegetation (Fosberg 1967), or more

specifically by three components: the vertical arrangement of species (i.e. the stratification of the vegetation); the horizontal arrangement of species (i.e. the spatial distribution of individuals); and the abundance of each species (Kershaw 1964). The spatial variation of impact effects were accordingly measured in the vertical as well as horizontal dimension.

SCOPE

An exploratory survey of the study area revealed that if site selection criteria were to be met, the scope would have to be more restricted than originally planned. The study was therefore limited to a beech-maple community adjacent to a trail that had been cleared 14 years earlier¹. The maple-beech community is the type most frequently intersected by ski trails in the Mont-Ste-Marie area. It was accordingly considered the most representative of potentially impacted vegetation types.

THEORETICAL CONTEXT

The problem area of the study -- the impact of open corridors on forest vegetation -- could be considered to fall within the realm of landscape ecology which studies the structure, function, and development of landscapes (Forman 1981). Significant mutual control is exerted by landscape elements or structural components (patches, corridors, matrix) through interactions involving flows of energy, mineral nutrients and species (Forman and Godron 1981; Forman 1983). The interaction of corridors with other landscape elements represents a key

¹

Data collection took place in the summer of 1984.

conceptual area of landscape ecology (Forman 1983). Corridors function as sources of environmental and biotic effects on the surrounding matrix (Forman 1983). This study focuses on this ecological role of corridors by attempting to measure biotic effects induced by environmental changes imposed by ski trails.

The study could also be considered within the confines of stress ecology, defined by Barrett (1981) as that subdiscipline which attempts to measure and evaluate the impact of natural or foreign perturbations on the structure and function of ecological systems. Stress is defined variously in the literature; however, all definitions share the common premise of a stimulus acting on a biological system and the subsequent reaction of the system (Rapport et al. 1984). Often used synonymously with 'disturbance' and 'perturbation', stress is generally considered to involve an interference with normal system function that exerts an energy cost to that system (Boesch and Rosenberg 1981). This energy cost results in community change. As noted by Godron and Forman (1983), disturbance causes a community or ecosystem characteristic (e.g. species diversity, nutrient output, biomass, vertical and horizontal structure) to exceed or drop below its common (homeostatic) range of variation. Stress effects are not necessarily negative. In fact, the persistence of some ecosystems depends on periodic disturbance (Vogl 1977, 1980), and as Odum et al. (1979) observe, disturbance induced by man can be beneficial at low levels of impact (e.g. enhance productivity) yet have adverse effects at higher levels.

Ecosystems vary considerably in their response to stress.

Two components of relative stability define this response: resistance--the ability of a system to resist displacement from its initial state when subject to perturbation (Webster et al. 1975; Vitousek et al. 1981), and resilience--the ability of a system to return to a reference state following a disturbance or stress period (Webster et al. 1975) once the limits of resistance have been exceeded. In attempting to measure and evaluate the stress effects on forest vegetation induced by disturbance corridors, this study conforms to the general objectives of stress ecology. The observed changes in the vegetation adjacent to the trail, measured in terms of vegetation structure and species composition (outside the range of variation of control samples)¹ could be considered measures of community resistance to corridor stress. As the measurement of resilience generally implies recovery after the removal of stress, yet the disturbance is sustained by corridor maintenance, this concept will be more difficult to apply. Nevertheless, evident efforts by the vegetation community to neutralize stress effects or to insulate itself from the disturbance could be considered as indicators of resilience.

In the context of the stress-response framework developed by Rapport et al. (1985), trail clearance would be considered as a terrestrial physical restructuring stress. This framework (table 1) provides overall context for this type of disturbance. Characteristic responses cited by these authors and relevant to

1

This range would reflect adjustment to predictable environmental changes, species interactions, and chance events.

Table 1

CHARACTERISTIC RESPONSE OF ECOSYSTEMS TO STRESS

	Nutrient Pool	Primary Productivity	Species Diversity	Size Distribution	System Retrogression
Harvesting of renewable resources					
Aquatic	*	*	-	-	+
Terrestrial	-	-	-	-	+
Pollutant discharges					
Aquatic	+	+	-	-	+
Terrestrial	-	-	-	-	+
Physical restructuring					
Aquatic	*	*	-	-	+
Terrestrial	-	-	-	-	+
Introduction of exotics					
Aquatic	*	*	*	-	+
Terrestrial	*	*	*	*	+
Extreme natural events					
Aquatic	*	*	-	-	+
Terrestrial	-	-	-	-	+

Note: +/- Signs indicate directions of change compared with normal functioning of relatively unstressed systems

* Characteristic response not sufficiently determined

Source: Rapport et al. 1985

the variables measured in this study are those related to species diversity, size distribution of species, and system retrogression.

LITERATURE REVIEW

Few attempts have been made to assess the vulnerability of an entire community to ecological changes resulting from trail proximity (Cole 1978). Previous corridor impact studies have been carried out in relation to ski slopes (Bayfield 1971; Hoffer 1981; Baiderin 1983); roads (Bates 1937; Frenkel 1970, 1974; Johnson et al. 1975); footpaths and hiking trails (Bates 1935; Peters 1972; Dale and Weaver 1974; Cole 1978); power transmission-line corridors (Boss 1974; Ludwig et al. 1977; Hessing et al. 1982); gas pipeline and other rights-of-way (Vasek et al. 1975; Niering 1958; Niering and Goodwin 1974; Anderson and Egler 1984); and seismic survey lines (Revel et al. 1984; Dougherty et al. 1986). With the exception of the road, hiking trail and seismic line studies, these investigations were primarily concerned with impacts on corridor vegetation using adjacent control plots to measure within-corridor change, or focused on vegetation control in rights-of-way. Even roadside disturbance observations have been confined to relatively narrow segments adjacent to highways within road rights-of-way (Frenkel 1970, 1974; Johnson et al. 1975) or outside areas of natural vegetation (Bates 1937). Studies that have measured hiking trail impact on adjacent vegetation have confined their observations to changes in groundlayer vegetation subject to trampling stress (Peters 1972; Dale and Weaver 1974; Cole 1978).

Corridor impact effects on more than one structural layer of adjacent vegetation were examined solely in the seismic line study by Revel et al. (1984). Even in this instance, measured variables were limited by the authors' primary interest in tree growth effects. This study was undertaken in a lodgepole pine-black spruce forest community in southwestern Alberta with the objectives of determining the effects of seismic lines on adjacent forest growth and examining on-line regeneration. Sample plots within and adjacent to seismic lines were aligned with the line edges; control plots were located 20-30 metres toward the forest interior. Study sites were selected to represent a variety of stand types (cover type, stocking density, and age), environmental conditions, and corridor age. Height and diameter measurements of trees were taken and increment cores were extracted. In addition to these measurements, the percentage cover of each species was estimated for tree, shrub, and herb layers.

None of the corridor studies that were reviewed systematically investigated impact effects along a transect from corridor edge to forest interior.

In view of the dearth of open corridor studies relevant to the project objectives, a review of vegetation studies of edges or ecotones between forested and non-forested land was carried out. Edges occur where plant communities meet or where successional stages or vegetative conditions within plant communities come together; areas influenced by the transition between communities or successional stages are called ecotones (Thomas et al. 1979). Edges can be inherent (i.e. result from

the meeting of two plant communities and originate from abrupt changes in natural factors such as soil, topography, bedrock, microclimate etc.); or induced (i.e. result from the meeting of successional stages or vegetative conditions within a plant community that are created by management practices or short-term natural events such as fire, disease, insect infestations, floods, erosion etc. (Thomas et al. 1978)). Edges may also be maintained, or advancing (not maintained and advancing with secondary succession (Ranney et al. 1981)). Edge configuration can also vary from abrupt to mosaic (Thomas et al. 1978). According to this terminology, corridor edges relevant to the current study would be classified as induced, abrupt, and maintained. The differentiation between 'edge' and 'ecotone' is not commonly made in the literature (See Ghiselin 1977; Smith 1980; Ranney et al. 1981) where 'edge' is often used to denote both boundary and ecotone¹. This expanded usage will be adhered to in this study.

The term 'edge effect' was first used by Leopold (1933) in relation to the high abundance and richness of wildlife encountered in these zones. This phenomenon is so predictable that edge characteristics (e.g. length, width, and configuration) are used as surrogates in the calculation of predictive indices of wildlife diversity and productivity (Patton 1975; Ghiselin 1977; Thomas et al. 1979). Edge effects are also characteristic of plant communities, and as noted by Thomas et al. (1979) for

¹
In the case of maintained edges, only one half of the ecotone exists interior to the maintained edge (Levenson 1976).

wildlife, result from the additive effects of the overlap of species ranges when two or more plant communities meet, and from the addition of species adapted to the environmental conditions of the ecotone created. The high abundance and richness of wildlife in edges is in fact a function of habitat diversity which is in turn defined by the food and shelter characteristics of the vegetation and abiotic environment. Wildlife and vegetation edge effects are therefore directly related.

Pioneering work on the vegetation characteristics of inherent edges between different forest types in relation to wildlife habitat value was carried out by Barick (1945, 1950). Studies of induced edges have investigated vegetation characteristics in relation to distance from edge margin (Wales 1972; Ranney et al 1981); aspect (Trimble and Tryon, 1966; Wales 1972; Ranney et al. 1981) edge age (Trimble and Tryon 1966; Ranney et al. 1981); edge maintenance (Ranney et al. 1981); community age (Whitney and Runkle 1981); or have compared characteristics in edge plots with those of interior control plots (Gysel 1957; Frei and Fairbrothers 1963; Runkle 1981).

Gysel (1951) studied and compared vegetation structure and species composition in openings and edges in beech-maple woodlands adjacent to agricultural fields in southern Michigan. Edge, interior, and opening plots were compared in terms of number and frequency of tree species, and of cover for seedling, vine, shrub, and herb species. General observations of tree form were also made. North- and south-facing edges in various successional phases of development were sampled. Because of variations in the past history of the edges studied, however, an

analysis of the influence of aspect could not be carried out.

Trimble and Tryon (1966) investigated the extent of border-tree crown expansion into openings of different age and varying size cut into Appalachian second-growth hardwood stands in West Virginia. They also examined the effect of aspect on the rate of crown growth of edge trees.

A floristic study of forest/field edges of a mature oak-hickory forest on the New Jersey piedmont (Frei and Fairbrothers 1963) investigated species presence, abundance (rare, common, abundant), and phenology in edge and interior sections. Wales (1972) studied north and south edges of the same forest. The edges studied were not maintained and had accordingly advanced with secondary succession. Sample sites were located along the forest/abandoned field edges and in the stand interior. Vegetation was sampled to a distance of 30 metres from each edge in contiguous strip plots aligned with the edge. Tree species density, diameter at breast height, and origin were sampled along with cover of the vine, shrub, and herb layer species. General observations of tree form were also noted. Comparisons were made among strips at the edges and forest centre. A detailed microclimatic study of north and south edges had been previously carried out by the author (Wales 1967) and provided valuable insight for the interpretation of results.

Forest/field edges and interiors of a disturbed (logged) second-growth stand and an undisturbed old-growth stand in a beech-maple forest in Ohio were compared by Whitney and Runkle (1981). Because of the need to minimize differences in soil

type, aspect could not be held constant, and sample plots were located along east-oriented edges in the second-growth stand and west-oriented edges in the old-growth stand. Tree species density and diameter at breast height were sampled at interior and edge plots. Variations in species density and basal area were examined in relation to age of stand (old growth, second growth) and position (edge, interior). Edge age was not considered.

A comprehensive study of deciduous forest island edges in the suburban and rural fringe area of Milwaukee, southeastern Wisconsin, was carried out by Ranney et al. (Levenson 1976; Brunner 1977; Ranney 1978; Ranney et al. 1981). Trees, saplings, shrubs, and woody groundlayer species were sampled in contiguous plots aligned with the forest/field edges, extending from edge to stand interior for a distance of 30 metres. Edges with north, south, east, and west orientations were sampled. Edge age was determined from increment borings of selected trees. The maintenance characteristics of each edge sampled was also recorded. Structural tree measurements (height, crown asymmetry, and dominance class) were taken for use in simulation models of forest edge dynamics. A selected review of forest island edge literature was also undertaken by Ranney (1977).

Results of canopy gap dynamics studies in Beech and Sugar Maple forests (Bray 1956; Runkle 1979, 1981, 1982, 1984; Nakashizuka 1983) also have some applicability to this investigation, although Gysel (1951) and Wales (1972) observed differences between the composition and structure of vegetation at edges and in openings.

Although not specifically related to induced edges produced by terrestrial physical restructuring, other investigations that have observed impact effects on a forest community in relation to distance from a man-induced disturbance source include studies of chronic gamma-ray irradiation of a late-successional oak-pine forest in New York (Woodwell and Whittaker 1968) and a boreal forest ecosystem in southeastern Manitoba (Guthrie and Dugle 1983); and investigations of stress effects of sulphur dioxide emissions at Sudbury, Ontario (Gorham and Gordon 1960; Luzon 1971; Freedman and Hutchinson 1979) and Wawa, Ontario (Gordon and Gorham 1963).

RATIONALE

An examination of the relevant literature in relation to the study objectives reveals that:

- o The impact of ski trail corridors on adjacent forest vegetation does not appear to have been studied;
- o The majority of corridor impact studies have stressed impact effects of corridor use on within-corridor vegetation rather than on vegetation adjacent to corridors;
- o Only one corridor study (Revel et al. 1984) investigated impact effects on more than one structural layer of adjacent vegetation; most studies confined observations to the groundlayer;
- o No corridor studies and only one study of induced maintained edges (Ranney et al 1981) investigated the spatial variation of impact effects with distance from the edge margin.

It accordingly appears that the investigation will fill gaps in the corridor impact literature in relation to type of corridor (ski trail) and the spatial variation of impact effects (both horizontal and vertical). It will supplement studies of induced

edges with respect to edge type (forest/ski trail) and topography (sloping). In view of the few existing empirical studies of this nature, the investigation will also make a contribution by validating existing findings and assessing the applicability of edge study findings to open corridor situations.

In the summary paper of a volume related to forest fragmentation, Burgess and Sharpe (1981) state:

"The strong interaction between elements of landscape mosaics... is fundamental to the dynamics of landscapes... Major unknowns are the time and distance decay rates of these interactions between any landscape element and those surrounding it."

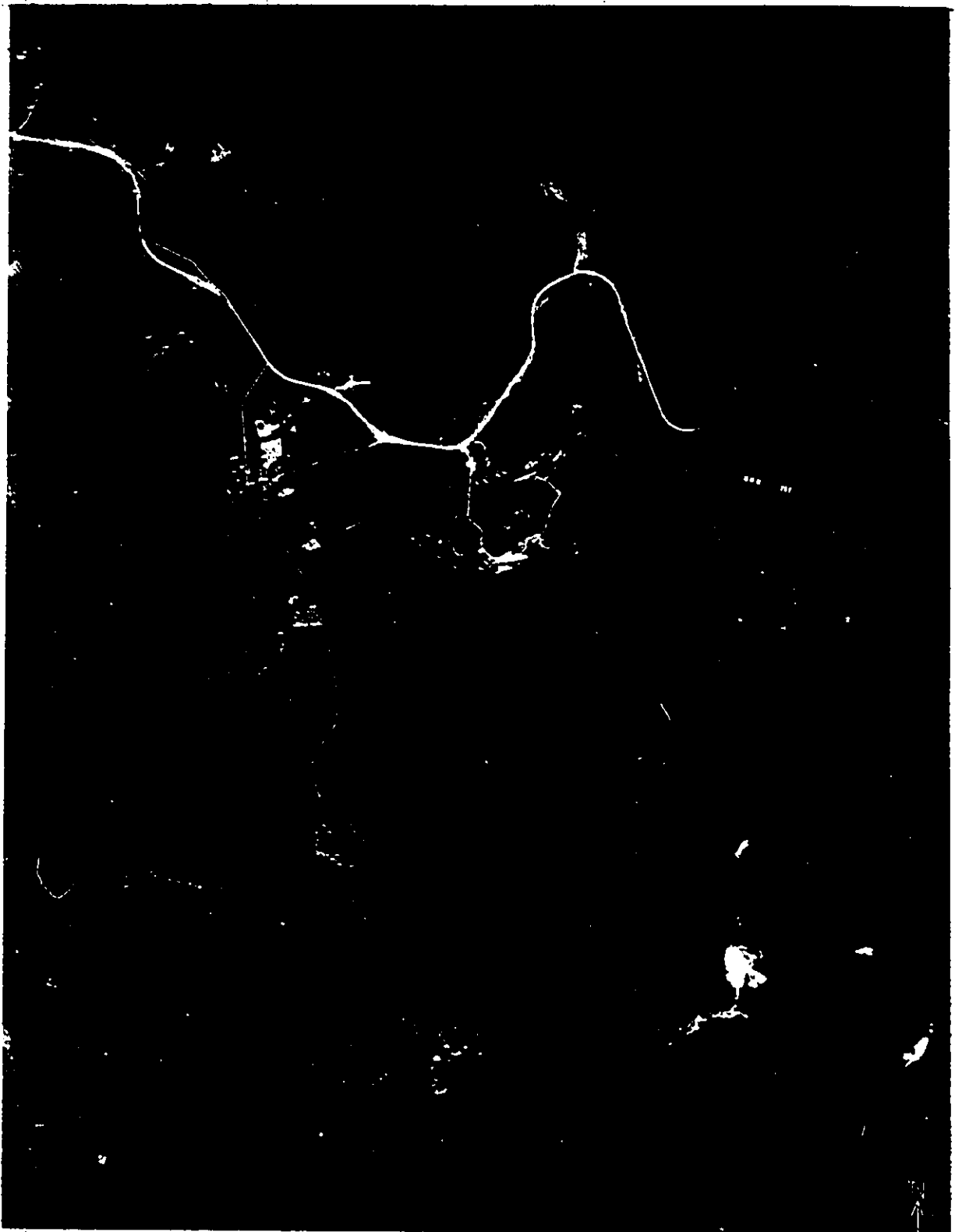
By focusing on the distance impact effects of open corridors on forest vegetation this study addresses one of these unknowns.

Finally, by contributing, if only in a small way, to the elucidation of the ability of ecosystems to withstand man-induced stress, the study will address an aspect of stability that urgently requires research (Hill 1975).

STUDY AREA

Physiography

Mont-Ste-Marie (fig.1) is located approximately 60 km due north of Ottawa in the southern part of Hinks Township, Gatineau County, Quebec, on the divide between the Gatineau and Lièvre tributaries of the Ottawa River. Its summit (Lat. 45 56 10 W, Long. 75 51 07 N), the highest point in the Gatineau Hills, reaches an elevation of 558 metres above sea level and a vertical height from base to summit of approximately 375 metres. The Gatineau Hills are part of the Laurentian Highlands of the



(Sample units shown as white rectangles)

Scale 1:35,000

Fig. 1 Study Area, Mont-Ste-Marie

Precambrian Shield (Bostock 1970). Topography in the area is quite diverse ranging from the flat lowlands of the Ryanville plain to the rolling-to- mountainous upland ski terrain.

Geology

The Precambrian Shield bedrock of the region was subjected to intense deformation, metamorphosis, and granitic intrusion in the Grenvillian Precambrian orogeny (one billion years before present), and later in the Precambrian era, and principally consists of intermediate intrusive rocks ranging from quartz monzonite to pyroxene diorite (Quebec Department of Natural Resources 1949, Geological Survey of Canada 1968).

Surficial Deposits

A geomorphic map of the area (Phipps 1974) reveals a variety of surficial materials including exposed rocky ridges and domes; debris-covered slopes with angular fragments derived from slope weathering and frost action; glacial moraine at the base of the slopes and surrounding the small lakes in the area; fluvial deposits of sand and gravel in the valley that drains Lac Fournier and issues onto the Ryanville plain; silt and clay deposits covering the lowlands adjacent to Lac Ste-Marie; and occasional small organic deposits scattered throughout the area.

Soils

Soils developing on these varied surficial deposits are likewise diverse and derive their primary characteristics (texture, structure, drainage, mineral composition etc.) from these parent materials. Soils sampled at the study site appear

to belong to the Orthic Humo-Ferric Podzol subgroup of the Podzolic order (Canada Soil Survey Committee 1978)¹ and conform to described characteristics of Podzols of the Ste. Agathe series (an earlier classification) found in northern Gatineau county (Lajoie 1962).

Climate

The regional climate, according to the Köppen classification, is Boreal Humid Continental (Energy, Mines and Resources, Canada, forthcoming).² Some climatic statistics relevant to plant growth are as follows :

Mean daily July temperature 18.3⁰C
Mean daily January temperature -13.5⁰C

Mean annual precipitation 866.6 mm³
Mean annual rainfall 650.8 mm
Mean precipitation May-September 433.0 mm

Average date of last spring frost May 29
Average date of first fall frost September 20
Average frost-free period 113 days
Annual degree-days above 5 C 1649.6

Maximum daylight hours 15.45 (June 21-22)
Minimum daylight hours 8.38 (December 21-22)
Mean annual hours of sunshine 1951.4
Hours of sunshine May-September 1139.4

¹
Without chemical analyses this classification is tentative. The soils could also be Eluviated Melanic Brunisols.

²
Climate statistics are those recorded for Maniwaki, Quebec (altitude 170 m above sea level) and represent the climatological recording period 1951-80 (Environment Canada n.d., 1982a, 1982b, 1982c).

³
Monthly precipitation in the growing season is higher than at other times of year but the variability is also higher.

Vegetation

In a regional forest classification context, the area lies within the Middle Ottawa Section of the Great Lakes-St. Lawrence forest region (Rowe 1972). The climax vegetation of the upland is deciduous forest dominated by Sugar Maple in association with Beech, Basswood and White Ash with occasional admixtures of Yellow Birch and Red Oak (Lafond and Ladouceur 1968)¹. The diversified topography and surficial deposits of the area support a variety of community types (fig. 2). Treeless exposure barrens on rock crests and at the summit support a dwarf shrub (e.g. blueberry/vaccinium spp.), moss and lichen community. A community of Red Oak and Red and White Pine occurs on rocky ridges and steep slopes with shallow soils. A transitional Beech-Red Oak community is found in exposed upland areas with slightly deeper soils and gives way to the most areally significant community of Sugar Maple and Beech on deeper soils at slightly lower elevations. On the lower, moister slopes, Sugar Maple is associated with Basswood, and toward the base of the mountain, in well drained situations, with Ironwood. The well-drained sand and gravel deposits in the valley support a Balsam Fir-White Pine community which gives way to a Balsam Fir-White Spruce association on the finer silt and clay deposits bordering the Ryanville plain. Most of the plain has been cleared for agricultural purposes.

¹ This climax community was designated l'érablière laurentienne (*Aceretum saccharophori laurentianum*) by Dansereau (1946) and is considered as a sub-association of the érablière order by Grandtner (1966).

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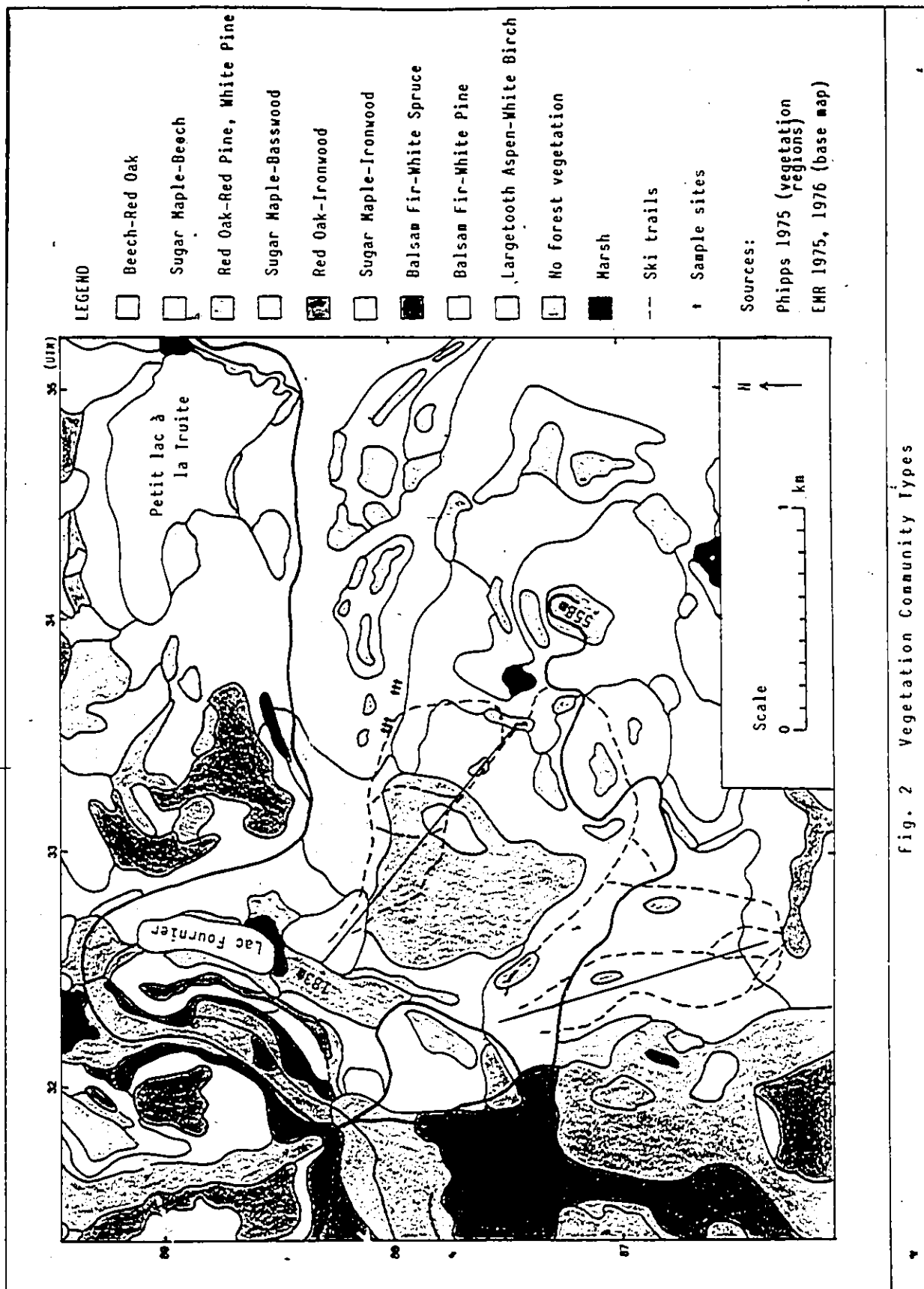


Fig. 2 Vegetation Community Types

Development History

Twenty years ago, in a floristic study of Mont Ste-Marie, Dore (1967) stated:

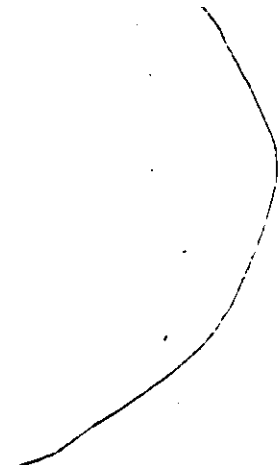
"On account of the ruggedness of the terrain, the slopes of Mont Ste Marie have long stood a wilderness of rock and forest and, despite their relative accessibility from valley roads, have not been overly fragmented by sportsmen nor excessively exploited by lumbermen. Presently, the covering vegetation could be said to be representative of the area and in an almost original state".

Accessibility was improved in 1962-63 when an unsurfaced road was cleared to the summit for the construction of a radar tower. The project was, however, abandoned after the tower was constructed. The land was purchased by the Mont-Ste-Marie Company for a ski resort development in 1965. Ski trails were cleared on the Côte Vanier side of the mountain and, by the fall of 1966, a chairlift was installed from the base to Ryan peak, west of the main summit. Following clearing, the trails and slopes were seeded with a coarse grass mixture of timothy and fescue. The second development phase took place in 1970 when ski trails were cleared and a chairlift was installed on the Cheval Blanc side of the mountain, leading from a base close to the southern end of Lac Fournier to a peak northwest of the main summit. These hills were also seeded after clearing and grading. Supplementing the introduced grasses, native vegetation rapidly colonized the cleared areas.

Trail maintenance at Mont-Ste-Marie is by mechanical mowers that are used to cut trail vegetation in the fall at the end of

¹
This section is based on Dore (1967) and on verbal accounts by Mont-Ste-Marie personnel.

the growing season. No herbicides or chemicals of any kind are used in trail maintenance, and no artificial snowmaking equipment has yet been installed on the Cheval Blanc side of the mountain where the study site was located. Verbal assurance was obtained from area personnel that the current and original edge margins are coincident (i.e. that subsequent trail widening did not take place). This could not be confirmed by aerial photography because of limited coverage. An aerial photograph of the area (Energy, Mines and Resources Canada 1975) appears in fig. 1.



METHODS

DATA COLLECTION

Site Selection

A variety of vegetation community types are supported by the elevation range and diverse topography of the Mont-Ste-Marie area. The superimposition of a preliminary map of vegetation communities (Phipps 1974) and a topographic map of the area (fig. 2) reveals that the vegetation community most frequently intersected by alpine ski trails is the beech-maple type. All trails of intermediate ability-level fall within this assemblage, with the exception of the upper reaches of some of these that grade into a beech-oak forest; the steeper expert slopes are cut through an oak-pine association. Although a comparison of effects on all three communities was initially considered, field investigation revealed that site selection criteria could not be met by the beech-oak and oak-pine associations. For this reason, and because the maple-beech community appears most representative of potentially impacted vegetation types in the area, it was selected for investigation. As other related studies have been carried out in maple-beech communities (Gysel 1951; Whitney and Runkle 1981; Ranney et al. 1981), this also presented the possibility of a direct comparison of results.

2

The objectives of the study dictated a highly stratified approach to site selection. To ensure that results would reflect trail impact effects rather than a response to natural abiotic variation, care was taken to minimize differences in environmental variables among sample sites.

Potential sample locations were first identified on maps and aerial photographs. Trail edge segments and complementary control areas were selected on the basis of similar community type, elevation, topographic position, slope inclination, slope aspect and edge orientation. To qualify, forest stands had to be of sufficient area to be considered unaffected by other trails or clearings (no other major disturbance within 30 metres of sample unit boundaries¹); and relatively homogeneous (to reduce within-sample variability). The final selection of sample sites took place in the field.

Because of the topographic diversity of ski terrain and dissection by other trails, the availability of sites meeting the above criteria was severely limited. Even an attempt at randomization in terms of sample unit placement along suitable edge segments had to be abandoned because of local terrain unsuitability or the obstruction of potential edge plots by large boulders or fallen trees. Three trail edge sample sites with south-southwesterly edge orientations were finally selected² as well as an undisturbed control site located 105 metres to the

¹This dimension was approximated from the literature (Wales, 1972; Ranney et al, 1981).

²Trail sites located adjacent to Carousel ski trail on Cheval Blanc side of mountain.

east along the base of the same general slope (fig. 3)¹.

Since beech dominates the canopy layer at most of the study sites, the community is referred to as beech-maple rather than maple-beech. Maple dominance is, however, more characteristic of the area as a whole.

Sample Plot Design

Sample plot design was systematic. Since the purpose of this investigation was to determine the spatial variation with distance from the trail edge, contiguous sample plots were aligned with the trail edge and extended into the forest interior for a distance of 30 metres². The location of sample units is shown in fig. 3, and the plot arrangement in one unit in fig. 4. General characteristics of sample units are given in table 2.

Three replicate sample units of 10x30 metres were outlined in both trail and control sections. Trail section units were separated (from west to east) by distances of 13.4 and 22.5 metres respectively; control section units were located immediately adjacent to one another. (Contiguity was necessitated by openings to the west and east of this section.) Each unit consisted of six contiguous 5x10 metre plots with their long

1

In an area of even terrain, a set of control plots interior to the trail section might have been adequate to represent unimpacted conditions of the forest interior. In the present study, however, the transect from trail edge to interior forest followed an ascending slope and effects related to slope position could not be ruled out. In order to separate slope effects from trail impact effects, therefore, a duplicate set of control plots and replicates had to be selected beyond the influence of the trail.

2

See note 1 on p. 22 above.

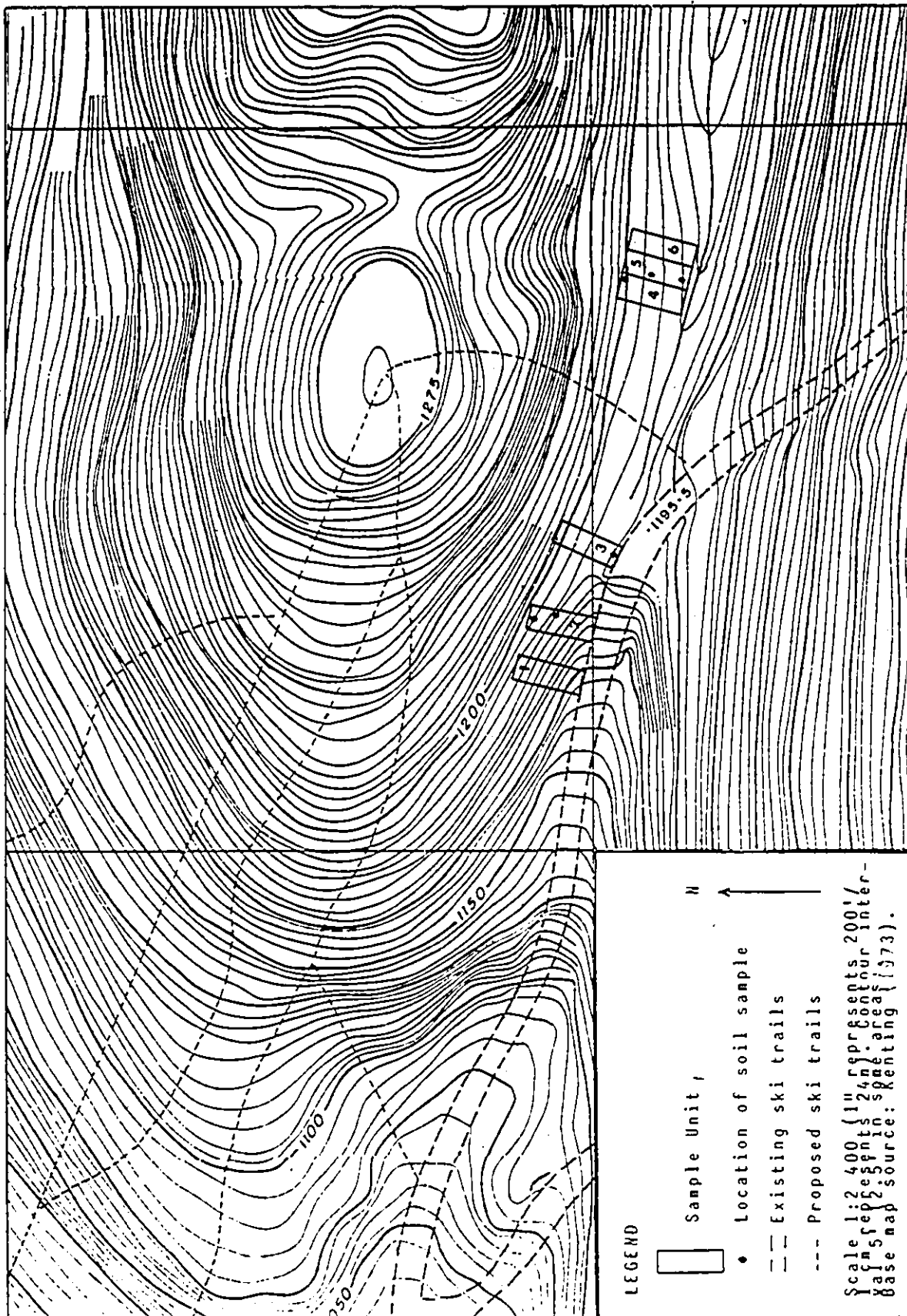
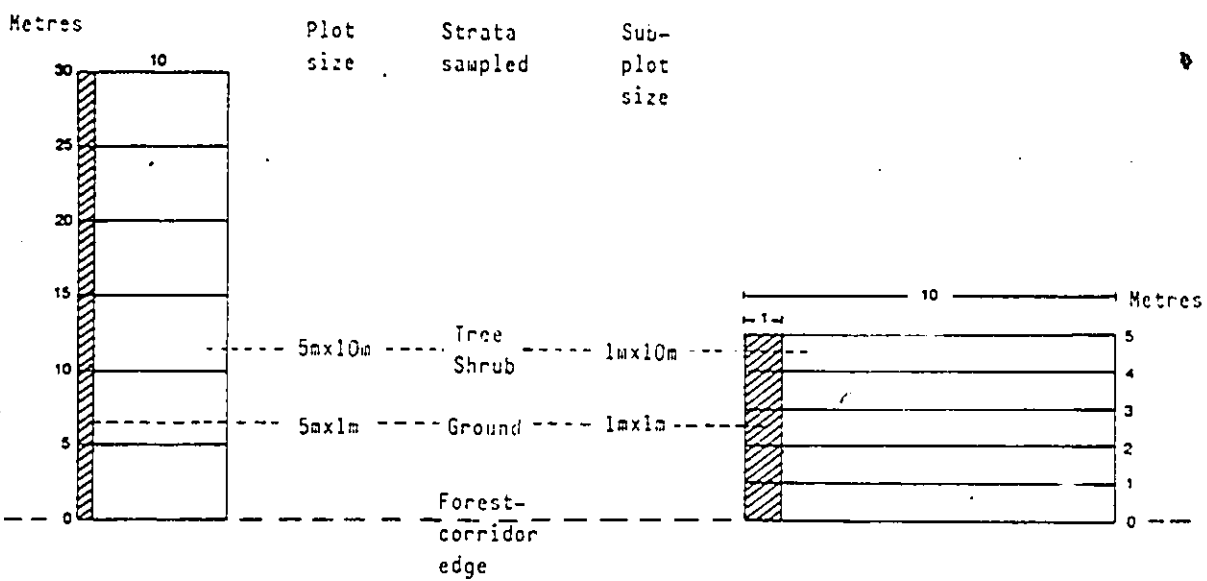


Fig. 3 Sample Sites

Forest interior



Ski trail corridor

A. Sample plot arrangement within one unit

B. Sample sub-plot arrangement

Fig. 4 Sample Plot Design

Table 2

GENERAL CHARACTERISTICS OF SAMPLE UNITS

Section	Unit	Edge Orientation (°)	Edge Maintenance Form	Average Slope (°)	Estimated Base Elevation (m)	Width of Ski Trail Corridor (m)
Trail	I	199	Stem Base/Canopy Dripline	15.5	356.6	16.0
Section	II	192	Canopy Dripline	15.3	359.7	16.0
	III	205	Stem Base/Canopy Dripline	8.5	362.7	13.2
Control	IV	195	--	15.0	362.0	--
Section	V	195	--	17.6	361.2	--
	VI	192	--	18.3	359.7	--

sides aligned with the trail edge. Control plots were aligned with the valley. Trees (>2.5 cm dbh, >5 m height) were sampled in three height classes, and shrubs (<2.5 cm dbh, >0.5 m height) in two structural layers in these plots. Groundlayer vegetation (<0.5 m height) was sampled in 1×5 m plots, located, when possible, at the western extremity of each tree/shrub plot. Lateral displacement of groundlayer plots was required in cases of obstruction by rocks or fallen tree stems. Plots were divided into one-metre-wide strips in order to derive frequency measures and to facilitate counting and cover estimation. This division also provided flexibility in distance-interval sampling by permitting a finer breakdown and the reaggregation of data into plot widths of multiples of one metre.

The selected tree plot size, comparable to that used for other related studies (Gysel 1951; Ranney et al. 1981), is relatively small for the sampling of canopy trees. However, because edge age at the time of sampling was only 14 years, significant change in the canopy layer was not anticipated for the primary variables measured and was expected to be limited to the structural adaptation of individual trees. Shrub data were sampled in the same plots as trees. The shrub layers should be accurately represented by the results since this plot size is somewhat larger than that used in comparable studies. The plot size used for the groundlayer is relatively standard for this layer and should adequately represent this stratum.

Variables Recorded

Vegetation characteristics that were recorded and measures that were derived are listed in table 3¹. The selected characteristics are standard variables used in vegetation sampling which could be expected to be sensitive to disturbance. A number of abundance measures (density, frequency, cover, and basal area) were used in order to investigate differential impact effects on these characteristics. Derived variables are defined in appendix I. The structural layers and height classes used for the recording of vegetation characteristics (table 4) were derived partly from conventional classifications and partly from field application.

Selected environmental site characteristics were recorded to supplement vegetation data. Among variables recorded were: light intensity, slope, microrelief, rock outcrop occurrence, soil characteristics, edge orientation, edge maintenance form, and width of ski trail corridor.

Sampling Methodology

Field work was carried out between June and October of 1984, with most vegetation data collected in the months of July and August².

Sampling units were delineated by taking compass bearings on the edge orientation and by extending unit sides towards the³

¹ Sampling was limited to vascular plants.

² Some ephemeral spring herb species may have recessed by the time of sampling and accordingly have escaped detection.

³ Adjusted for magnetic declination.

Table 3

RECORDED VEGETATION CHARACTERISTICS AND DERIVED MEASURES

Strata	Recorded Variables	Derived Measures
PRIMARY CHARACTERISTICS		
Ground Shrub Tree	Stem count/species	Density Relative density Frequency Diversity (species richness)
Ground Lower shrub	Cover class/species/stratum	% cover Relative cover
Upper shrub Tree	Areal cover/species/stratum	% cover Relative cover
Tree	cbh	dbh Mean diameter Basal area
SECONDARY CHARACTERISTICS		
Tree	Orientation of longest branches	
Tree	Inclination of stem	
Tree	Height of lowest branch; number of branches below breast height	
Tree Shrub	Dead branches, stems, stumps	

cbh -- circumference at breast height (1.3 m)

dbh -- diameter at breast height

Table 4

VEGETATION HEIGHT CLASSES

Vegetation Stratum	Stratum/Class Definition
Tree	>5 m height >2.5 cm dbh
T1	>20 m
T2	10-20 m
T3	<10 m
Shrub	>0.5 m height <2.5 cm dbh
S1	2-5 m
S2	0.5-2 m
Ground	<0.5 m height
G1	<0.5 m

forest interior, perpendicular to the edge orientation. Plots and their subdivisions were outlined with plastic tent pegs and polypropylene cord, using a 30-metre steel tape measure. Height measurements for the ground and lower shrub layers were approximated by the author's knee height and reach, respectively. The upper shrub layer and tree layer heights were visually estimated but checked, when estimates proved difficult, with the aid of a relascope.

Stem counts per species were carried out in the one-metre-wide subplots (1x10 m for trees and shrubs; 1x1 m for the ground-layer). Two one-metre wooden pole segments were used in areas of dense shrub vegetation to delimit manageable sections for counting.

Cover¹ was estimated for the ground- and lower shrub layers in five cover classes (table 5) derived from the Braun-Blanquet (1932) cover-abundance scale. For the tree- and upper shrub layers, percentage cover values were obtained by the conversion² of aerial cover estimates. For all layers, estimates were made for individual species in each stratum, and for each stratum as a whole disregarding species and overlap. Plants providing cover in a plot were included in an estimate regardless of their stem location.

Circumference at breast height (cbh) was measured for all trees (>8 cm cbh / >2.5 cm dbh) to the nearest half centimetre

¹ The proportion of ground occupied by a perpendicular projection of the aerial parts of individuals of a species (Goldsmith and Harrison, 1976).

² See appendix I for explanation of the two sampling approaches.

Table 5

VEGETATION COVER CLASSES

Cover Class	% Cover	Class Mid-Point
0	<1	--
1	1-5	2.5
2	5-25	15.0
3	25-50	37.5
4	50-75	62.5
5	75-100	87.5

with a cloth tape-measure at a height of 1.3 metres above the ground.

Light intensity readings were taken on two cloudless days¹ in early September² within one hour of noon Eastern Standard Time. Measurements were obtained with a Gossen-Erlanger Sixtomat exposure-meter held horizontally, oriented toward the edge, at 1.3 metres above the ground. Readings were taken along three transects extending from edge to interior and aligned with the sides and centre line of each unit. Values were recorded in the open corridor and at the centre of each (5x10 m) plot along each transect. In each instance, light intensity and time were recorded. Values were subsequently converted to percentages of corridor illumination.

Although recording procedures were standardized and multiple recordings taken within each plot, a number of factors could affect the reliability of the light intensity data. Firstly, the exposure-meter scale was graduated in units of increasing magnitude rather than absolute values. When converted to absolute values, therefore, reliability decreases with increasing light intensity, since the variation in the order of one magnitude is much more significant at the upper end of the

¹ Recordings in July would have been representative of optimal conditions in the growing season, and would therefore have been preferable. With limited resources available, however, first priority was assigned to vegetation sampling. It is, moreover, doubtful that a significant difference in results would have been obtained, particularly in terms of relative values.

² Since standard time deviates from local time (i.e. time at the local meridian) by only +4 minutes (Thompson 1970), adjustment for local time appeared unwarranted.

scale. Secondly, light intensity can vary considerably within one plot depending on local canopy cover and sidelighting. In addition, although recordings were taken on relatively windless days, some movement of crown foliage resulted in variability in the amount of light reaching the meter. The extremely limited recording period should also be borne in mind.

Microrelief for each plot was described by degree of irregularity according to a four-level classification that graduated from smooth to very irregular. The occurrence of rock outcrops and boulders was also recorded.

Slope measurements were recorded in degrees of slope with a Brunton transit at the sides and centre of each unit and its constituent 5x10 metre plots, along interior boundaries.

Soils were sampled in both trail and control sections at three sites representative of lower-, mid-, and upper-slope conditions (fig. 3). Rocky areas with shallow soils were avoided in site selection. Pits were dug to a depth of 0.5m, and profile characteristics were noted. Variables recorded were: horizon depth and boundary type; colour, texture, structure, and consistence of each horizon; drainage and stoniness of site. Munsell (1954) Soil Colour Charts were used for colour determinations in the field. Samples of each horizon were taken for laboratory verification of field observations.

DATA ANALYSIS

Approach

Preliminary analysis of the data involved the calculation of mean values and standard deviations for sample replicates, the derivation of basic indices, and the comparison of samples in terms of distance effects by statistical tabulation and graphic display. All primary vegetation characteristics (table 3), and all structural layers were reviewed individually in this phase of the analysis. Data summarization was subsequently obtained by computer-assisted multivariate analyses which involved the calculation of similarity/distance measures and the ordination of sample data. Graphic displays of the reduced data were then examined for distance effects. Density and frequency data were used in this part of the analysis¹ which focused on the shrub and ground layers that were shown by the preliminary review to be most affected by the presence of the open corridor with respect to the variables measured. A diameter-size-class ordination of density data for the tree layers was also carried out and was examined for distance effects and possible successional trends.

Data Aggregation

The two shrub layers were aggregated for the multivariate analysis, but a separate analysis was performed on the ground layer. The shrub layers were combined to facilitate data handling. The combination of these layers was justified on the

¹ Cover values, as estimates, were considered less reliable for quantitative analysis.

0

basis of a similar response to trail impact of the tree species component that was identified in the preliminary review. It should be borne in mind, however, that shrub species were mainly confined to the lower shrub layer. The shrub and ground layers were analyzed separately because: (1) sample plot size was not the same¹; (2) the two layers were characterized by different species; and (3) survival ratios of tree species seedlings are not the same for the two layers². For a subsequent multivariate analysis, species density data for the tree layers were divided into diameter size-classes (table 6).

In addition to aggregation by structural layer and diameter size-class, different levels of data aggregation in terms of plot size were experimented with during the analysis. Two levels were used in the final analysis: (1) 5-metre distance intervals (5x10m tree/shrub plots; 5x1 m ground plots) for the univariate analysis involving all structural layers and for the diameter-size-class ordination of tree data, and (2) 3-metre intervals (3x10 m tree/shrub plots; 3x1 m ground plots) for the remainder of the multivariate analysis³.

Derived Variables

Derived variables (table 3) are defined in Appendix 1. Mean values were obtained by the averaging of replicate values.

¹ Frequency, one of the variables used, is dependent on sample size.

² Tree seedling mortality is much higher in the groundlayer (Forcier 1975).

³ Although the sample design would have permitted a finer breakdown, a minimum of 9 subplots (3x3 replicates) was considered necessary for the derivation of reliable frequency values.

The standard deviation values used to represent variability are the best estimate of the standard deviation ($\hat{\sigma}$)¹.

Multivariate Analysis

A reduction in the dimensionality of the density and frequency data for the shrub and ground layers was obtained by:

- 1) The transformation of species-by-sample matrices, where applicable, by the calculation of resemblance/distance measures, and
- 2) The ordination of species and/or samples using the original or derived resemblance value matrices.²

Characteristics of the resemblance (Gower coefficient) and distance (information analysis) measures used are outlined in Appendix II.

Since the structural and compositional variation of vegetation was being investigated along a distance gradient, an ordination approach to summarizing samples and species relationships appeared appropriate. Two ordination techniques were used in the analysis in an attempt to clarify relationships among variables and to substantiate apparent trends in the data: correspondence analysis and principal component analysis.³ Correspondence analysis (Hill 1973, 1974; Legendre and Legendre 1983) was used to ordinate samples and species using frequency and density data for the shrub and ground layers at the

¹The correction factor $\sqrt{n/n-1}$ is applied to the sample standard deviation because of the small sample size (Gregory 1978).

²The ordering of a set of data points with respect to one or more axes (Pielou 1984).

³See appendix II for description of techniques.

3-metre interval level of subplot aggregation. Principal component analysis was used to ordinate samples using sample similarity matrices based on the Gower coefficient and derived from density data for the shrub and ground layers. As for the correspondence analysis, a 3-metre interval level of subplot aggregation was used. In an attempt to establish successional trends, principal component analysis was also used for a diameter-size-class ordination of tree species density data using a 5-metre level of subplot aggregation. For this analysis, species density data for each size-class in each plot was considered as a separate entity. The size-classes are listed in table 6.

Graphic displays of the ordination results were examined for distance effects. In addition, graphs of similarity/information distance between trail edge and other plots were constructed.

Table 6

DIAMETER SIZE-CLASSES

Class	dbh (cm)	Number of Stems/Structural Layer			
		T1	T2	T3	Total
1	20.0+	35	6	--	41
2	10.0-20.0	1	31	3	35
3	5.0-10.0	--	19	47	66
4	2.5-5.0	--	--	132	132

RESULTS

ENVIRONMENTAL CHARACTERISTICS

Environmental variables considered in the initial selection of sample sites were elevation, topographic position, slope inclination, slope aspect, edge orientation, edge maintenance form, and width of trail (fig. 3; table 2). Measurements of these and additional variables were made to ensure that site characteristics did not vary significantly between trail and control sections. With the exception of light intensity, the results of these measurements confirmed that such was indeed the case. As would be expected, light intensity was higher in the trail section.

Light Intensity

Results of the light intensity measurements, expressed as a percentage of open corridor illumination, are shown in figure 5. Data reliability considerations are discussed in the methods section (pp. 24-25). It is immediately apparent from the diagram that light intensity was significantly higher in the trail section, particularly from 0-15 metres of the trail edge, and that although the differential between the two sections decreased toward the interior, it still existed at 30 metres. The

variability of light intensity values was also higher in the trail section. The mean trendlines for the two sections are noticeably different. Whereas control section values increased toward the interior/upslope, trail section values decreased abruptly between the edge and adjacent plots, increased, and then decreased again with a final upturn from 25-30 metres consistent with the control trend.

Slope

Slope ranged from strong to very strong (CANSIS 1983) throughout the study area with the exception of the level to very gentle slope on the upper part of unit 3 in the trail section. Although mean slope differences were not substantial, some variation existed in the pattern of steepest slope. Slope variability was generally higher in the trail section, particularly from 15-30 metres where very low slope values occurred in Unit 3. The average slope of the ski trail adjacent to the study area was 9° . Slope profiles are shown in figure 6 together with mean slope and standard deviation values. Average unit values recorded at the top of each section are given in table 2.

Microrelief

Microrelief within the study area generally varied from slightly irregular to irregular. Mean plot designations were as follows:

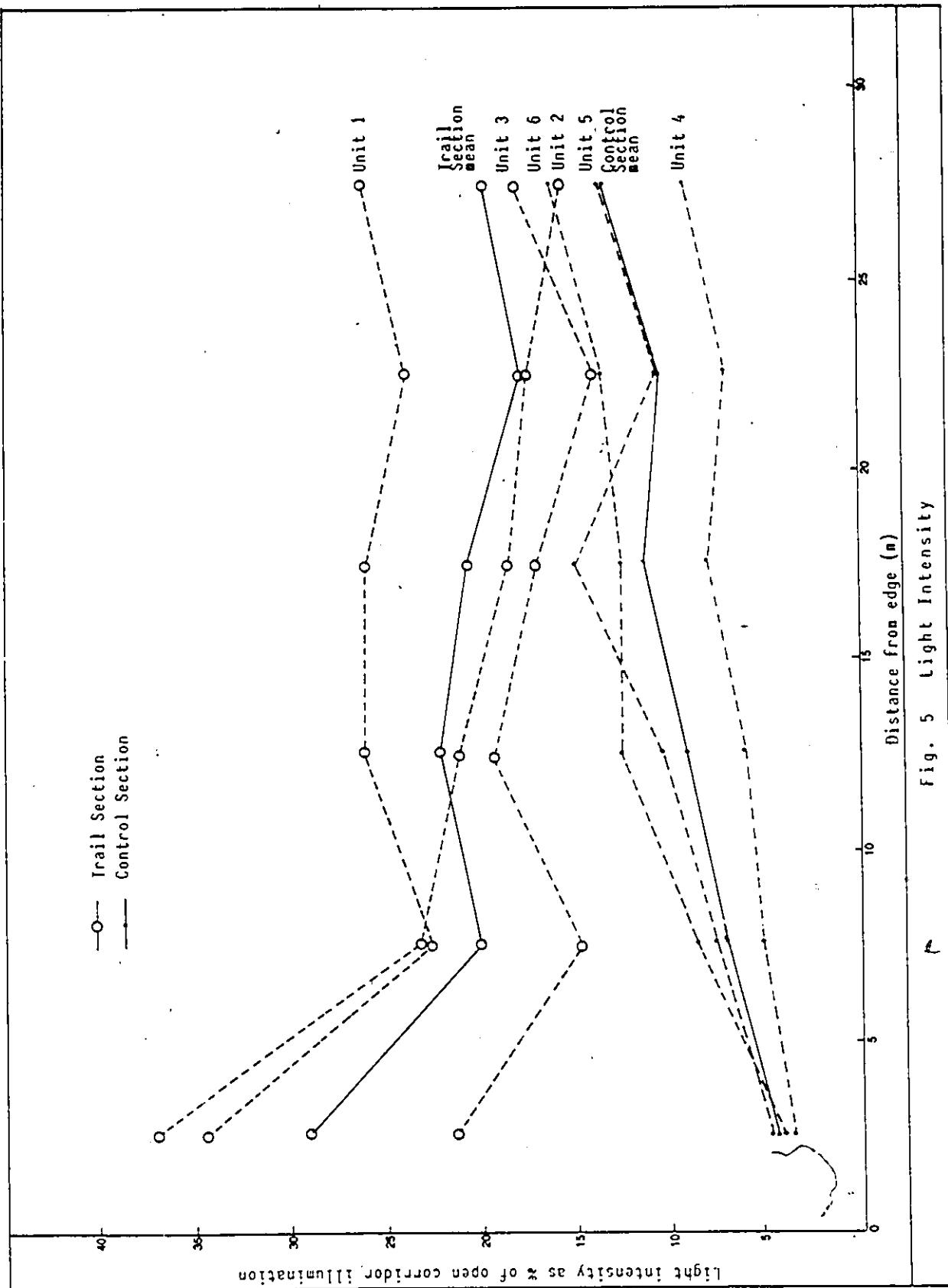


Fig. 5 Light Intensity

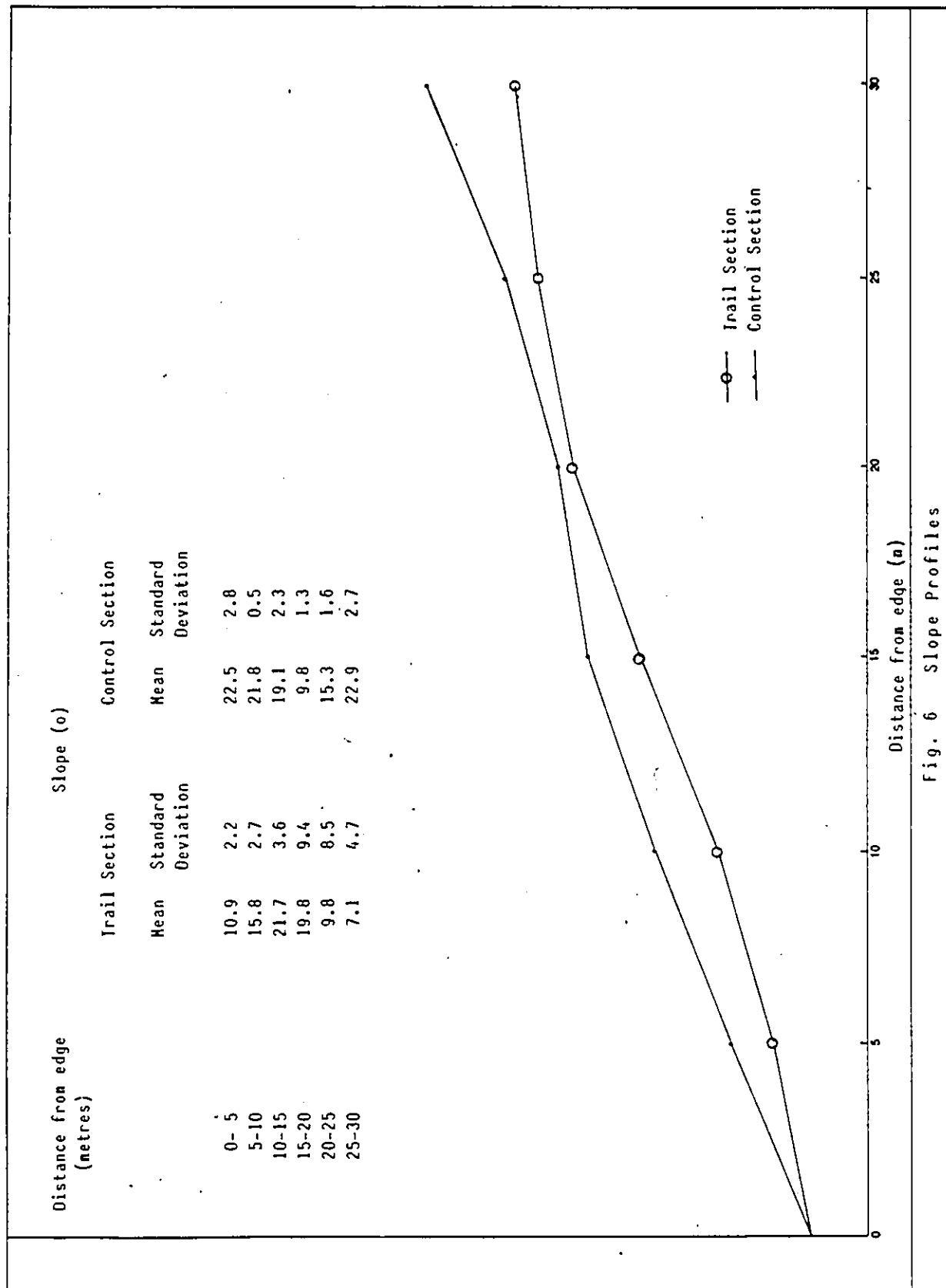


Fig. 6 Slope Profiles

Microrelief

Trail Section Control Section

Distance from Edge (metres)

Slightly irregular	10-15	0-10
	20-30	15-25
Irregular	0-10	10-15
	--	25-30
Very irregular	15-20	--

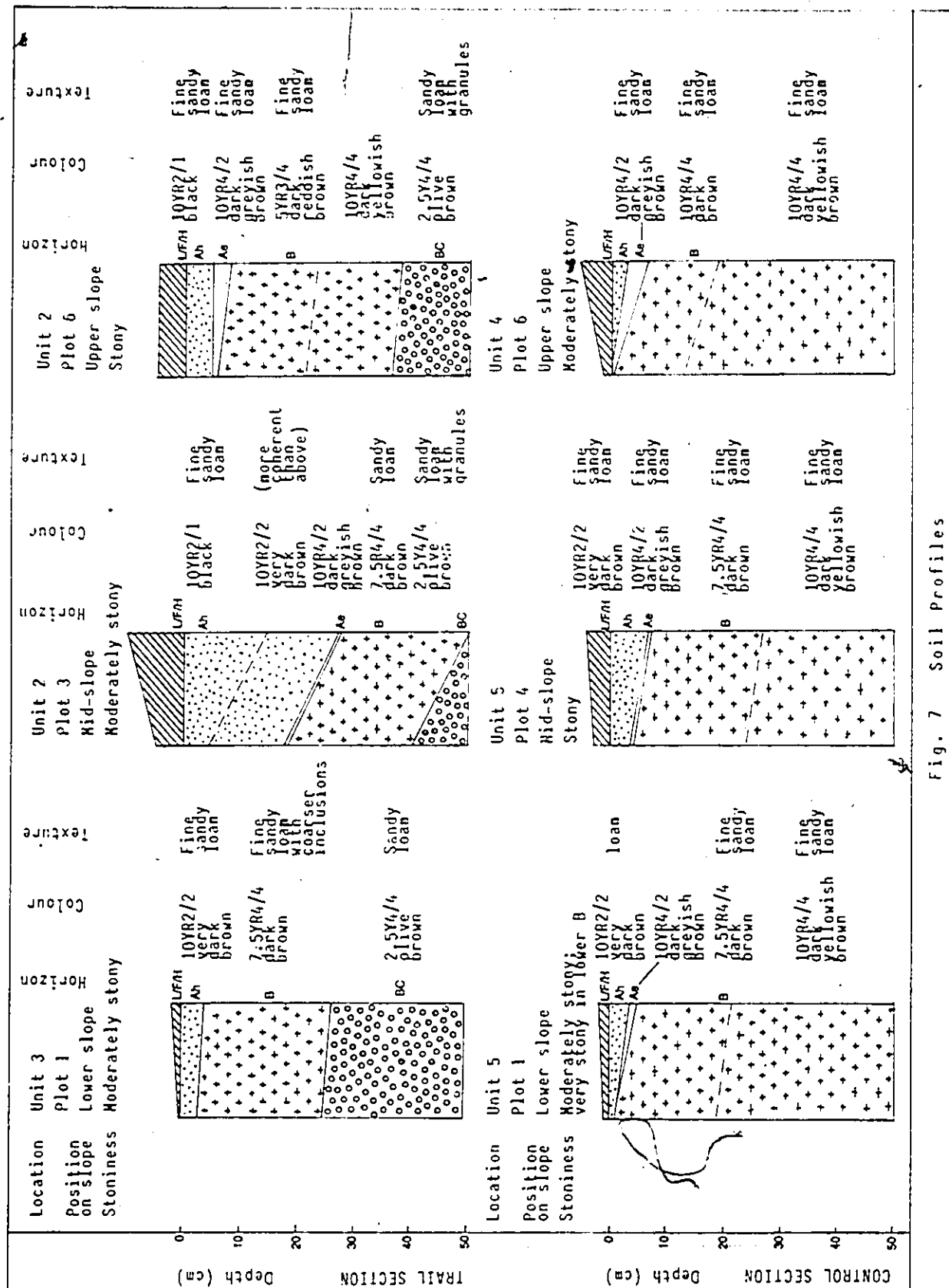
Rock Outcrops and Boulders

Rock outcrops occurred in the study area from mid-to-upper slope (trail section 10-25 metres; control section 10-15, 25-20 metres). Boulders, common throughout the area, were absent only in the trail section plots from 10 to 25 metres.

Soils

Soil profiles for the six sample sites, to a depth of 0.5 metre, are illustrated in figure 7. The location of sample sites (lower-, mid-, and upper slope in both trail and control sections) is shown in figure 2. Profile characteristics suggest that, according to the Canadian System of Soil Classification (Canada Soil Survey Committee 1978), the soils belong to the Orthic Humo-Ferric Podzol subgroup of the Podzolic order¹. Soils in both sections generally exhibited the same sequence of horizons. Typically, profiles consisted of: a layer of forest litter (L/F/H: 0-5 cm); an A horizon enriched with organic matter (Ah: 3-5 cm); a leached A horizon (Ae: 0-4cm); a dark brown B horizon (18-45 cm) that was sometimes differentiated in colour by

¹Chemical determinations would be required to confirm this classification. If the chemical properties do not meet the requirements of a podzolic B horizon, the soils might be classified as Eluviated Melanic Brunisols.



0 a change in hue from reddish- to yellowish brown toward the bottom; and a BC horizon of olive brown sandy loam that is shown only on the trail section profile diagrams, but was also sampled in the control section, with a soil auger, at greater depth.

Because of the undulating nature of the terrain and the variation in slope and rock outcrop, soil depth varied considerably within the study area. Stoniness in soils generally varied from moderately stony to stony, the latter being characteristic of the sites within plots of least slope. Stones were subangular and of variable size at all sites. Soil drainage was good at all sites and the soil moisture regime was fresh (Jones et al. 1983). Roots formed a dense mat in the organic A horizon of all profiles, and generally extended to the bottom of the B horizon.

The only notable difference between soil profiles in both sections was in B-horizon depth, which was greater in the control section. It is not possible to identify definitive trends related to position on the slope from the few sites sampled. The alluvial A horizon did, however, appear to be best developed in the upper slope profiles, and the organically-enriched A horizons best developed at mid slope. The latter may be a function of microrelief.

VEGETATION CHARACTERISTICS

Vegetation results are presented by structural layer. Principal findings relevant to trail impact are summarized in Table 7. Impact effects are also evident from the composite models of the six trail section and control section plots that appear in the form of structural diagrams in figure 8. A complete list of species, organized according to distributional pattern, and indicating the limit of distribution for edge species, is given in appendix IV.

For each structural layer, characteristics of species richness, density, cover, and composition are derived from the univariate analyses. Results of the multivariate analyses are then presented.

Of the multivariate analysis techniques used, correspondence analysis was the most useful in identifying the distance, magnitude, and abruptness of impact effects. Results are displayed in the form of scatter diagrams and transect profiles of axes. Principal component analysis was less helpful in demonstrating the edge effect; as a consequence, results for this technique are only presented for the groundlayer and for the more successful size-class analysis of trees. Sample

Table 7

SUMMARY OF PRINCIPAL FINDINGS RELEVANT TO TRAIL IMPACT

Variable	Structural Layer	G1						S2						S1					
		0-5	5-10	10-15	15-20	20-25	25-30	0-5	5-10	10-15	15-20	20-25	25-30	0-5	5-10	10-15	15-20	20-25	25-30
Impact Distance**																			
Species Density		x						x	x					x	x				
Species Frequency		x	x					x	x					x	x				
Gradient Discontinuity		x								(x)									
Species Abundance/Size																			
Density		+	-					+	+	(+)	(-)			+	+				
Variability								(+)	+	+				+	+				
Cover		+	(-)					+	+	(+)	(-)			+	+				
Variability								(+)	+	+				+	(+)				
Mean Tree Diameter														+	(+)				
Variability																			
Species Richness		+	-					+	+	(+)				+	(+)				
Variability								+	+					+	(+)				
Species Composition																			
Species Importance@																			
Edge		+						+	+					+	+				
Herb		+						+											
Shrub		+						+	+					+					
Tree		-						+	+					+	+				
Sugar Maple*		-	(+)	+	+			-	+	+		-	-	-	+	+			
Beech*		-	(-)	+	+	+		-	-	-	-	-	-	-	+	-			
Species Dominance																			
Sugar Maple		o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	x	o	x
Beech																			

Legend

- +/- Highest/lowest values within study area
- (+)/(-) High/low values but within control range or exceeded beyond 15 metres of trail edge
- x Effect noted
- o Effect noted but same as control
- (x) Effect suggested

Notes

** Ordination results

@ Density

+/- Deviation from theoretical density greater than 2

(+)/(-) Deviation from theoretical density greater than 2 but not greater/less than control values

Table 7, Contd.

SUMMARY OF PRINCIPAL FINDINGS RELEVANT TO TRAIL IMPACT

Variable	Structural Layer	T3						T2						T1					
	Distance from Trail Edge (metres)	0-5	5-10	10-15	15-20	20-25	25-30	0-5	5-10	10-15	15-20	20-25	25-30	0-5	5-10	10-15	15-20	20-25	25-30
Impact Distance**																			
Species Density		x	(x)	(x)															
Species Frequency																			
Gradient Discontinuity																			
Species Abundance/Size																			
Density		+																	
Variability		+																	
Cover		(-)*	*	*	*														
Variability		+																	
Mean Tree Diameter		-*						(+)											
Variability								+											
Basal Area										(+)									
Variability		+								(+)									
Species Richness		+	(-)																
Variability		+																	
Species Composition																			
Species Importance																			
Edge		+																	
Herb																			
Shrub																			
Tree		(+)																	
Sugar Maple		-	+	+		-	-	-	+	+	+	+	(-)	-	-	-	-	-	-
Beech		-	-	-		+	+		-	-	-	-		+	+	+	+	+	+
Species Dominance																			
Sugar Maple		x	x	x						x	x								
Beech					o	o	o	o	o				o	x	x	o	o	o	o
Structural Adaptation																			
Stem Inclination to Edge		x												x	x	(x)	(x)		
Branch Orientation to Edge		x						x	(x)					x	x	(x)			

Legend

Notes

+/- Highest/lowest values within study area

** Ordination results

(+)/(-) High/low values but within control range or exceeded beyond 15 metres of trail edge

* Sugar Maple +

x Effect noted

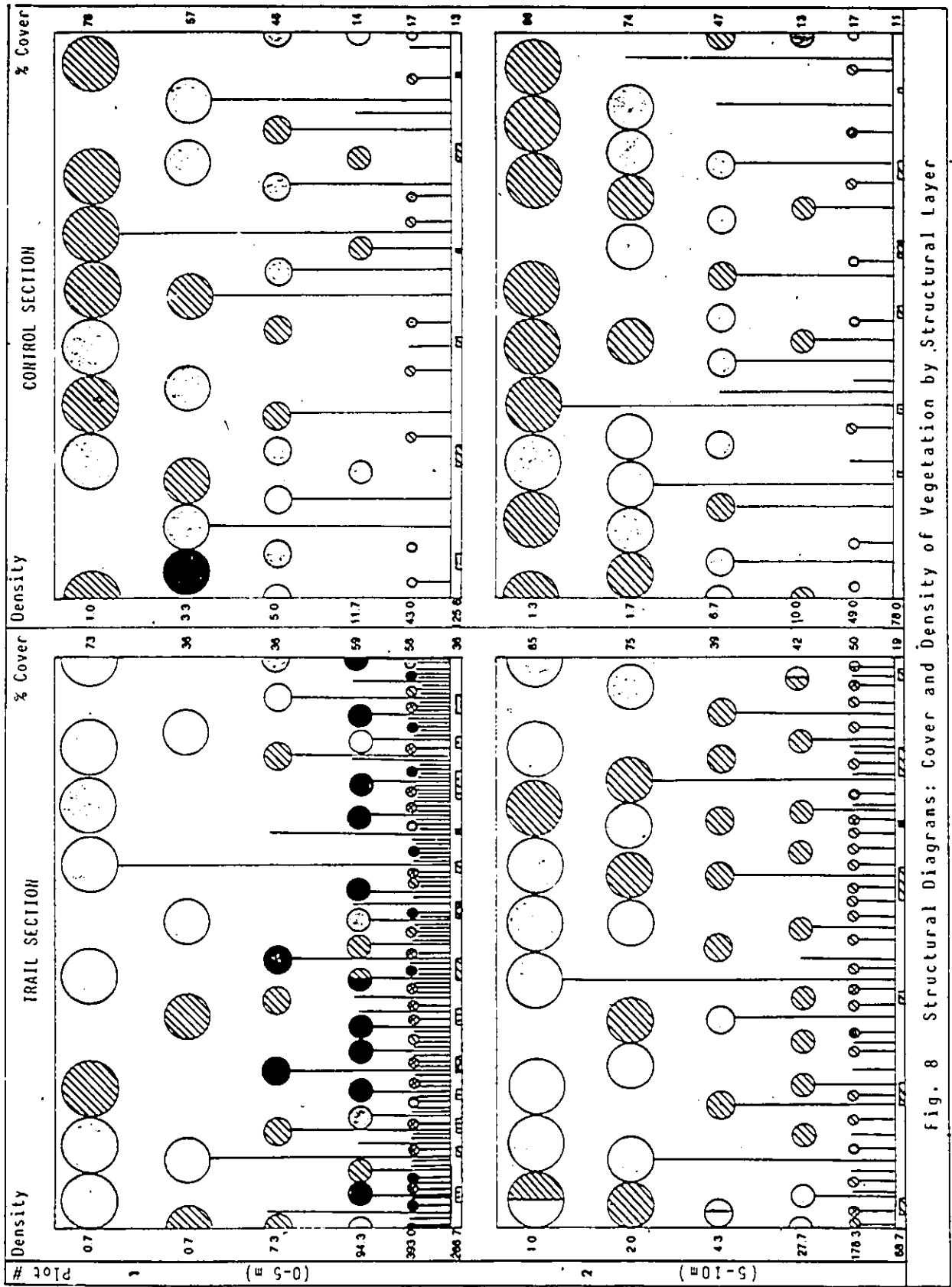
o Density

o Effect noted but same as control

+/- Deviation from theoretical density greater than 2

(x) Effect suggested

(+)/(-) Deviation from theoretical density greater than 2 but not greater/less than control values



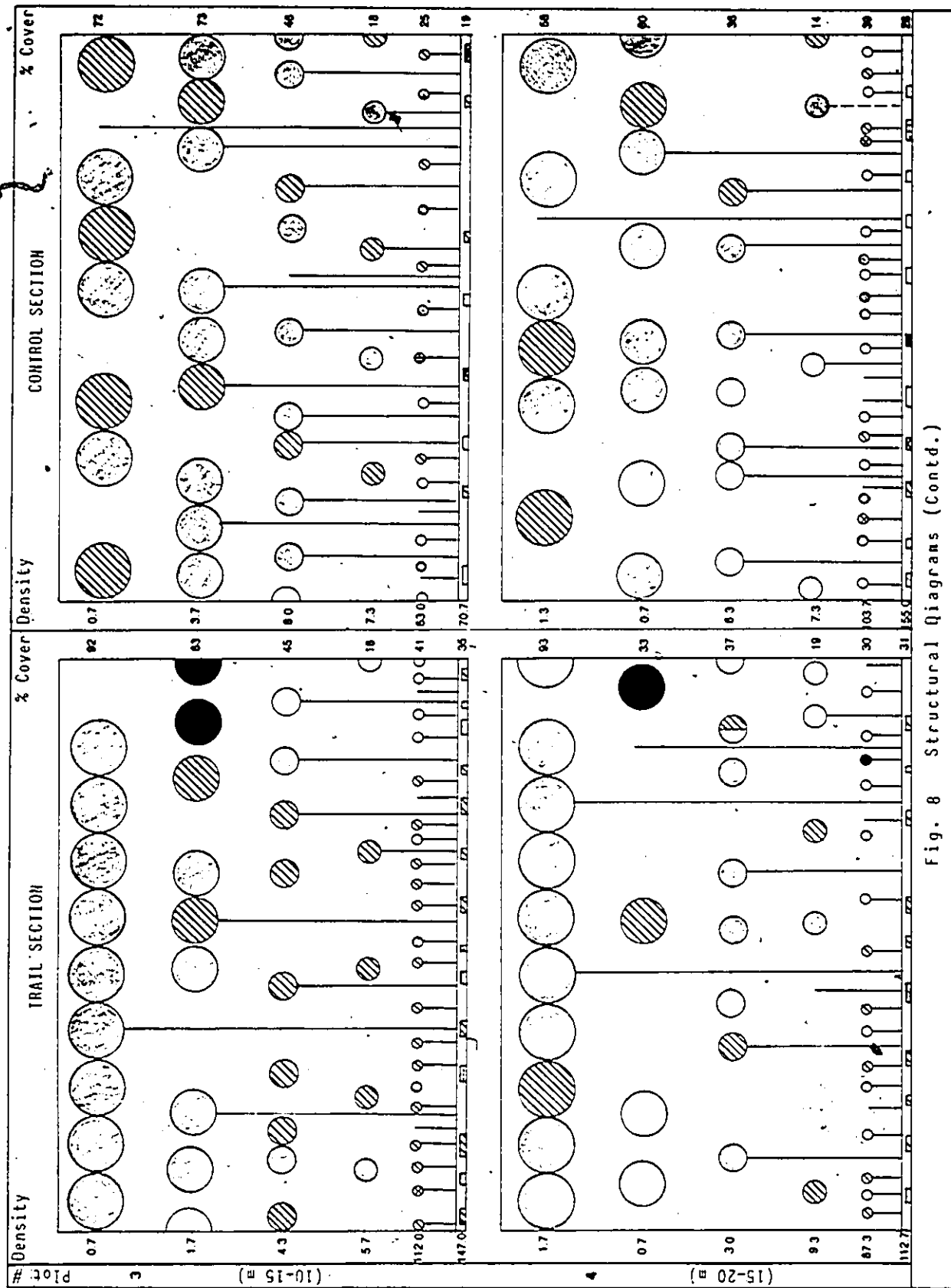


Fig. 8 Structural Diagrams (Contd.)

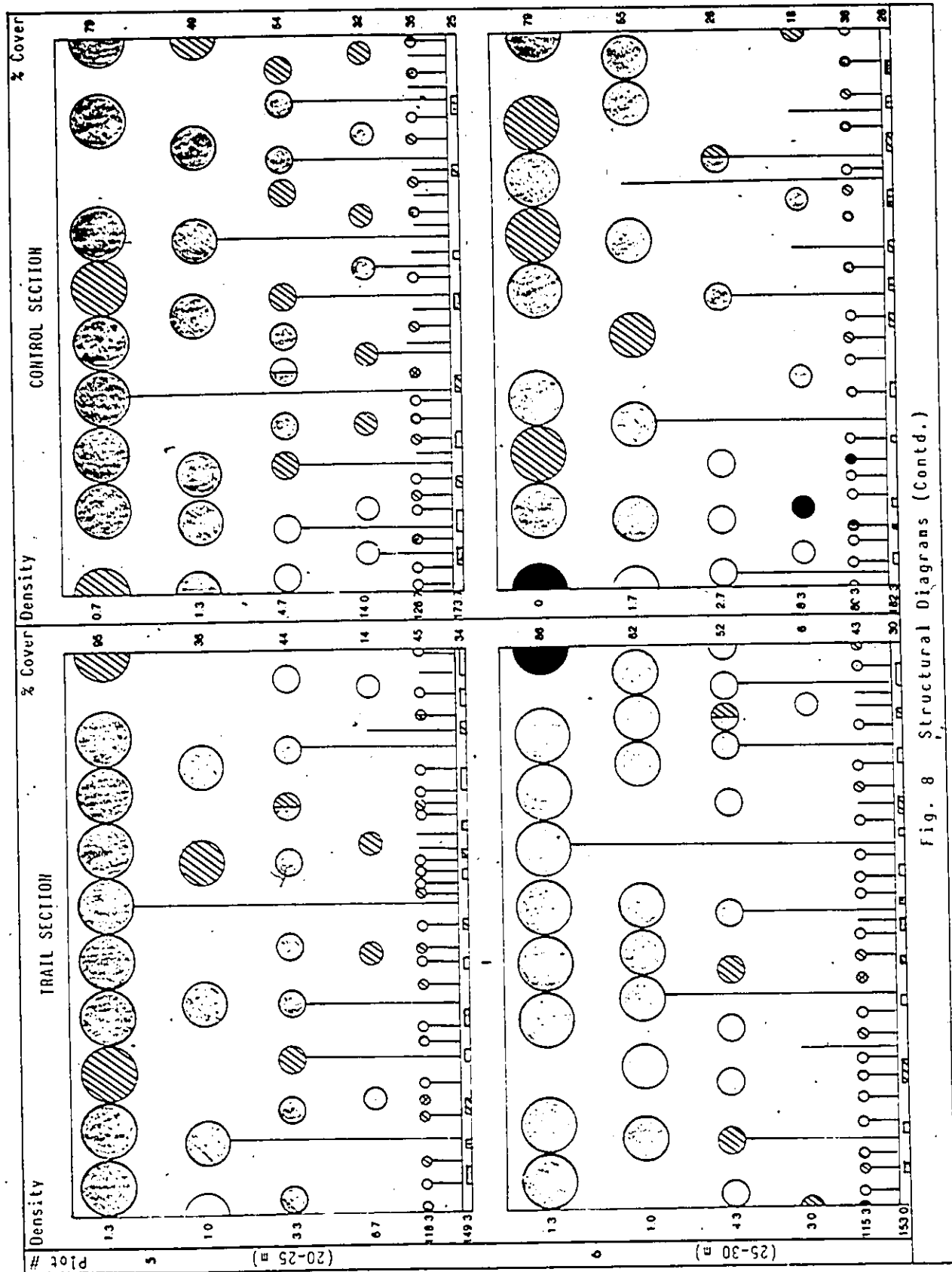
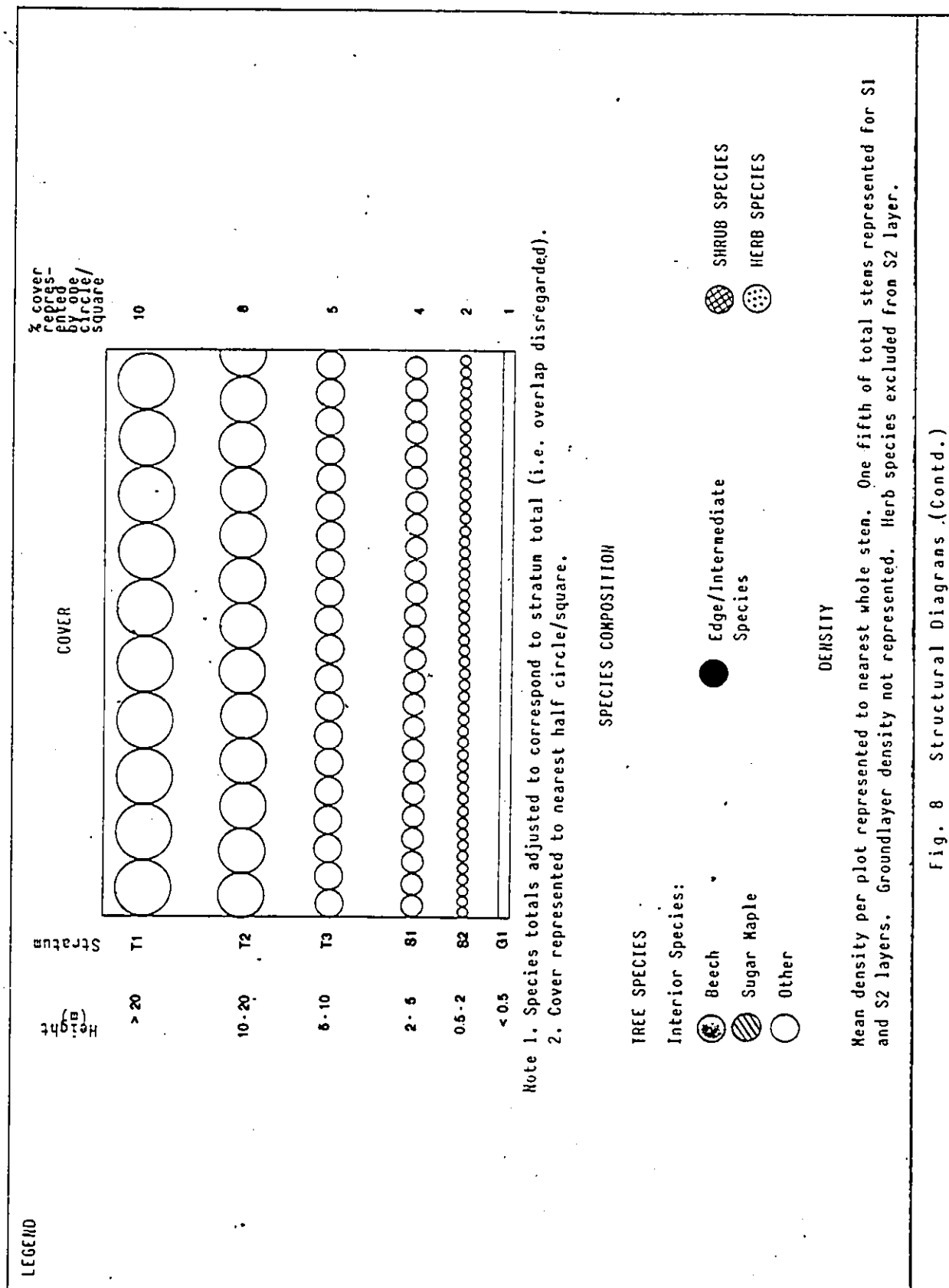


Fig. 8 Structural Diagrams (Contd.)



distance/similarity values based on information analysis and on the Gower coefficient, for species frequency and density respectively, provided additional insight into impact effects. Results are displayed in the form of graphs of similarity/information distance between trail edge and other plots. Numerical results for all multivariate analyses appear in Appendix III.

Groundlayer (<0.5 metres)

General Characteristics

Highest values for species richness, density and cover occurred in the trail edge plots (0-5 metres). For all three variables, trail values more than doubled those of their control counterparts and more than tripled the lowest overall values (table 8; figs. 9-11). These high values were largely due to an increase in the relative importance of herb species, and to a lesser extent, shrub species; tree species abundance was depressed in these plots.

In contrast to the edge plots, lowest values for species richness, density and cover¹ occurred in the adjacent trail plots (5-10 metres)... Tree species abundance remained depressed in these plots. Trail section values stabilized from 10-30 metres at levels within the control section range, although trail section cover values were slightly higher than control values throughout. Within the control area, highest values for species richness, density, and cover occurred in the most interior/ upslope plots.

¹ Cover values were lowest in the trail section but within the range of variation of control samples.

Table 8

SPECIES RICHNESS, DENSITY, COVER, AND BASAL AREA BY STRUCTURAL LAYER AND DISTANCE FROM EDGE

Stratum	Variable	Distance from Edge (metres)												
		0-5		5-10		10-15		15-20		20-25		25-30		
		Trail	Control	Trail	Control	Trail	Control	Trail	Control	Trail	Control	Trail	Control	
G1	Species Richness	M	15.0	6.3	4.3	6.3	8.3	7.0	7.7	8.3	7.0	9.7	8.3	12.0
		S	2.6	0.8	1.6	1.3	2.6	1.0	1.4	1.7	2.0	0.9	4.1	5.3
	Density	M	266.7	125.6	68.7	78.0	147.0	70.7	112.7	155.0	149.3	173.7	153.0	182.3
		S	74.8	76.5	45.9	16.6	41.9	21.4	13.1	62.4	114.2	94.0	173.0	61.2
	Cover	M	36.0	13.4	19.2	10.7	35.3	19.0	30.5	28.0	34.3	25.2	30.3	26.0
		S	8.7	9.4	11.8	6.3	2.3	4.6	2.0	2.8	22.3	6.7	11.9	5.3
S2	Species Richness	M	20.0	3.3	8.3	3.7	7.0	5.0	6.7	7.0	6.3	8.0	5.3	7.3
		S	3.0	1.2	4.6	1.1	1.0	1.0	2.4	2.0	2.2	1.7	1.6	2.2
	Density	M	430.7	43.0	181.3	49.0	112.7	63.0	89.0	103.7	119.3	128.7	116.0	182.0
		S	52.2	17.8	66.4	28.6	34.4	19.7	8.7	21.6	53.6	31.4	13.9	14.8
	% Cover	M	58.3	17.0	49.7	17.3	40.7	25.0	30.3	38.7	45.0	35.0	42.5	37.7
		S	7.6	6.9	16.4	4.2	12.0	5.3	5.3	5.5	8.9	3.5	8.5	8.4
S1	Species Richness	M	8.3	2.3	3.3	2.0	2.0	2.0	2.7	3.0	2.0	3.3	1.7	3.3
		S	1.7	0.7	1.2	1.0	1.0	1.0	0.4	1.0	1.0	0.7	1.5	0.7
	Density	M	94.3	11.7	27.7	10.0	5.7	7.3	9.3	7.3	6.7	14.0	3.0	8.3
		S	87.2	6.3	14.1	10.1	4.0	3.1	3.6	2.6	7.2	7.0	4.4	6.1
	% Cover	M	59.3	14.0	42.0	12.7	17.7	18.0	19.3	14.3	13.7	32.0	6.3	18.3
		S	23.9	5.2	11.1	12.9	8.5	4.0	5.9	3.5	9.8	5.6	5.9	7.2

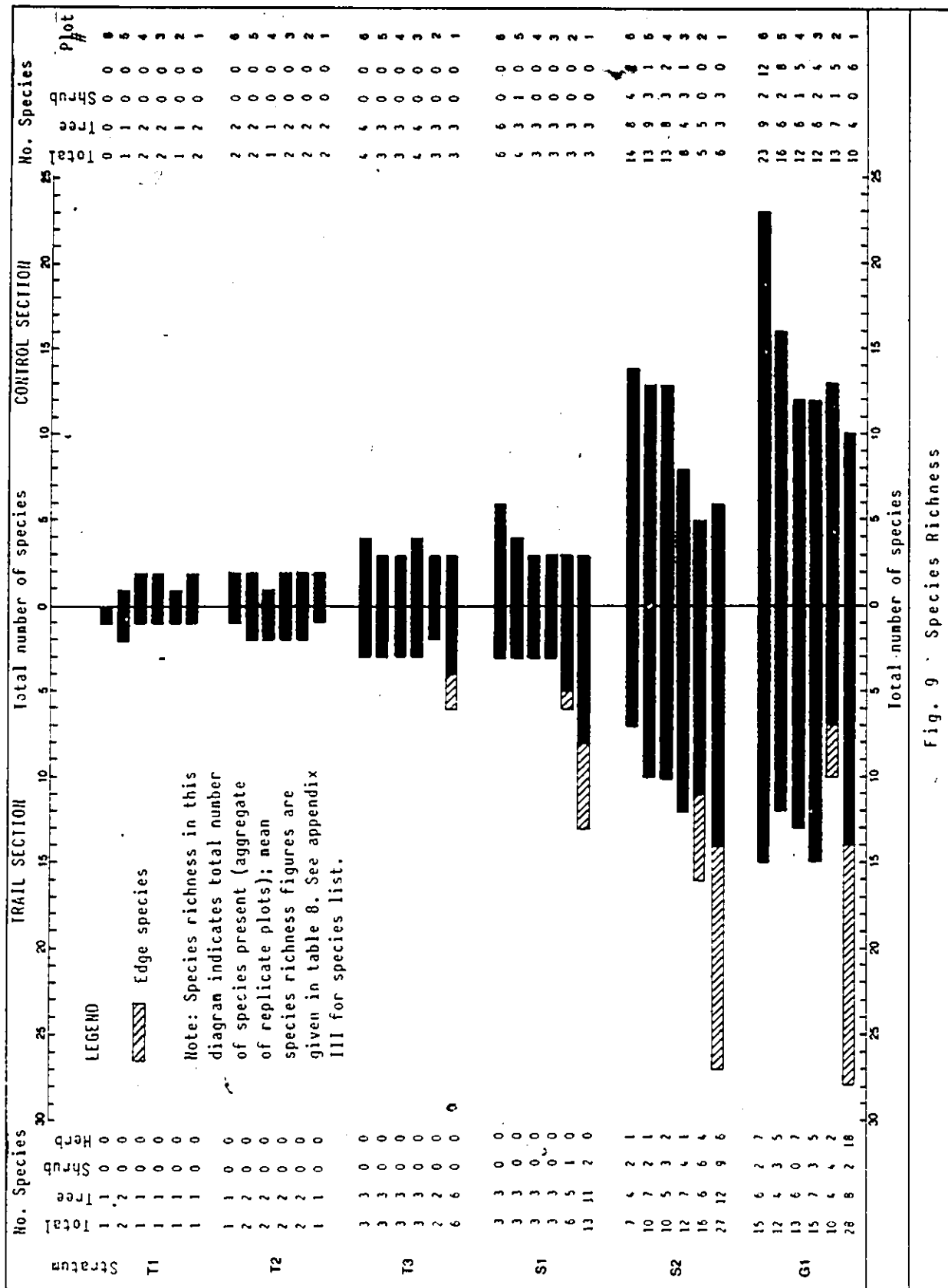
M--Mean M--Mean S--Standard Deviation

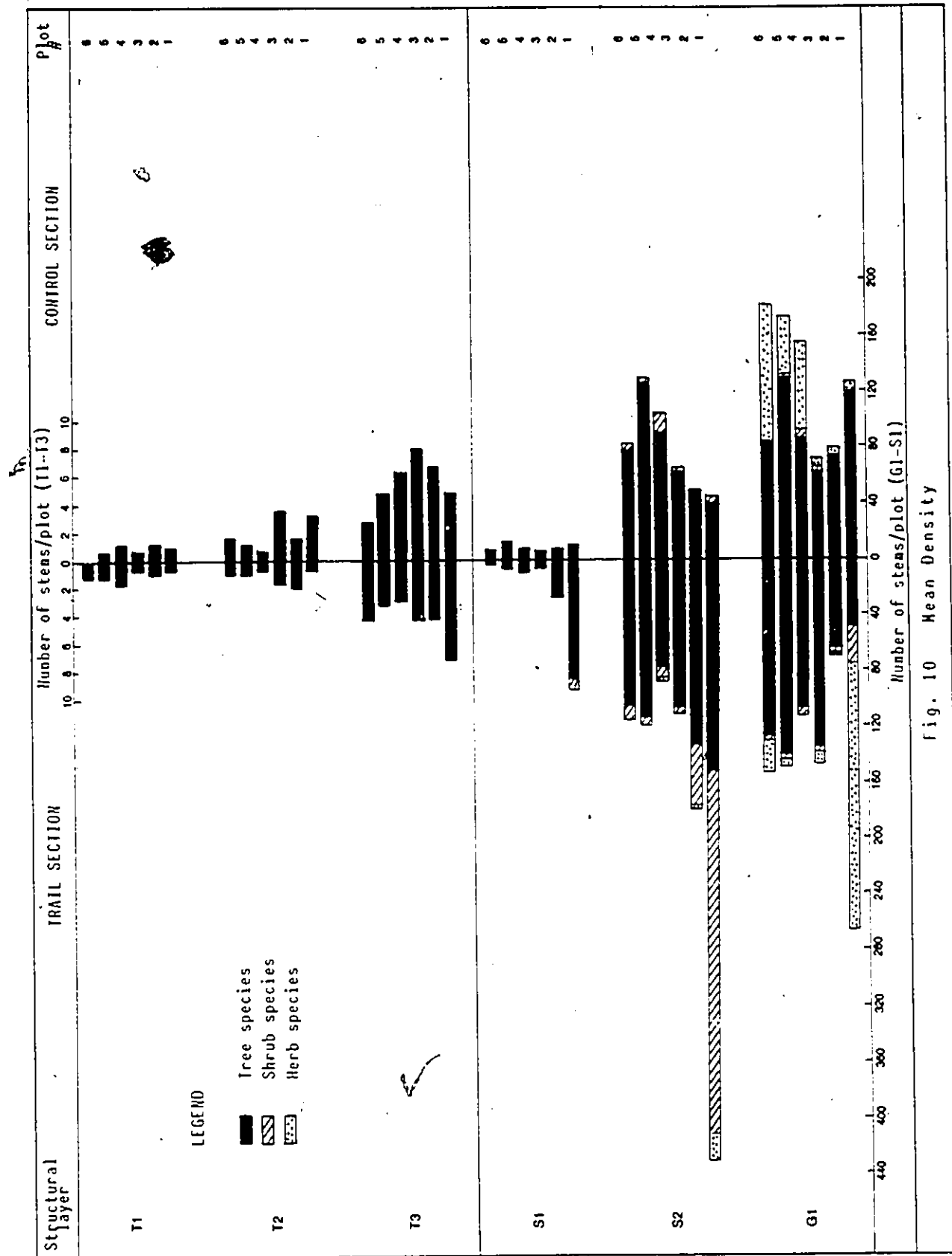
Table 8, Contd.

SPECIES RICHNESS, DENSITY, COVER, AND BASAL AREA BY STRUCTURAL LAYER AND DISTANCE FROM EDGE

Stratum	Variable		Distance from Edge (metres)											
			0-5		5-10		10-15		15-20		20-25		25-30	
			Trail	Control	Trail	Control	Trail	Control	Trail	Control	Trail	Control	Trail	Control
T3	Species Richness	M	3.3	1.7	1.7	2.3	2.0	2.3	1.3	2.3	1.7	1.7	2.3	1.7
		S	1.5	0.5	0.6	0.7	0.0	0.7	0.6	0.7	0.5	0.5	1.4	0.5
	Density	M	7.3	5.0	4.3	6.7	4.3	8.0	3.0	6.3	3.3	4.7	4.3	2.7
		S	5.0	2.6	1.2	2.2	2.4	2.0	1.0	2.2	1.2	2.0	1.6	0.4
	% Cover	M	36.0	45.7	39.0	47.0	45.3	46.0	37.0	36.3	44.3	53.7	52.0	26.3
		S	31.5	18.0	11.0	27.9	13.6	15.1	4.6	10.7	8.2	10.8	12.8	8.1
	Basal Area (cm ²)	M	75.7	100.9	84.5	86.4	45.7	114.5	91.9	95.7	76.9	78.4	126.4	54.1
		S	134.1	70.2	35.5	44.1	65.2	13.3	91.6	57.6	34.0	56.4	18.0	13.4
	Mean Diameter (cm)	M	3.4	4.9	4.4	3.9	3.6	4.0	5.8	4.0	5.0	4.4	5.6	4.7
		S	0.5	0.6	1.0	0.5	0.3	0.5	1.4	0.7	1.4	0.4	1.4	1.3
T2	Species Richness	M	0.7	1.7	1.0	1.0	1.0	1.7	0.7	0.7	1.0	1.0	1.0	1.0
		S	0.6	0.5	0.0	0.0	1.0	0.5	0.6	0.6	0.0	1.0	0.0	0.0
	Density	M	0.7	3.3	2.0	1.7	1.7	3.7	0.7	0.7	1.0	1.3	1.0	1.7
		S	0.6	1.6	0.0	1.1	1.5	1.1	1.1	0.6	0.0	1.5	0.0	0.5
	% Cover	M	36.3	56.7	75.3	73.7	63.3	73.3	32.7	60.3	36.3	49.0	62.3	54.7
		S	26.8	30.3	11.2	10.8	25.2	21.0	11.0	29.9	17.3	34.5	17.1	17.4
	Basal Area (cm ²)	M	191.7	232.3	386.6	144.4	184.8	696.6	96.9	154.0	110.9	584.7	289.7	292.8
		S	230.6	214.7	376.7	179.8	217.8	293.8	114.1	144.5	46.9	610.4	197.5	257.1
	Mean Diameter (cm)	M	18.3	8.9	15.7	10.1	11.5	14.7	13.1	17.1	11.7	20.3	18.5	14.3
		S	7.9	1.7	0.9	1.7	2.8	4.9	5.4	2.9	2.7	0.4	6.5	5.0
T1	Species Richness	M	0.7	1.0	1.0	0.7	0.7	0.7	1.0	0.7	1.0	0.7	0.7	0.0
		S	0.6	1.4	0.6	0.6	0.1	0.6	0.0	0.6	1.0	0.6	0.6	0.0
	Density	M	0.7	1.0	1.0	1.3	0.7	0.7	1.7	1.3	1.3	0.7	1.3	0.0
		S	0.6	1.4	1.0	1.2	0.6	0.5	0.5	1.2	1.5	0.5	1.2	0.0
	% Cover	M	72.7	76.0	84.7	86.0	92.3	72.0	93.0	58.0	95.3	79.0	86.0	79.0
		S	20.8	16.5	5.8	12.0	7.5	37.3	1.7	31.1	6.8	20.0	22.5	14.7
	Basal Area (cm ²)	M	551.3	681.8	1008.4	1745.6	589.8	366.1	1712.1	1097.1	1715.8	665.8	1109.8	0.0
		S	527.7	849.2	1271.5	1573.6	687.9	318.1	683.5	955.7	2423.4	606.0	978.0	0.0
	Mean Diameter (cm)	M	32.2	28.6	34.3	39.9	32.3	26.5	36.1	30.7	29.9	35.6	32.2	0.0
		S	6.3	0.7	7.2	5.0	12.9	0.9	1.5	2.1	0.9	4.7	2.1	0.0

M--Mean M--Mean S--Standard Deviation





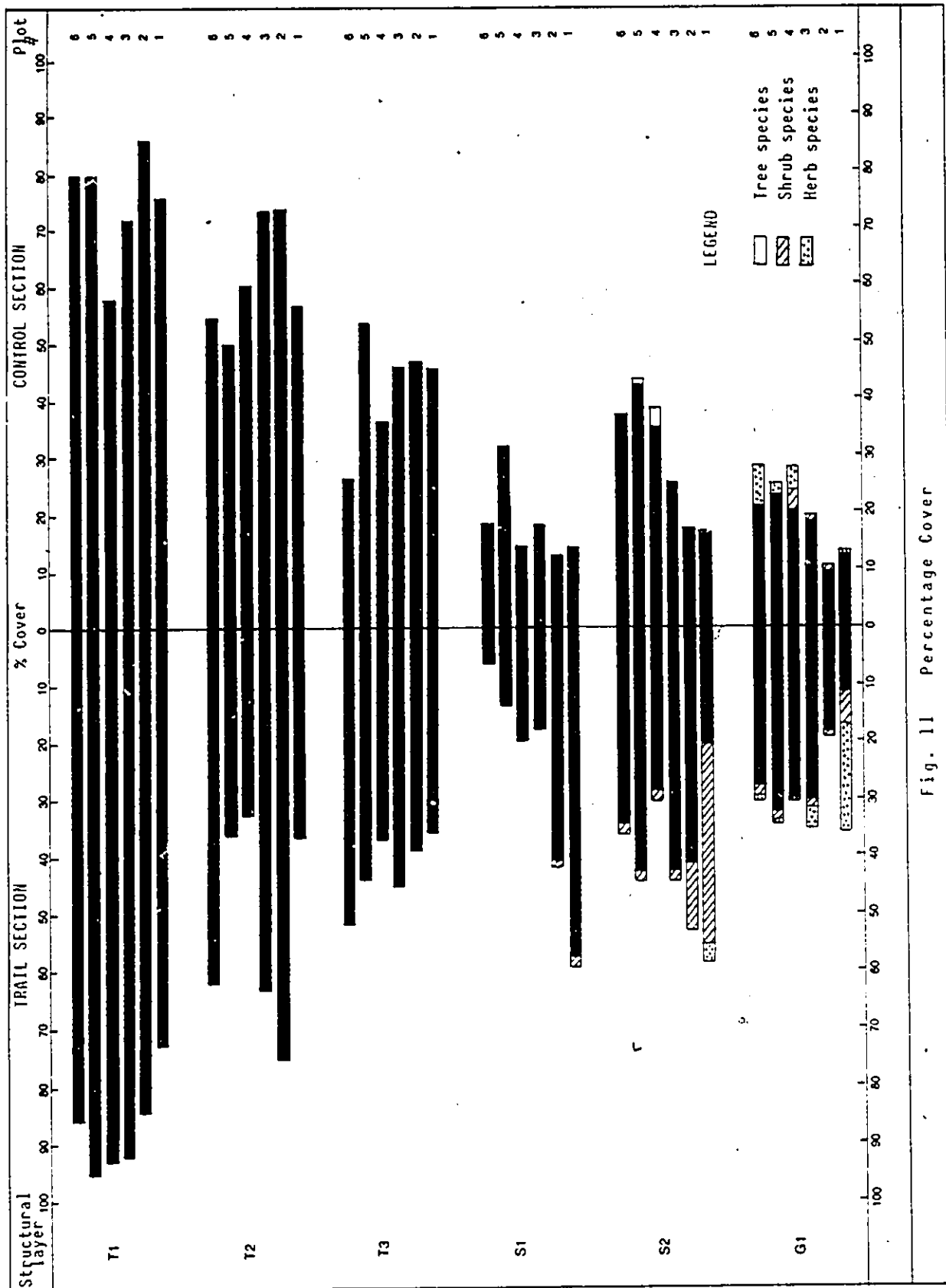


Fig. 11 Percentage Cover

Species Composition

Species are grouped according to distributional pattern as edge, intermediate, or interior species. Definitions of these groups and a species list are given in appendix IV.

It is apparent from this list and from figure 9 that a significant number of species were found exclusively at the trail edge. Beyond 5 metres of the trail margin, however, edge species were virtually absent in the groundlayer. Although species diversity was high in edge plots, the most notable contributors to high herb species abundance were Acuminate Aster (Aster acuminatus) and Northern White Violet (Viola pallens; Raspberry (Rubus idaeus), and to a lesser extent, Bush Honeysuckle (Diervilla Lonicera) were responsible for the elevated shrub species abundance. Although tree species abundance was depressed to 10 metres, Sugar Maple (Acer saccharum) dominated the groundlayer from 5-30 metres.

Density, deviation from theoretical density¹, and frequency of the principal interior tree species are illustrated in figures 12-14. Relative density and cover values for all interior tree species were depressed at the trail edge. (High negative deviation scores on figure 13 graphically illustrate these low values for density.) In addition to being the most important interior tree species in the groundlayer, Sugar Maple was more important in the trail section than in the control section from lower to mid slope (6-21 metres) although frequency was slightly depressed to 9 metres. American Beech

¹ See appendix I for explanation of deviation index.

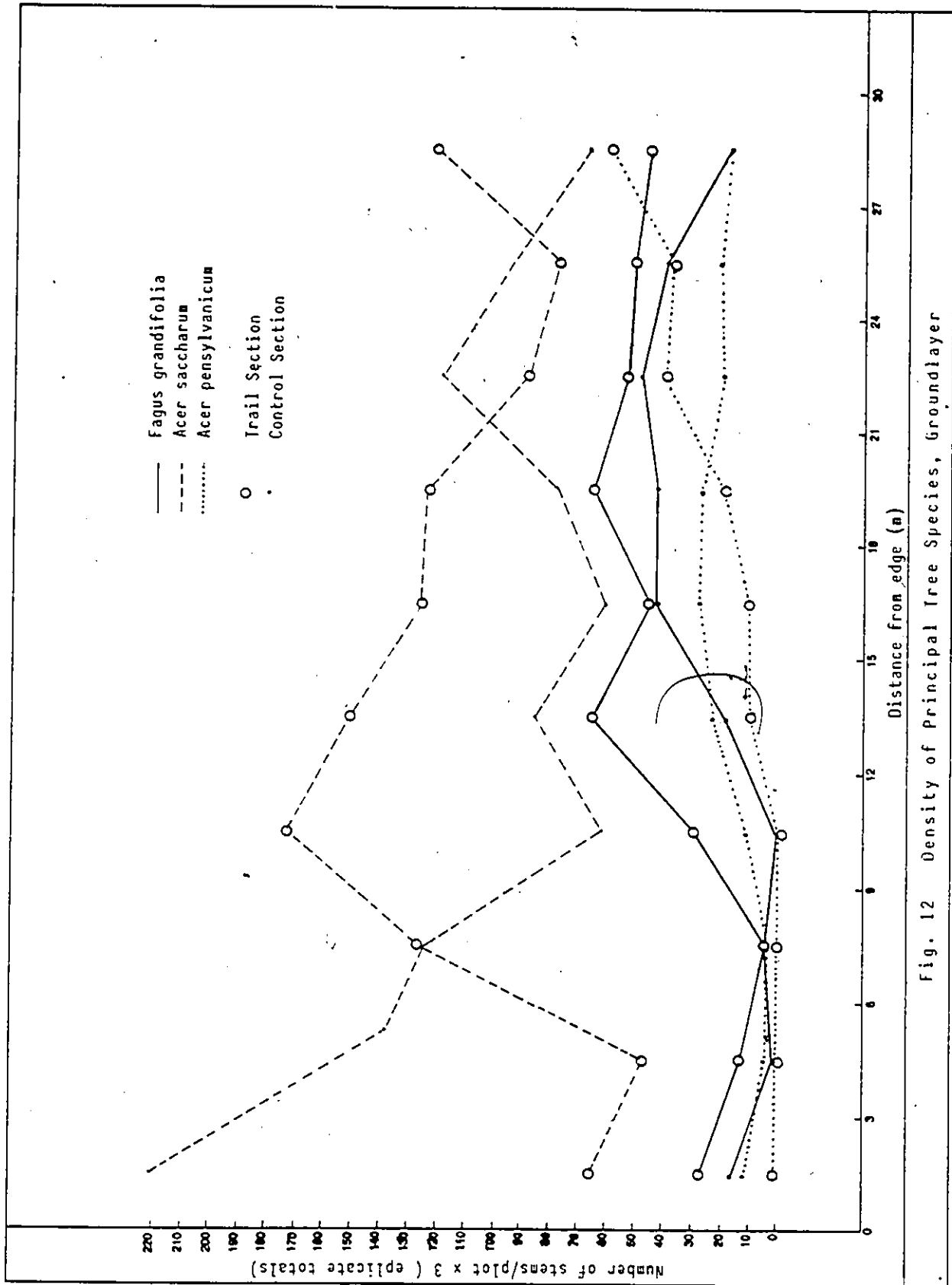


Fig. 12 Density of Principal Tree Species, Groundlayer

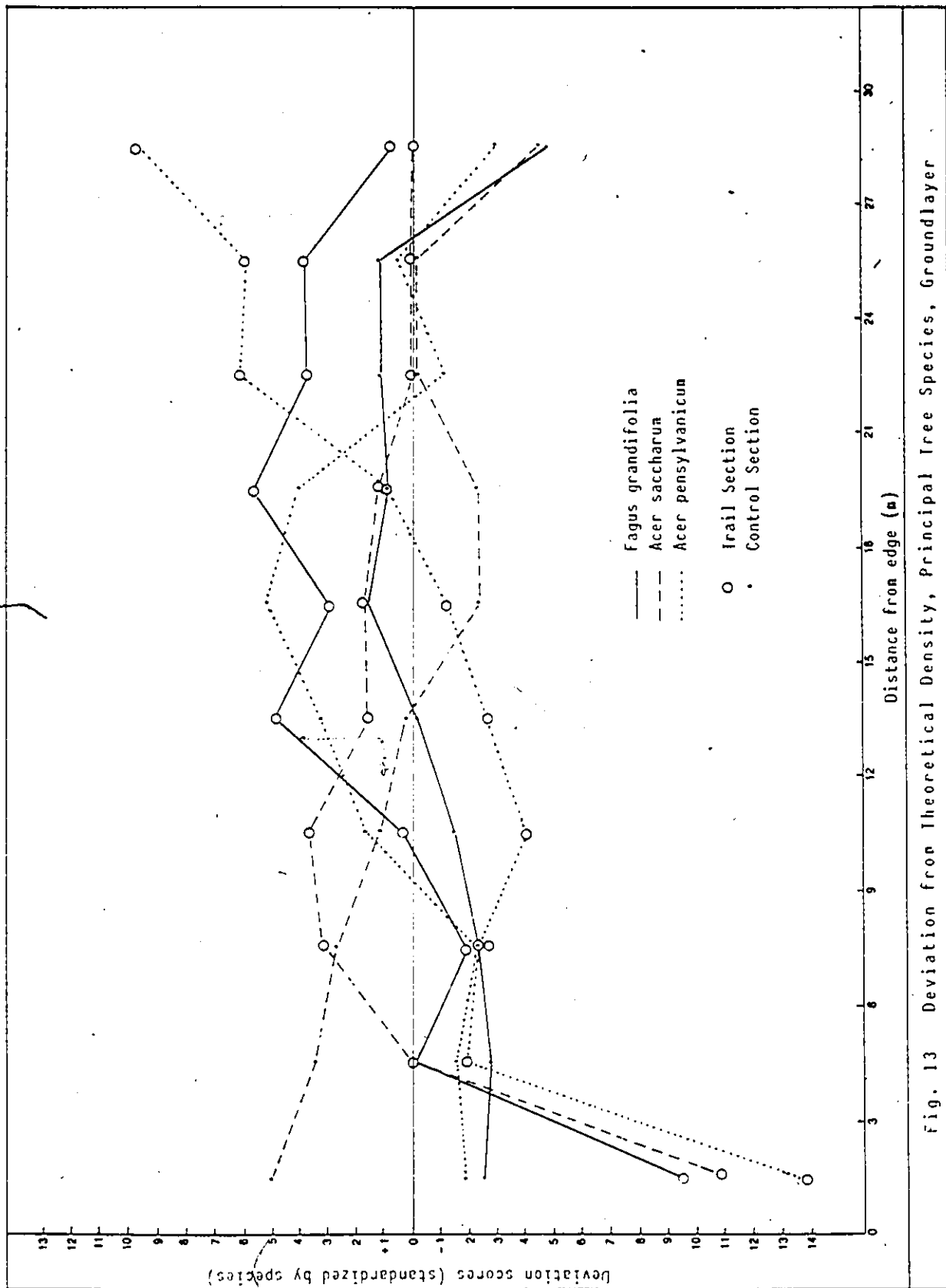


Fig. 13 Deviation from Theoretical Density, Principal Tree Species, Groundlayer

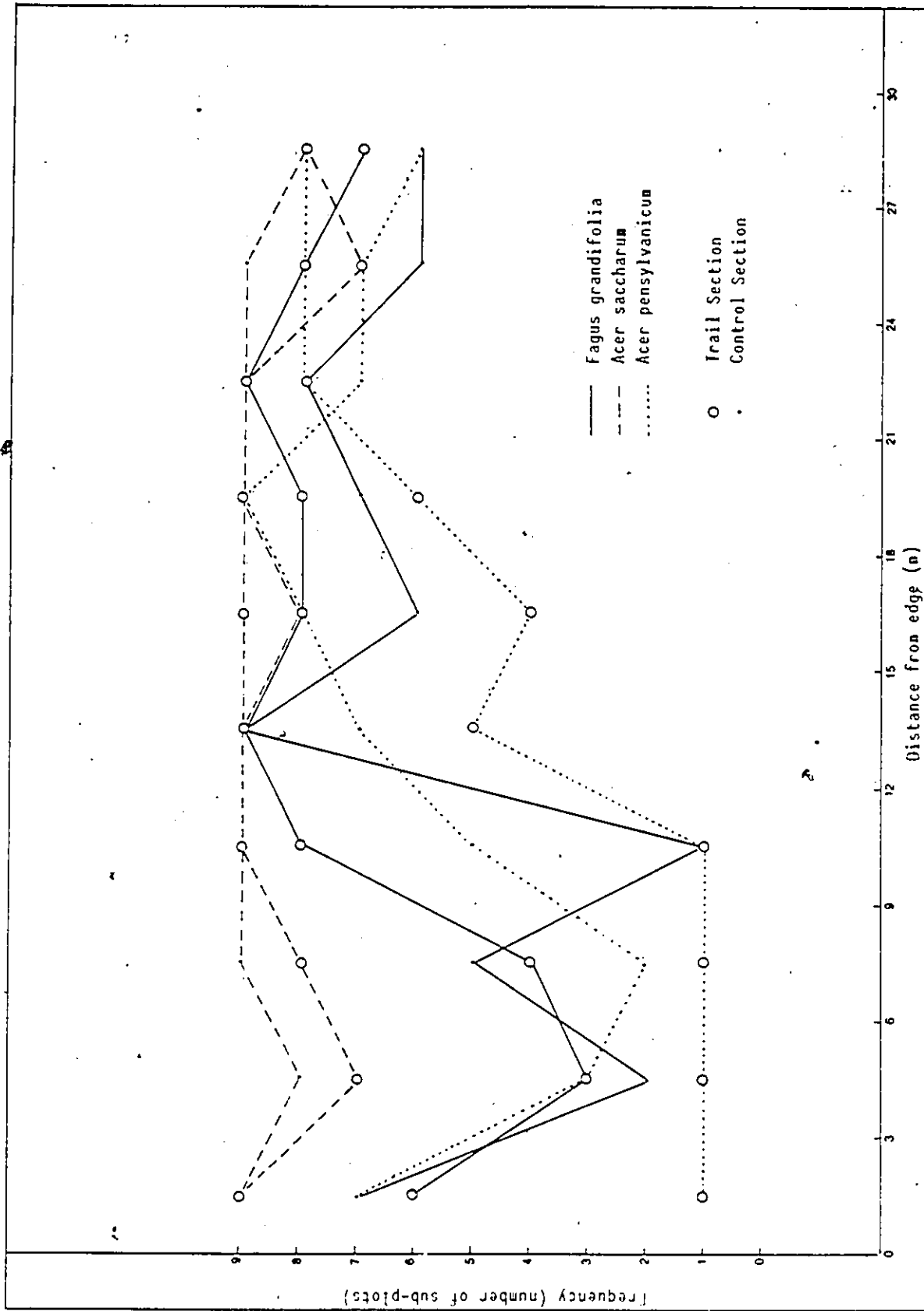


Fig. 14 Frequency of Principal Tree Species, Groundlayer

¹
(Fagus grandifolia) was more or equally important in the trail-
as in the control section beyond the edge plot (3-30 metres
density, cover; 9-30 metres, frequency). Distributional patterns
for Striped Maple (Acer pensylvanicum)² and Red Maple
(Acer rubrum) were similar in both sections; both increased in
importance upslope.

Multivariate Analysis

The first axes of the correspondence analyses (CA) of
groundlayer sample plots by species frequency and density (figs.
15-16) and the second axis of the principal component
analysis (PCA) of plots by species density (fig. 18)
demonstrate the trail impact (edge effect) in terms of these two
variables. Transect profiles of these axes (figs. 17, 19) show
that trail impact is clearly evident from 0-5 metres for density
and 0-9 metres for frequency.³

An abrupt change occurs for species density (3-6 metres,
PCA; 6-9 metres, CA) as interior conditions are restored. This
discontinuity is largely attributable to the herb species
component (fig. 20) for which the degree of sample similarity to
the trail edge plot does not vary significantly beyond the edge
plot. Tree species, conversely, show a progressive decline in
similarity to the edge plot toward the interior (upslope).

¹
Hereafter referred to as Beech.

²
A subcanopy species.

³
Trail impact is measured from the edge to the point where
values within the control range are encountered. The control
range is taken to represent the range of natural variation.

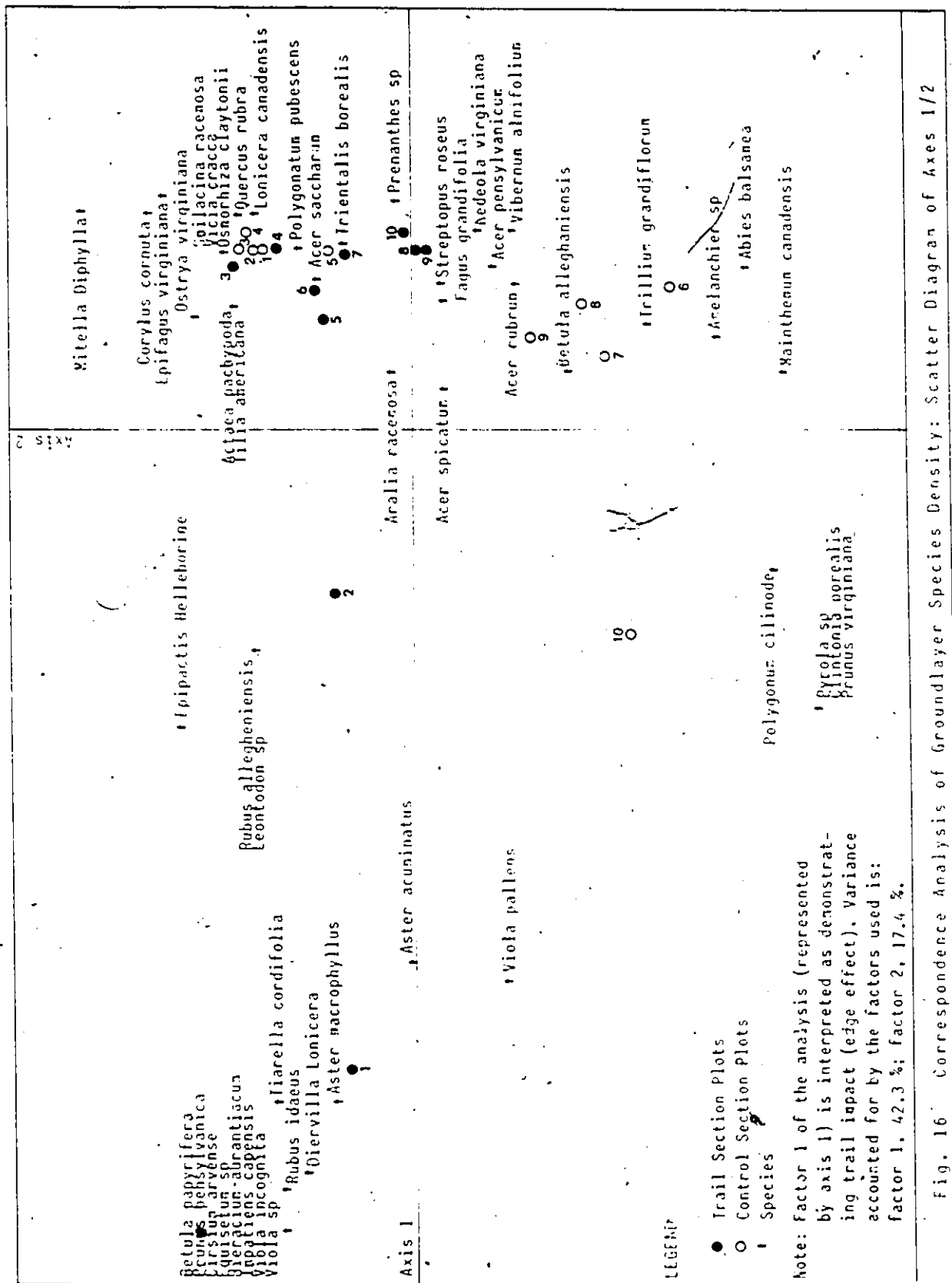


Fig. 16 Correspondence Analysis of Groundlayer Species Density: Scatter Diagram of Axes 1/2

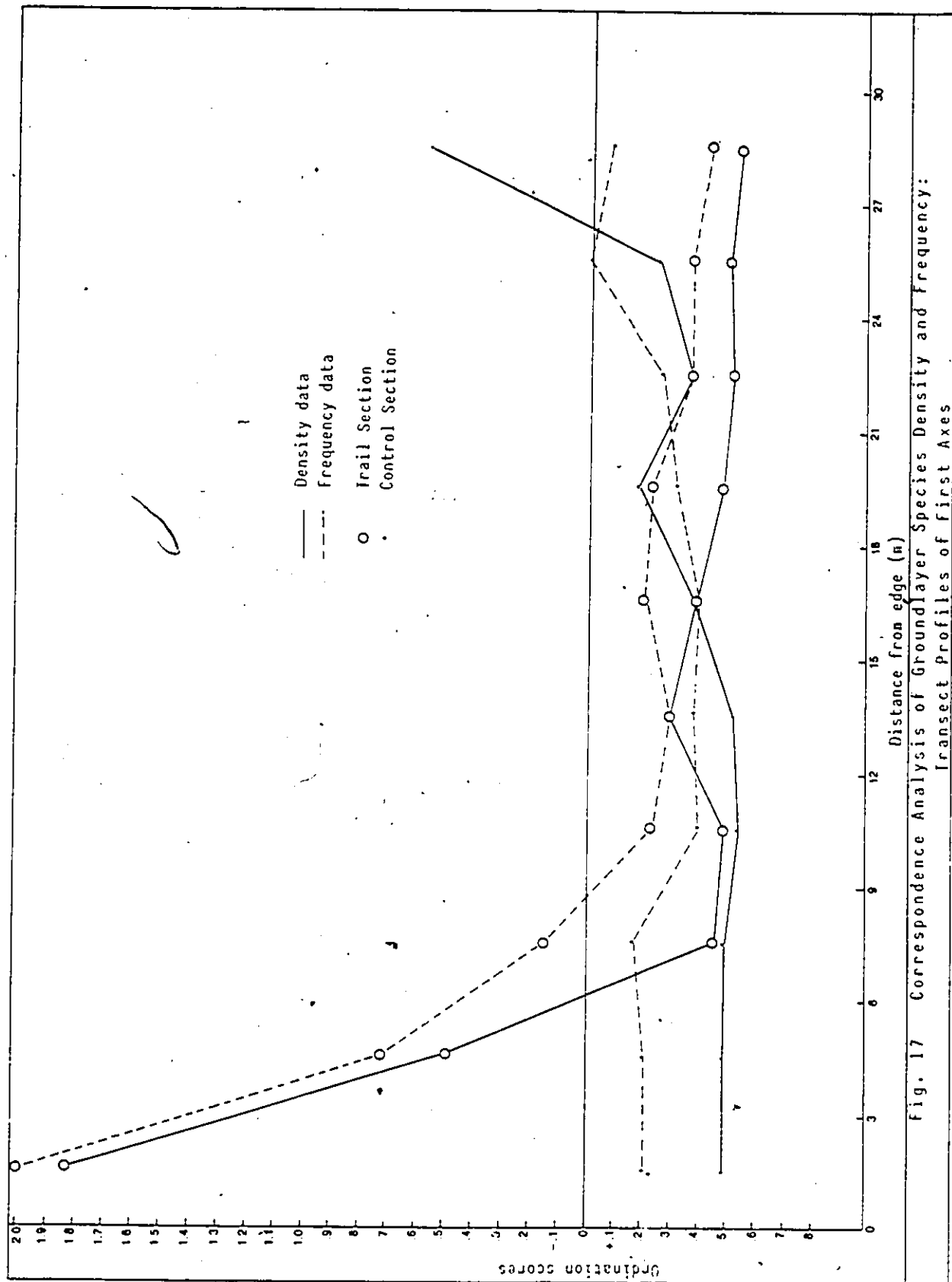


Fig. 17 Correspondence Analysis of Groundlayer Species Density and Frequency:
Transect Profiles of first Axes

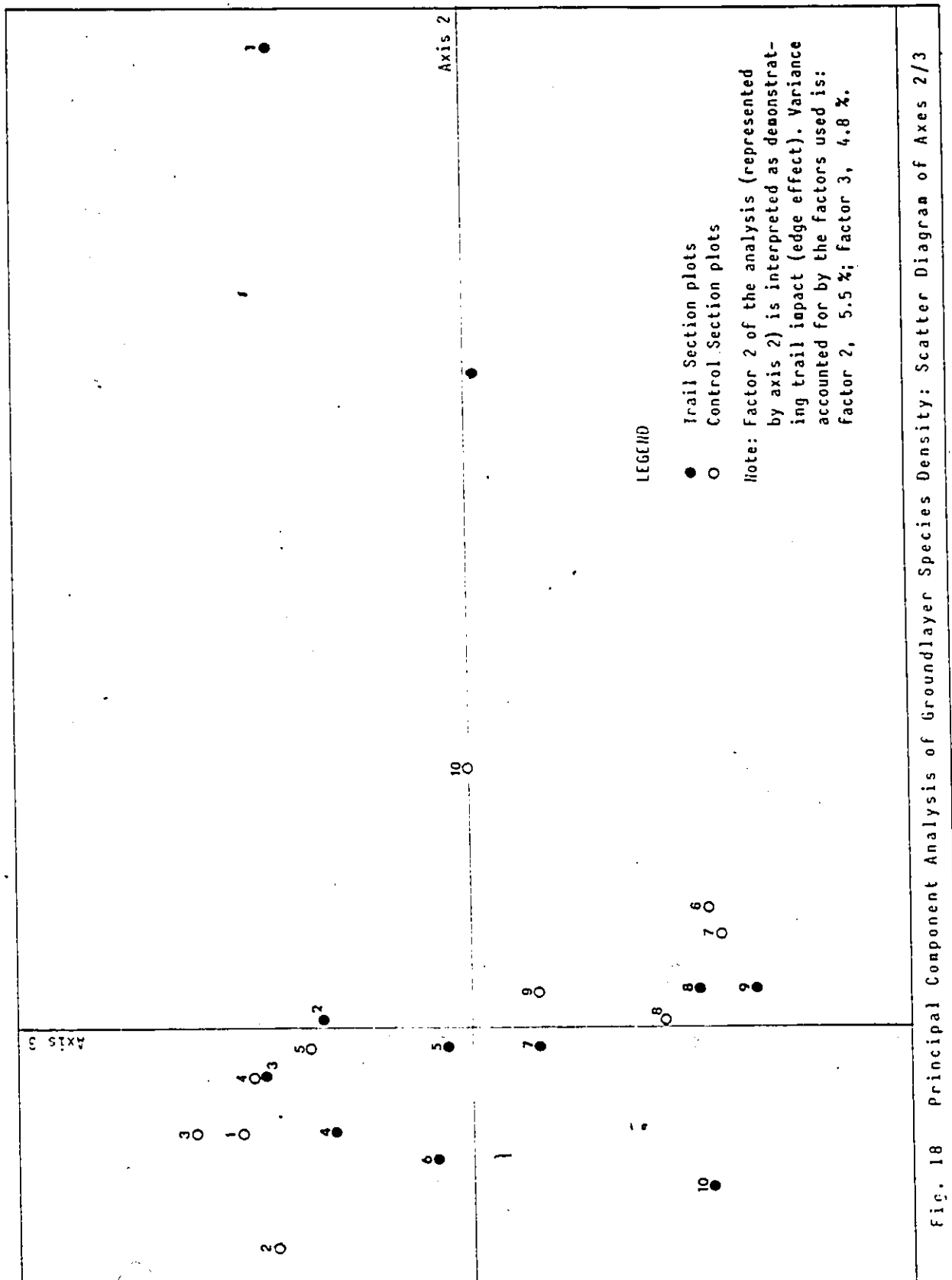


Fig. 18 Principal Component Analysis of Groundlayer Species Density: Scatter Diagram of Axes 2/3

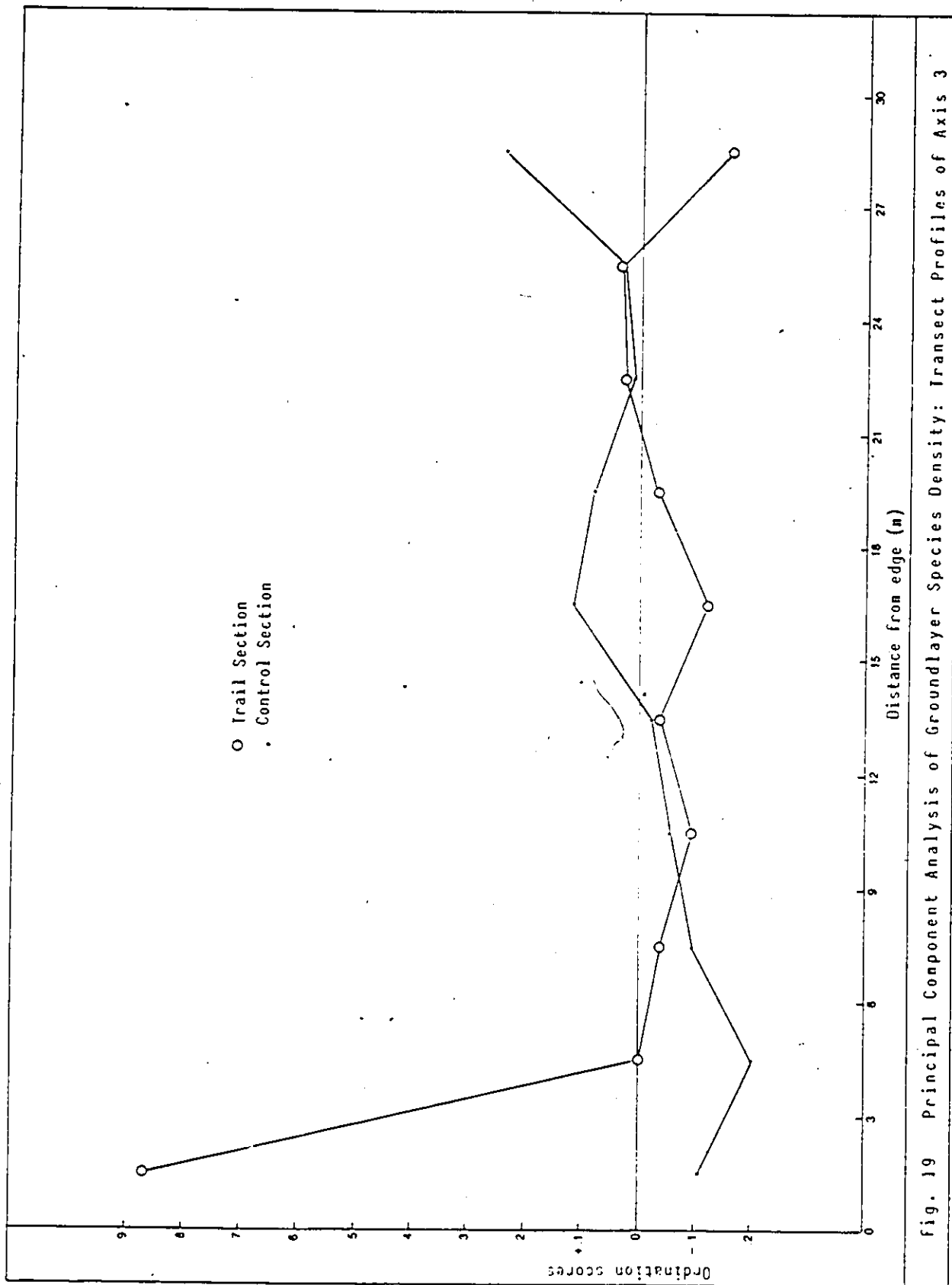


Fig. 19 Principal Component Analysis of Groundlayer Species Density: Transect Profiles of Axis 3

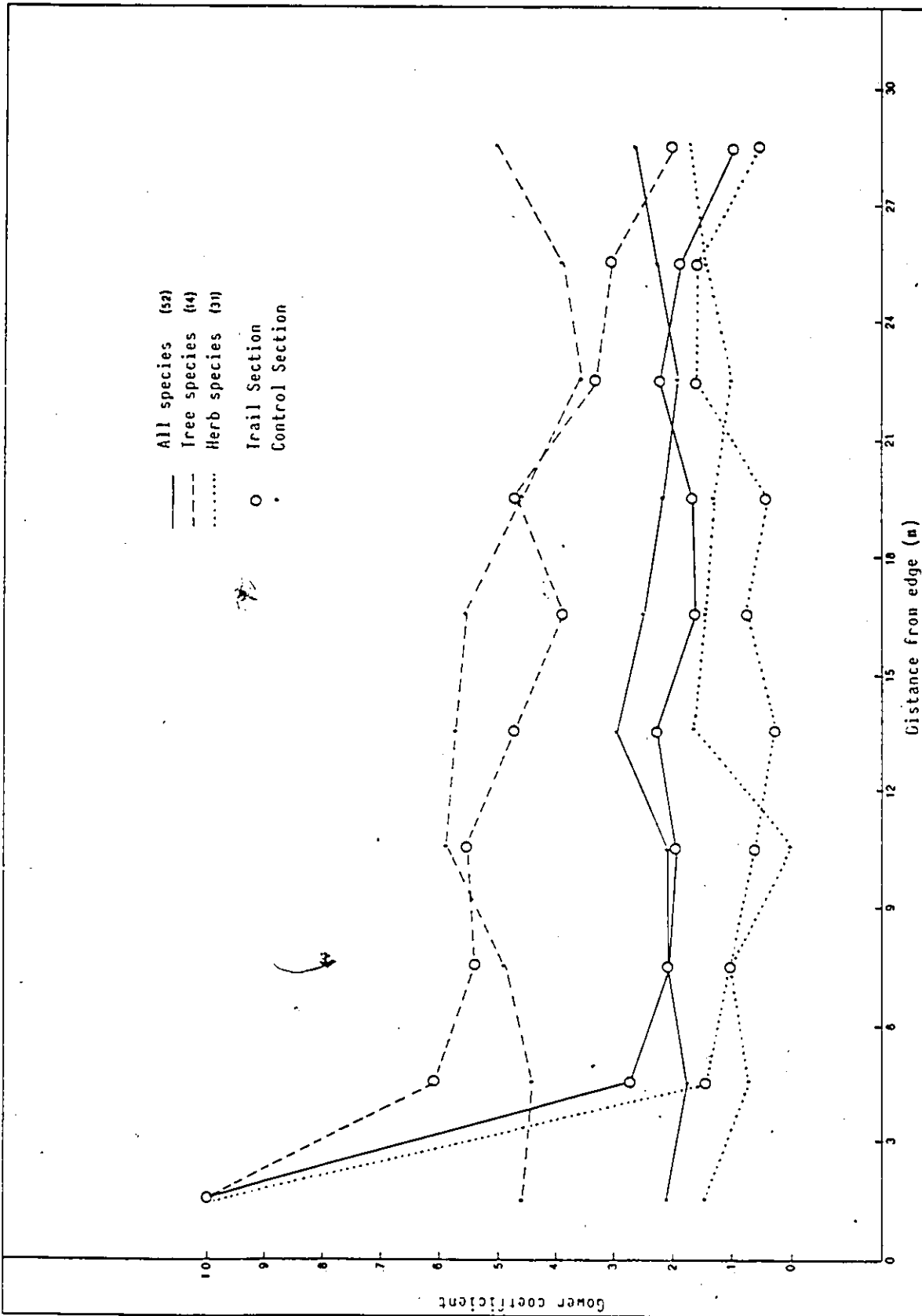


Fig. 20 Similarity Between Irail Edge and Other Plots 1: Gower Coefficient of Groundlayer Species Density

Change for species frequency is more gradual than for density (fig. 17), and ordination scores stabilize from 9-12 metres.

The scatter diagrams and transect profiles show impact effects in terms of magnitude as well as distance and continuity. According to the CA, the magnitude of change between the first two trail plots (3-metre intervals) is approximately equal for species density and frequency (fig. 17); between edge and interior sample plots, however, it is greater for species density than for frequency. (The PCA of density data increases the ordination distance between the first two plots but diminishes the range between edge and interior plots.) A far greater discrepancy exists between the first two trail plots in herb species than in tree species (figs. 20-21), a discrepancy that is more pronounced for species density than for frequency.

In the control section, ordination scores peak upslope (27-30 metres for density; 24-30 metres for frequency) where they exceed values of their trail section counterparts. The most interior (upslope) control plots are accordingly most similar to the impacted trail plots. This similarity appears to be based on the presence of a few (intermediate) species found in rocky areas in the upper control plots that are characteristic of the trail edge and adjacent plots.

A secondary "non-edge" gradient is exhibited by interior

The differences between the two ordinations of density are largely due to the fact that doubly-standardized CA (by species and by sample) tends to emphasize the distinctiveness of samples in terms of species composition, whereas the resemblance measure used for the PCA (Gower coefficient), although standardized by species range, still appears to emphasize abundances of the most dominant species.

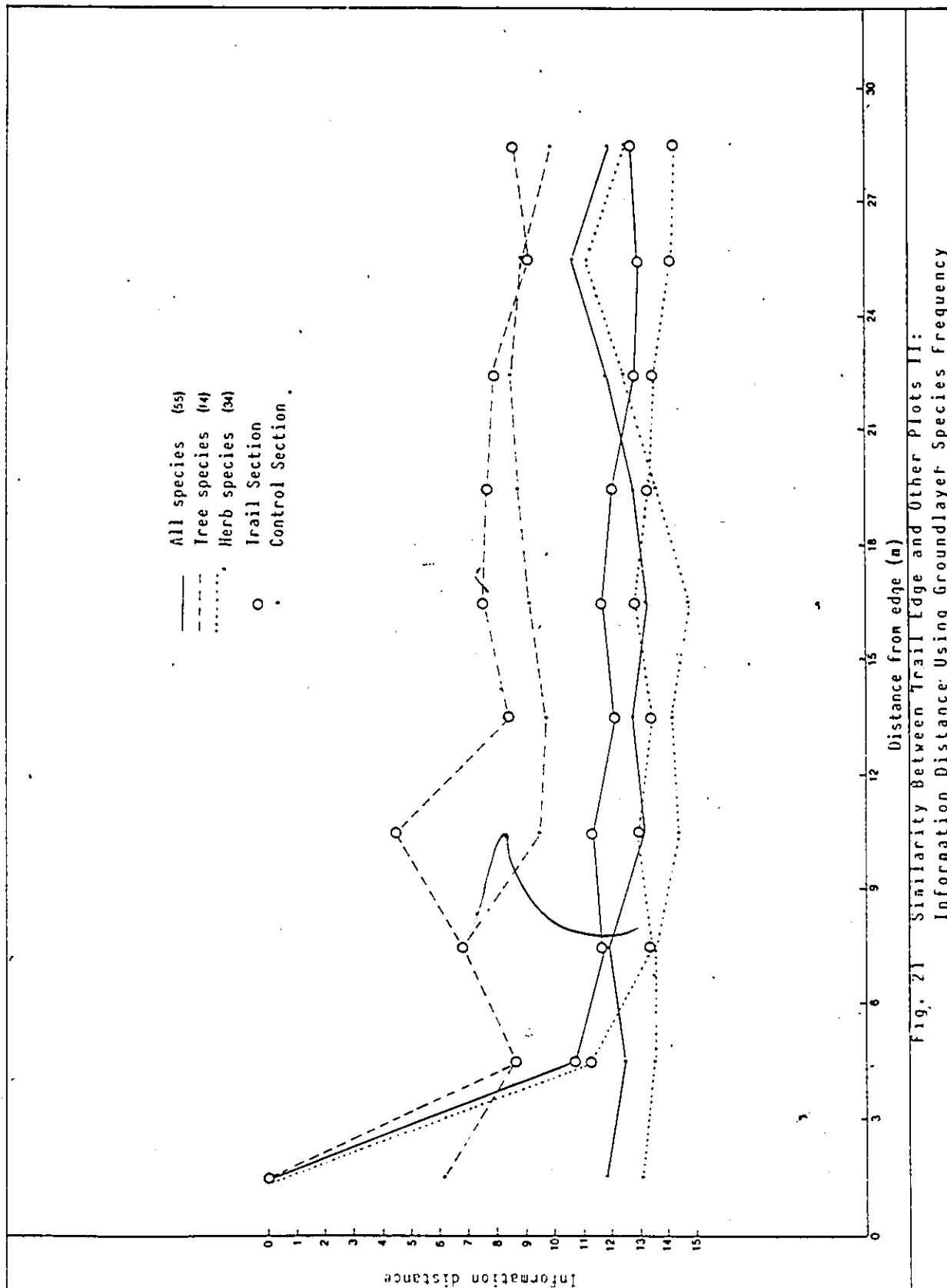


Fig. 21 Similarity Between Trail Edge and Other Plots II:
Information Distance Using Groundlayer Species Frequency

plots that relates to their position on the slope and appears to correspond to the distributional pattern of interior species. This gradient appears along the secondary axis shown in all three ordination diagrams¹. Upslope plots trend toward the lower parts of the diagrams, with upslope control plots farthest placed along this axis on the CA diagrams. The gradation appears partly due to the importance of Sugar Maple in the lower-to-mid slope plots and to the increasing importance of Striped Maple and Red Maple toward the interior (upslope). The characteristic presence of additional species towards the top of the control section appears to account for the lower placement of the interior control plots.

The placement of species on the two CA scatter diagrams is consistent with their grouping according to distributional pattern as edge, intermediate, and interior species². The strong complement of edge species responsible for the separation of edge and interior sample plots is evident on both diagrams.

Shrub Layers

S2 Layer (0.5-2 metres)

General Characteristics

Highest values for species richness, density, and cover occurred in the trail edge plots (table 8; figs. 9-11). These high values were largely due to a significant increase in the relative importance of shrub species. Although tree species

¹ Axis 3 was selected over axis 2 in the CA scatter diagram of species frequency (fig. 15) as it more clearly demonstrates this gradient.

² See appendix IV.

declined in relative importance adjacent to the trail, absolute values remained above the control range. The adjacent plots had the next highest values as well as the highest variability for these characteristics (table 8; figs. 9-11). High variability for density and cover persisted to 15 metres. Lowest values for these variables, found in the control counterparts of the trail edge plots, were notably lower than trail edge values (i.e. by magnitudes of ten for density, six for species richness, and three for cover). Trail section values came within the control section range from 10 to 30 metres, although they continued to exceed comparable control values to 15 metres¹. Density and cover values continued to decrease and were lowest in the trail section from 15-20 metres. Species richness values decreased to 30 metres. In the control section, species richness, density and cover values increased upslope. Species richness values exceeded comparable trail section values from 15-30 metres.

Species Composition

In accordance with findings for the ground layer, edge species were important adjacent to the trail in the lower shrub layer and generally extended farther from the trail margin to a distance of 8 metres (fig. 9; appendix IV). The extremely high abundance of shrub species adjacent to the edge was largely accounted for by three species of the Rubus genus, in the following order of importance: Raspberry (Rubus idaeus), Allegheny Blackberry (Rubus allegheniensis), and Flowering

¹ One of the three trail replicate units exceeded the control range for density and cover from 0-15 metres.

Raspberry (Rubus odoratus). Bush Honeysuckle was also relatively abundant in this layer. The interior shrub species Mooseberry (Viburnum alnifolium) and, to a lesser extent, American Fly-Honeysuckle (Lonicera canadensis) increased in importance beyond 8 metres of the trail edge.

A number of edge and intermediate tree species were also important near the trail margin in the lower shrub layer, notably White Birch (Betula papyrifera) and Yellow Birch (Betula alleghaniensis). Other edge species present were Willow (Salix sp.), Trembling Aspen (Populus tremuloides), and Pin Cherry (Prunus pensylvanica).

The relative importance and distributional patterns of the principal interior tree species were similar for both shrub layers. Density, deviation from theoretical density and frequency of these species are shown in figures 22-24. Both Beech and Sugar Maple were depressed in the trail edge plots (fig. 23). As in the groundlayer, Sugar Maple exceeded Beech in relative importance (density, cover) throughout the trail section and in most of the control section. As noted for the groundlayer, but to an even greater degree, trail section values for Sugar Maple exceeded control values from lower to mid slope. The density, frequency, and cover of Beech were depressed throughout the trail section in the lower shrub layer.

Sl Layer (2-5 metres)

General Characteristics

Highest values for species richness, density and cover, as well as the highest variability for these characteristics,

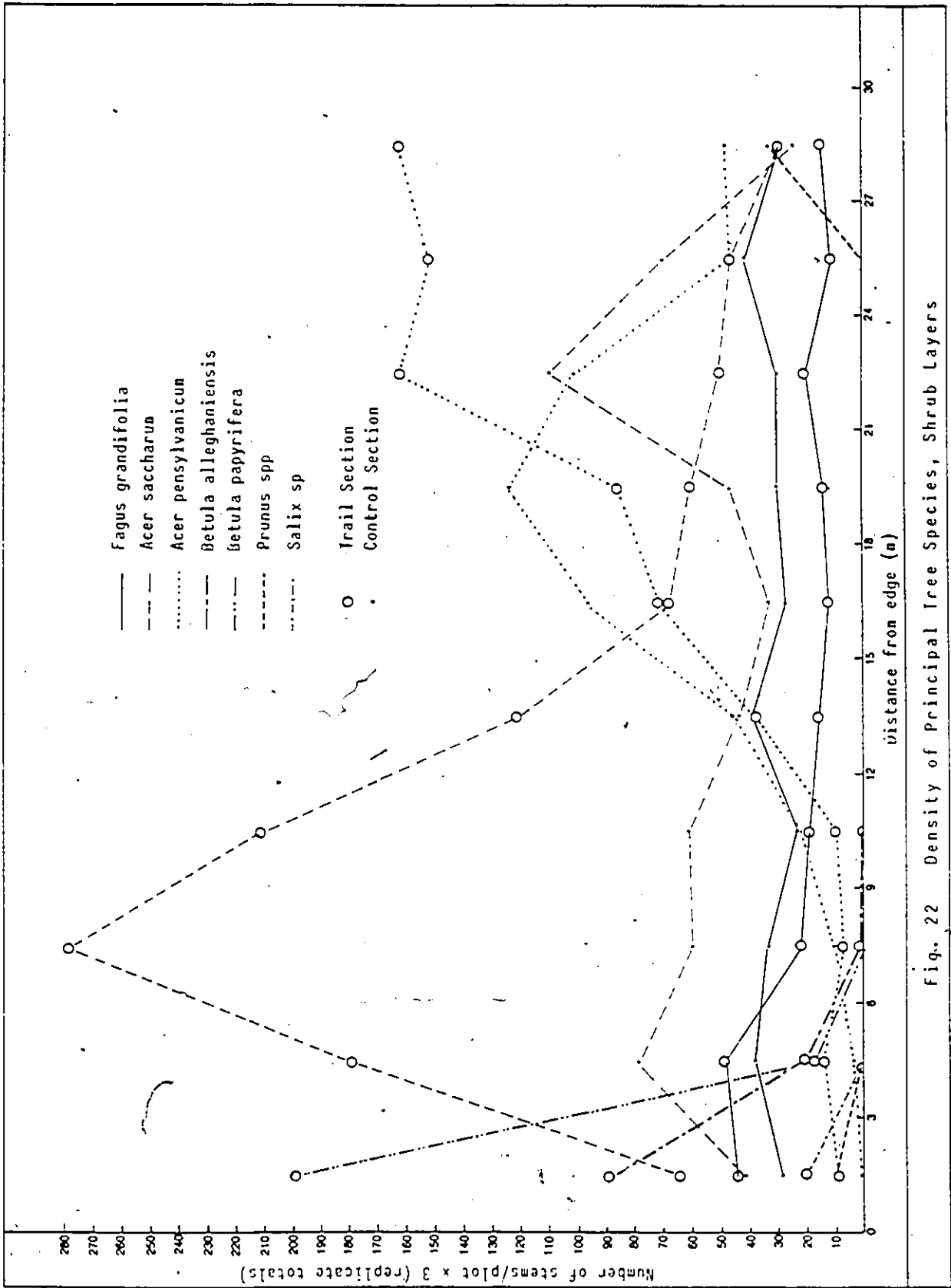


Fig. 22 Density of Principal Tree Species, Shrub Layers

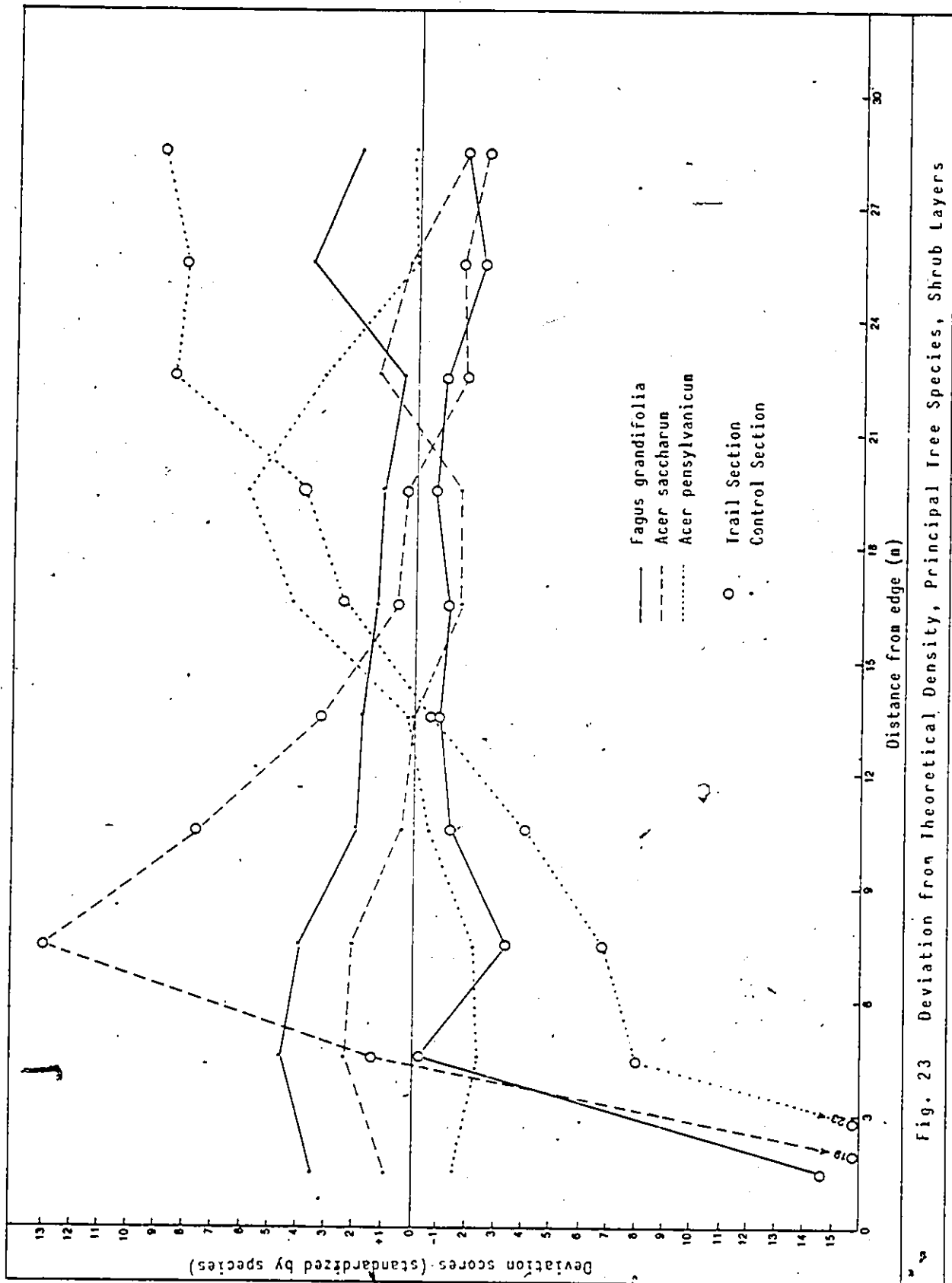


Fig. 23 Deviation from Theoretical Density, Principal Tree Species, Shrub Layers

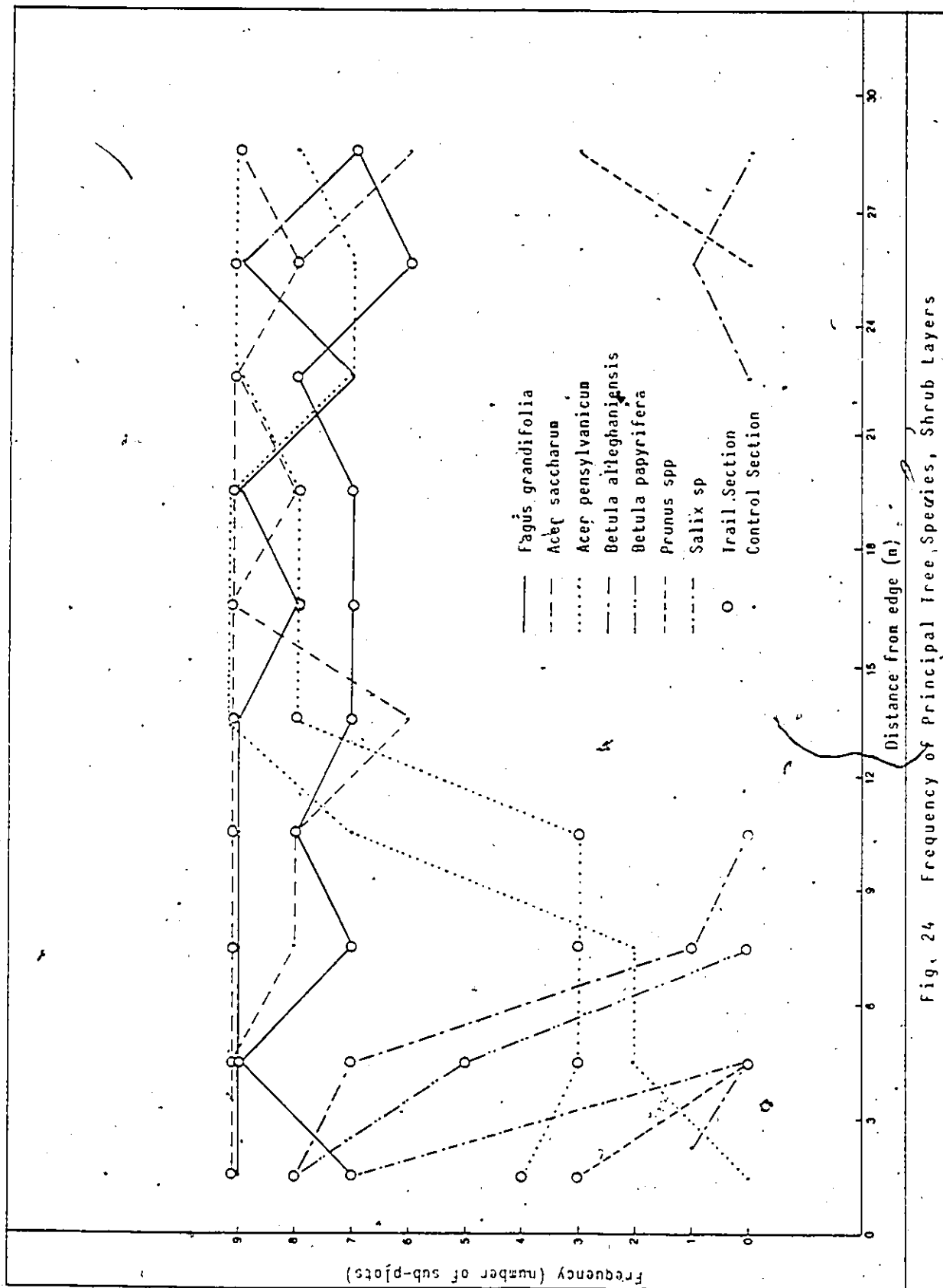


Fig. 24 Frequency of Principal Tree Species, Shrub Layers

occurred in the trail edge plots (table 8; figs. 9-11). High values were the result of an increase in the importance of tree species. Elevated values for these variables continued in adjacent plots. Lowest values for all three characteristics occurred in the most interior trail plots. Trail edge values significantly exceeded those in their control counterparts (i.e. by magnitudes of eight for density and four for species richness and cover). Values came within the control section range from 10 to 30 metres where species richness stabilized; density and cover values, however, continued to decrease to 30 metres. Control section values increased and exceeded trail values from 20-30 metres.

Species Composition

Edge and intermediate tree species were important in this layer close to the trail margin. White Birch, and to a lesser extent, Yellow Birch, were most abundant. Other edge tree species present were Willow and Pin Cherry. The relative importance and distributional patterns of interior species for both shrub layers were discussed above.

S1 and S2 Layers

Multivariate Analysis

Some differences in trail impact effects on ground and shrub layers are apparent from a comparison of the edge effect axes of the respective correspondence analyses (shrub layer scatter diagrams, figs. 25-26; transect profiles, fig. 27; groundlayer scatter diagrams, figs. 15-16; transect profiles, fig. 17). Most

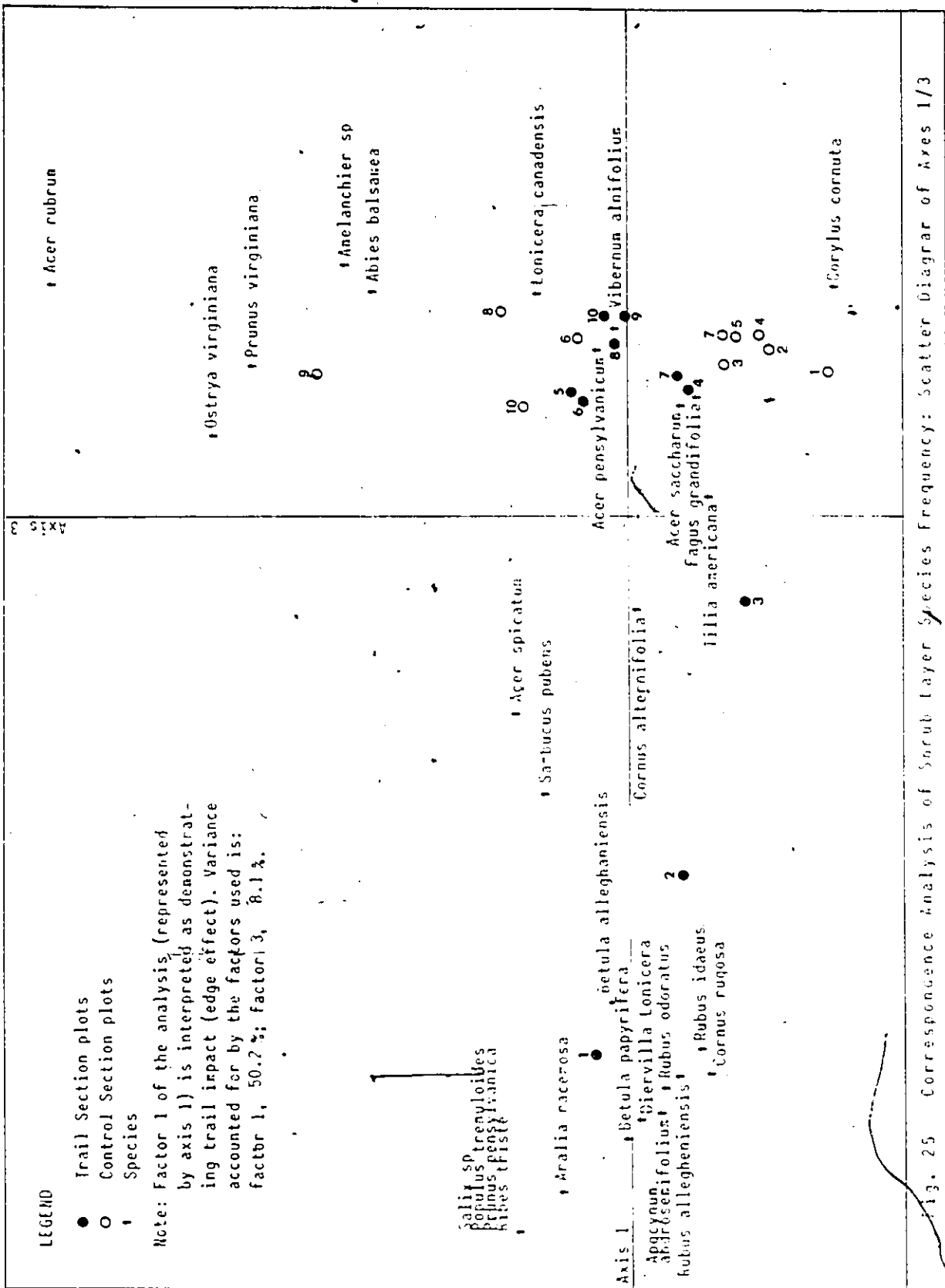


Fig. 25 Correspondence Analysis of Scrub Layer Species Frequency: Scatter Diagram of Axes 1/3

LEG 16

- Trail Section plots
- Control Section plots
- † Species

Note: Factor 1 of the analysis (represented by axis 1) is interpreted as demonstrating trail impact (edge effect). Variance accounted for by the factors used is: factor 1, 50.5 %; factor 2, 10.6 %.

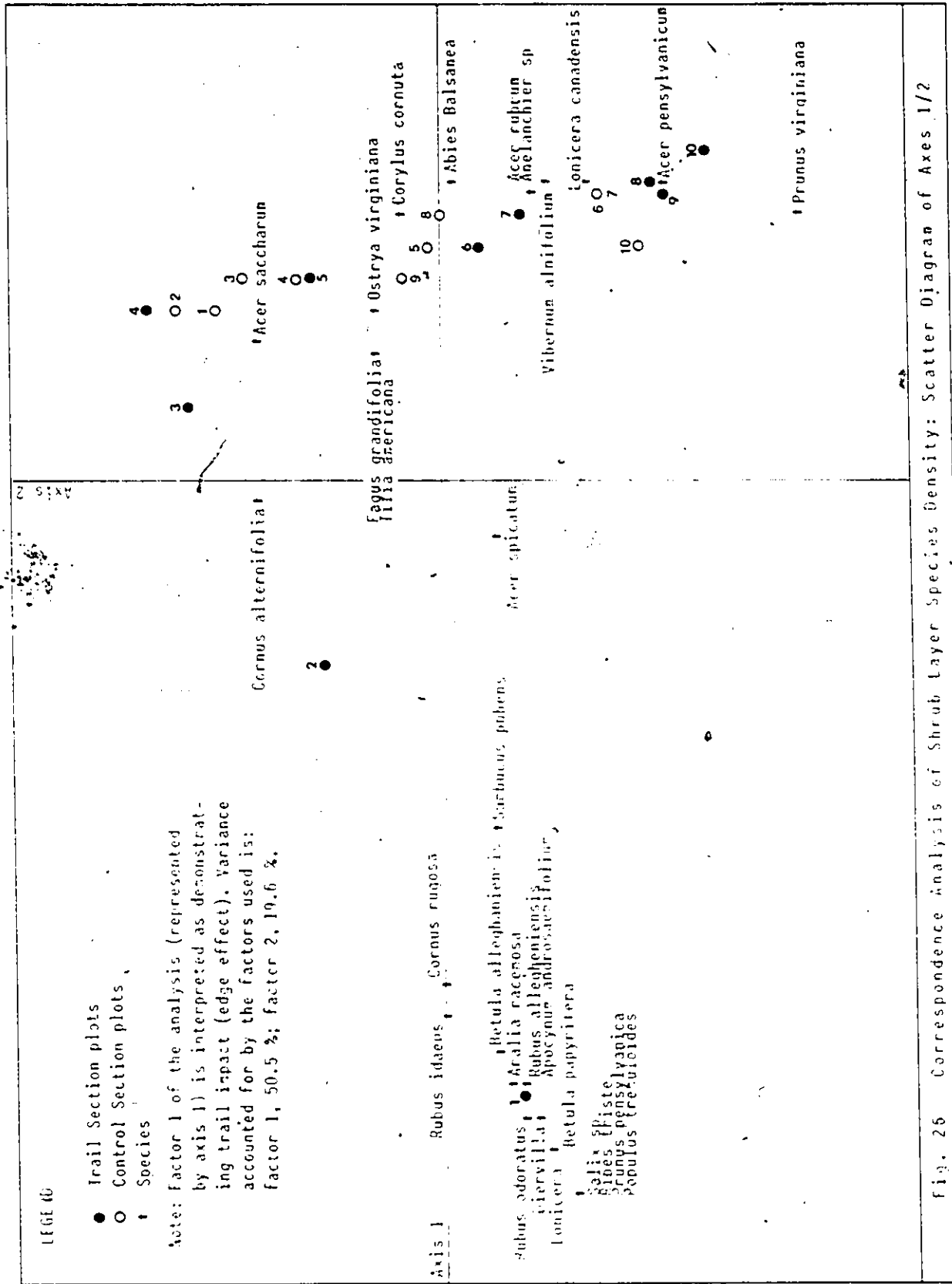


Fig. 26 Correspondence Analysis of Shrub Layer Species Density: Scatter Diagram of Axes 1/2

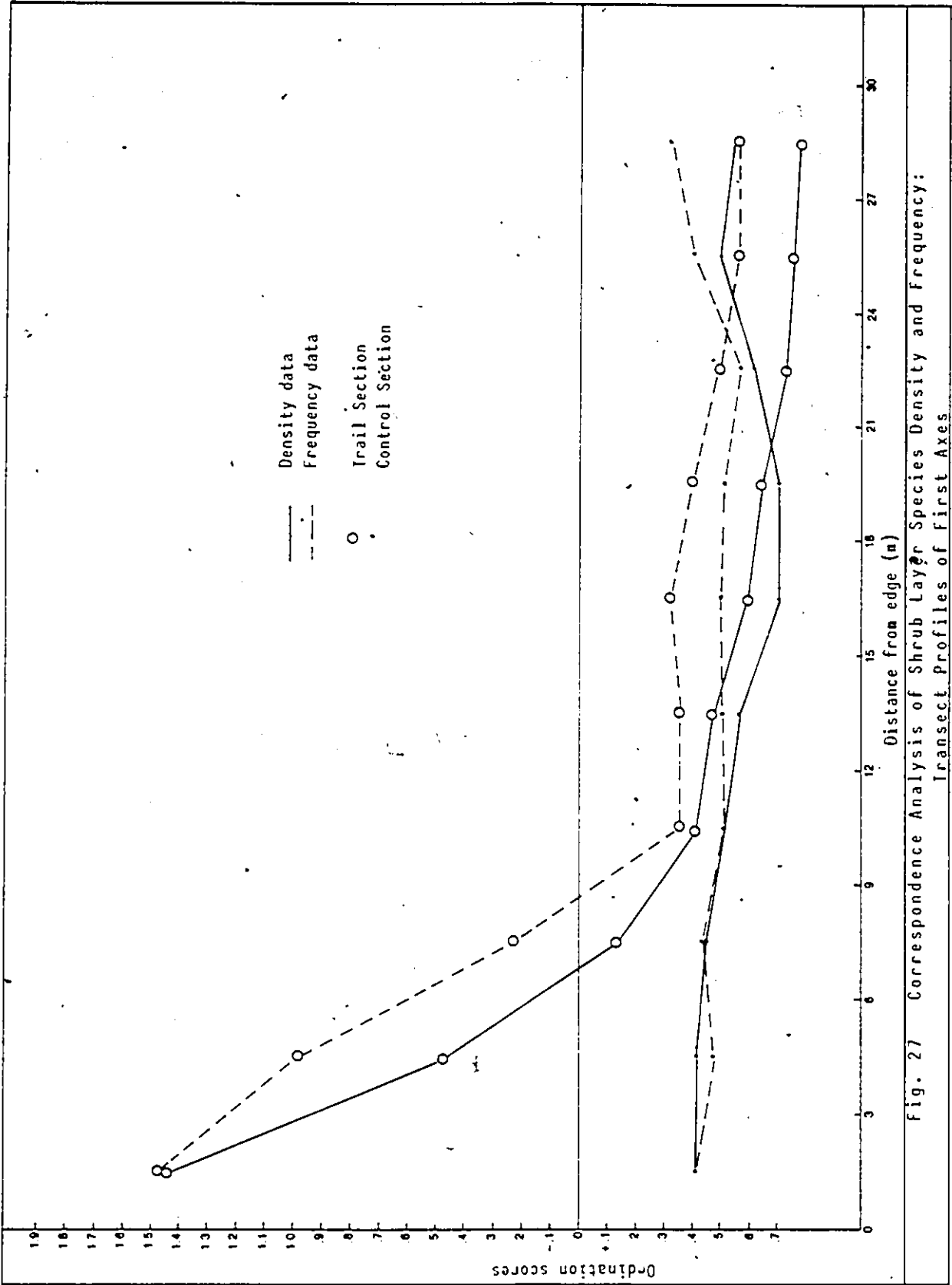


Fig. 27 Correspondence Analysis of Shrub Layer Species Density and Frequency: Transect Profiles of First Axes

apparent is the fact that impact extends to a greater distance from the edge in the shrub layers, most notably from 0-10 metres for both density and frequency. For both frequency and density, impact is evident for a greater distance for shrub species than for tree species (figs. 28-29).

The transition from edge to interior conditions is far less abrupt for density of the shrub layers than of the groundlayer, as ordination scores show a steady decline throughout with distance from the edge (fig. 27). The transition is, however, more abrupt for frequency. The magnitude of change between edge and interior is slightly less for the shrub layers in general although it is greater for the tree species component. This magnitude of change is not significantly greater for species density than for frequency (fig. 27), but is greater for shrub than for tree species (figs. 28-29). The degree of change between the first two plots (3-metre intervals) is much less in the shrub- than in the ground layer.

As observed for the ground layer, control section ordination scores peak and exceed trail section values upslope (21-30 metres for density; 24-30 metres for frequency). However, the similarity of the trail and control section most interior (upslope) samples is far greater for the shrub layer than for the ground layer, and the similarity of the upslope control plots to the impacted trail plots much less.

A secondary ordering of interior plots according to position on the slope is also evident on axis 2 of the CA shrub layer

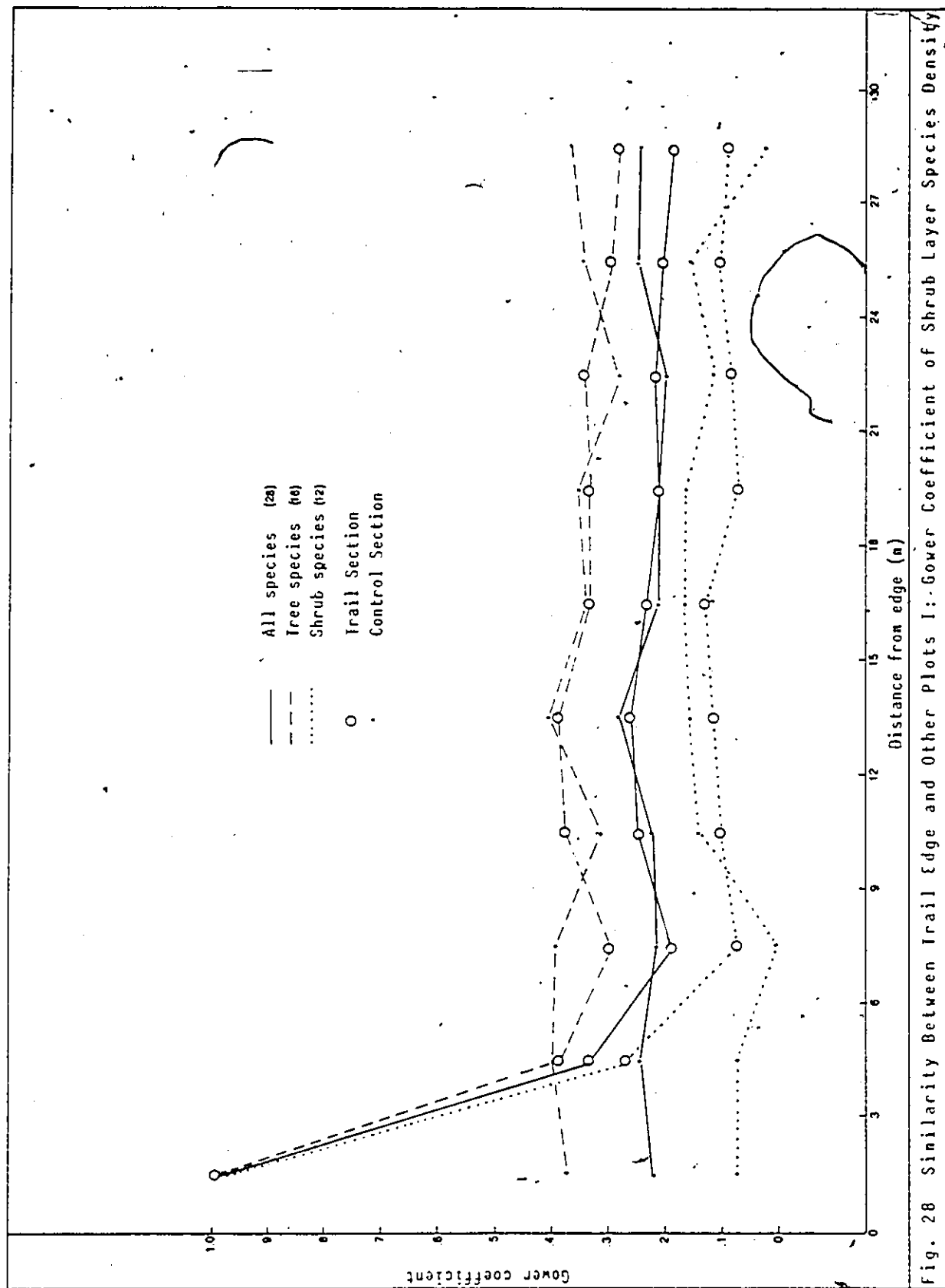


Fig. 28 Similarity Between Trail Edge and Other Plots 1: Gower Coefficient of Shrub Layer Species Density

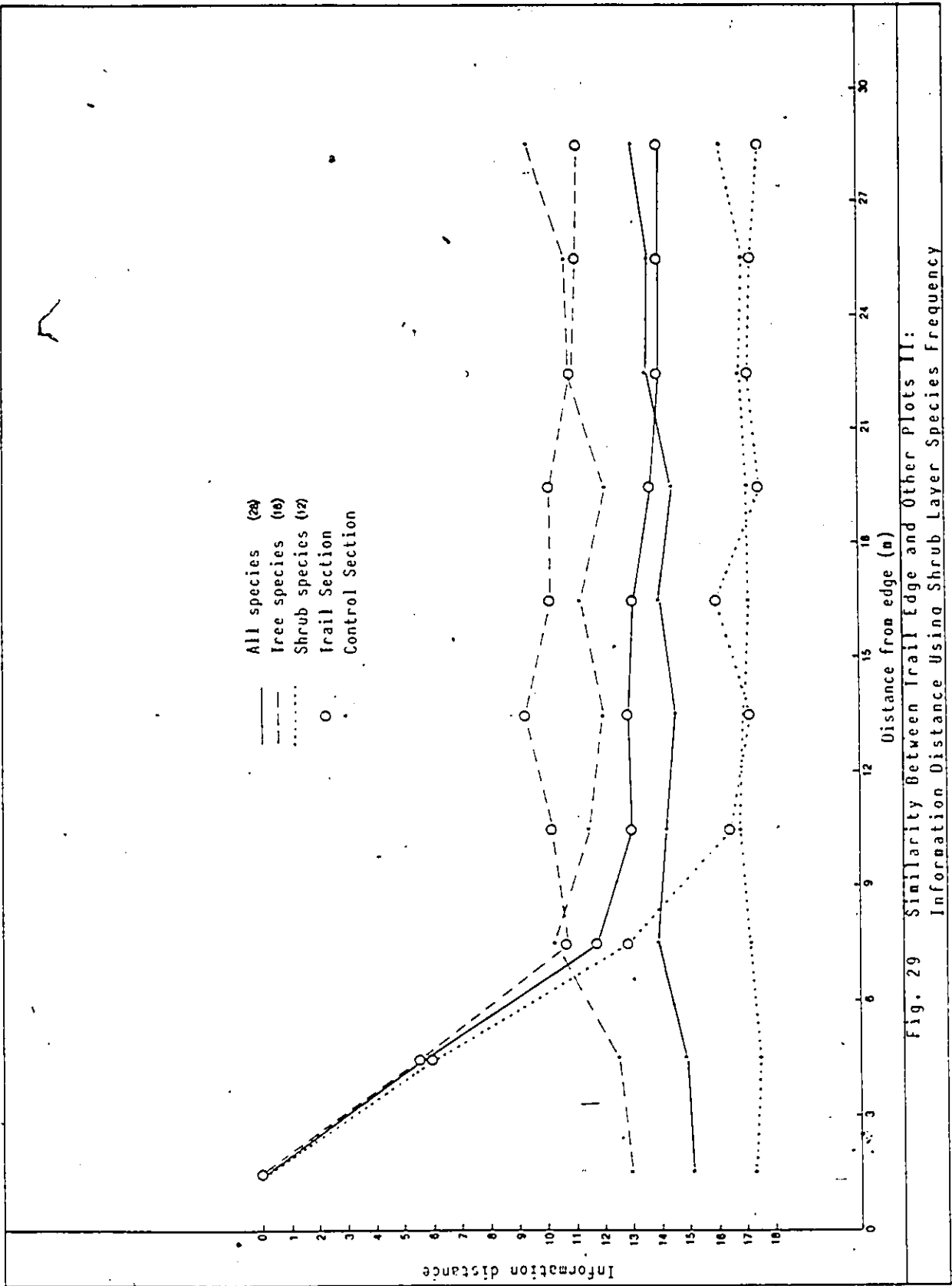


Fig. 29 Similarity Between Trail Edge and Other Plots II:
Information Distance Using Shrub Layer Species Frequency

density scatter diagram (fig. 26)¹. As for the groundlayer, this ordering appears to be related principally to the importance of Sugar Maple in the lower-to-mid-slope plots, and of Striped Maple in upper-slope plots. The appearance of a few species upslope, particularly in the control section (e.g. Red Maple, Serviceberry (Amelanchier sp.) and Choke Cherry (Prunus virginiana) contribute to this ordering. A further ordering by a higher-level axis of the CA (not shown) makes a separation between trail and control plots. The relative importance of Beech (high in control section, low in trail section) appears to be primarily responsible for this division.

As observed for the ground layer, the placement of species on the CA scatter diagrams is consistent with their grouping according to distributional pattern as edge, intermediate, and interior species. An important component of edge species is again evident from these diagrams.

Tree Layers

T3 Layer (<10 metres; <2.5 cm dbh)

General Characteristics

In the lowest tree layer, the trail edge plots were the most variable in terms of species richness, density, cover and basal area (table 8). They also contained the highest species richness and density values (figs. 9-10)². Again these high values were due to the presence of edge and intermediate species. The

¹ Some vertical ordering, particularly of control plots, is also evident on axis 3 of the CA frequency diagram (fig. 25).

² Density values highest in trail section but exceeded at mid slope in control section.

0
density of interior tree species was severely depressed in these plots¹. In contrast, mean tree diameter values were lowest in the edge plots (fig. 30)². Edge plot cover values were lowest in the trail section and second lowest in the study area (fig. 11)³. Two factors appeared to contribute to low cover values of edge species. Firstly, because of the proximity of these species to the trail margin, and the strong inclination of stems toward the edge, a large part of the cover lay outside the edge plots. Secondly, because of the clearing, no compensating cover was contributed from outside on the edge side of these plots.

Species richness and density values stabilized from 5-30 metres at levels generally comparable to or lower than the control section. Cover values remained lower than control values from 0-10 metres.

Species Composition

Edge and interior species of importance at the trail edge were White Birch, Willow, and to a lesser extent, Yellow Birch. Beyond the edge, Sugar Maple became dominant in the lower trail section and exceeded control values from 5-20 metres. Density and cover values for Beech were low in the trail section from 0-15 metres, but exceeded control section values from 20-30 metres. In the upper trail section (15-30 metres) and throughout the control section, Beech exceeded Sugar Maple in density and cover.

¹ Absent from units 1 and 2; extremely low in unit 3.

² Highest for Sugar Maple.

³ Relative cover for Sugar Maple high from 0-15 metres.

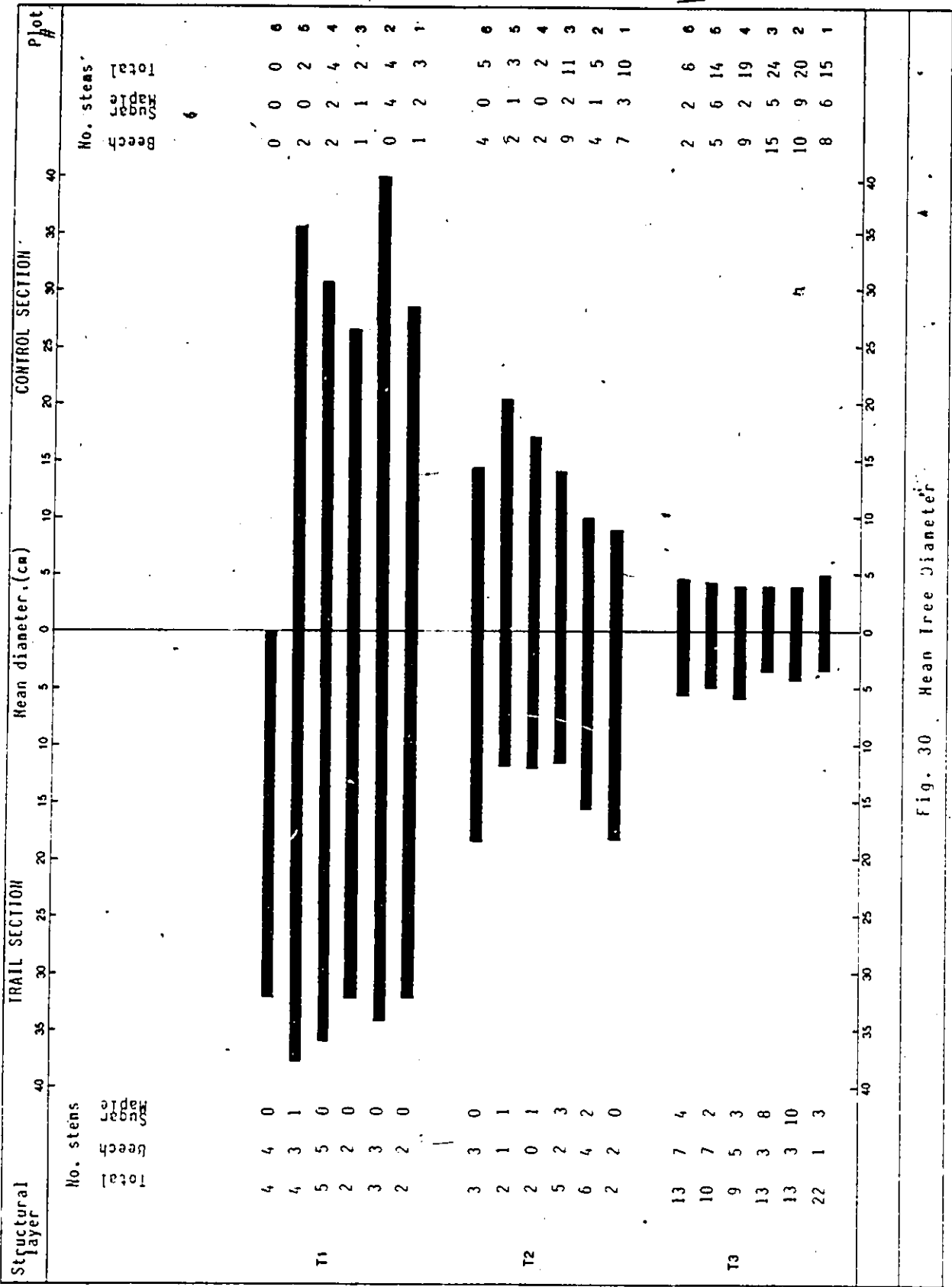


Fig. 30 Mean Tree Diameter

Striped Maple occurred with low abundance throughout the trail section but increased in importance in the upper part of the control section.

T2 Layer (10-20 metres; >2.5 cm dbh)

General Characteristics

The measured vegetation characteristics appear to show few clear impact effects at the trail edge in the subcanopy layer. Mean tree diameter values, however, exceeded control values from 0-10 metres, and showed a decreasing trend from 0-15 metres that opposed the control trend (fig. 30). Density was low in the trail edge plots (fig. 10). Although cover values were generally lower in the trail- than in the control section, they slightly exceeded control values from 5-10 metres (fig. 11).

Species Composition

Only two species--Beech and Sugar Maple--were consistently found in the subcanopy layer. In addition to these species there was only one occurrence each of Ironwood (Ostrya virginiana) and Yellow Birch. Beech was the most dominant species throughout the study area in terms of cover, and in the control section in terms of density. Control section density values invariably outnumbered trail section scores. Sugar Maple was dominant in the trail section in terms of density from 10-20 metres and exceeded control section values for the same species from 5-20 metres.

T1 Layer (>20 metres; >2.5 cm dbh)

General Characteristics

No trail impact effects were apparent at the trail edge for the primary vegetation characteristics in the canopy tree layer. Cover and basal area were higher in the trail- than in the control section from 10-30 metres. Differences, however, were probably primarily related to natural variation in density and species composition and not to effects associated with the trail. No canopy trees were sampled in the most interior control plots.

Species Composition

Only Beech and Sugar Maple were found in the sample plots although Yellow and White Birch contributed minimally to canopy cover. With only one occurrence of Sugar Maple, Beech was the dominant species throughout the trail section and consistently occurred at higher densities than in the control section. Sugar Maple exceeded Beech in importance only on the lower slope in the control section (from 0-10 metres).

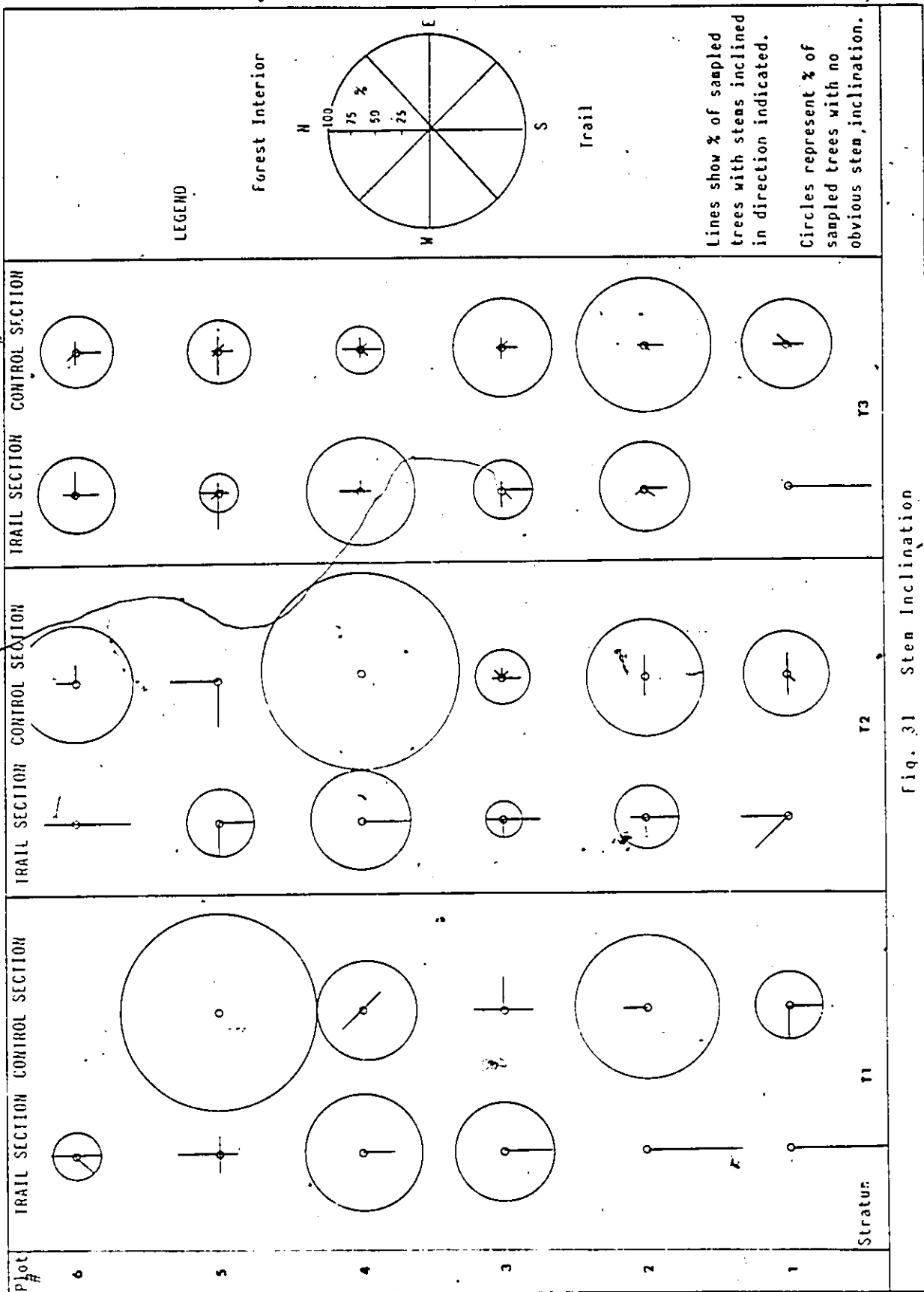
T1, T2, and T3 Layers

Structural Adaptation of Trees

Results of observations concerning stem inclination and the orientation of longest branches for the three tree layers are shown in figures 31 and 32. Stem inclination in the direction of the trail was evident for the greatest distance from the edge in the canopy layer.

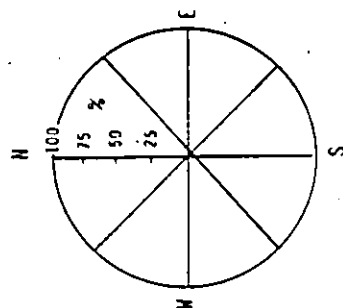
All canopy trees sampled from 0-10 metres had a noticeable

South on the diagrams, but more precisely, south-southwest.



LEGEND

Forest Interior



Trail

Lines show % of sampled trees with stems inclined in direction indicated.

Circles represent % of sampled trees with no obvious stem inclination.

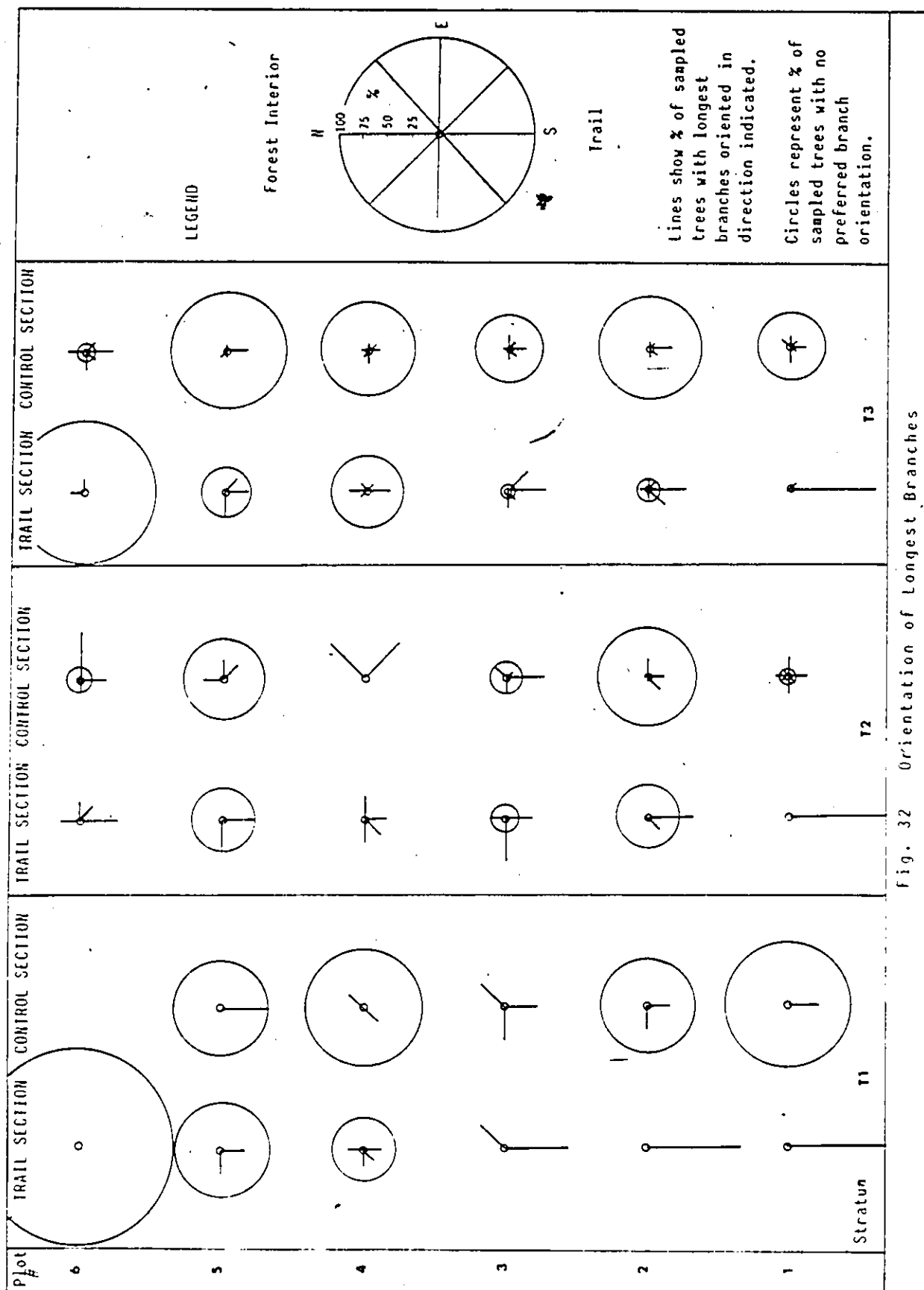


Fig. 32 Orientation of Longest Branches

lean toward the edge, and those sampled from 10-20 metres showed either a lean toward the edge or no noticeable lean in any direction, the frequency of the latter increasing toward the interior. The orientation of the longest branches followed a similar pattern, with trail impact noticeable to 15 metres.

The subcanopy layer, on the other hand, showed no apparent effect in terms of stem inclination in the edge plots, but did show a preferred orientation of longest branches in the direction of the trail from 5-10 metres and exclusive orientation in that direction from 0-5 metres.

Trail impact on the lowest tree layer was very strong for both variables from 0-5 metres. The combined effect of these variables resulted in most cover of trees located close to the edge (particularly Willow) lying outside of the edge plots. In this tree layer, and to a lesser extent the others, change in the pattern of branching was not confined to the longest branches. Most branches appeared on the trail edge side, with the inside of stems often clear, whereas in the control plots there was a greater incidence of completely clear stems, stems with no preferred branch orientation, or stems with a locally preferred orientation of branches related to competitive interaction with other trees.

Results concerning the height of lowest branches and the number of branches below breast height were inconclusive because of incomplete recording. It was apparent from the results, however, that for the lowest tree layer, the mean height of the lowest branch was less in the trail edge plots than in the

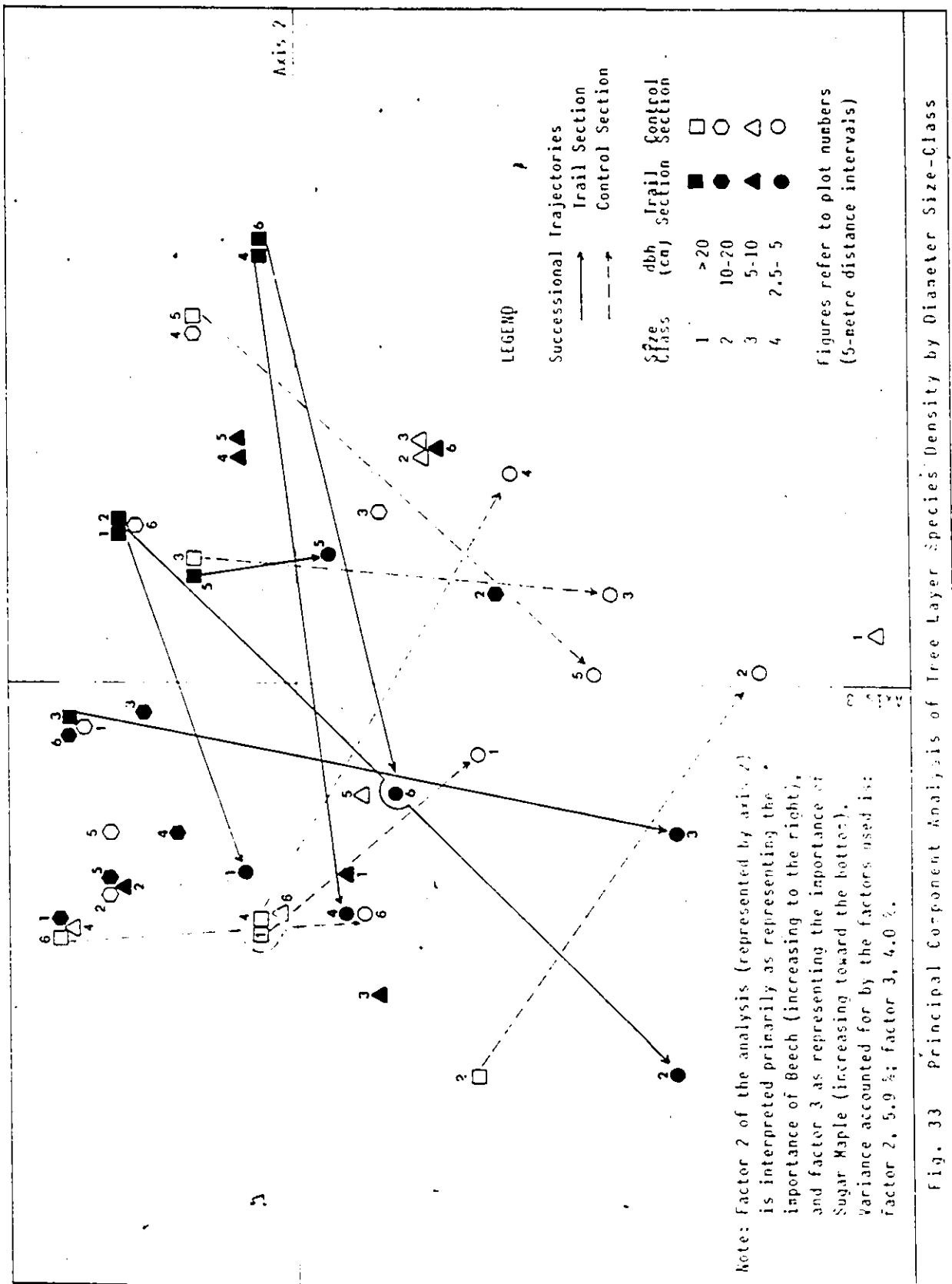
control counterparts. The incidence of dead branches or truncated leaders was also lowest in the trail edge plots.

Multivariate Analysis

The diameter-size-class ordination of tree species density, by principal component analysis, is illustrated in fig. 33. The main purpose of this ordination was to trace successional trajectories (Goff and Zedler 1972; Austin 1977; Enright 1982) by considering the size-class distribution of different species within a plot to indicate the probable successional replacement sequence. The diameter size-classes and their equivalence to structural layers are outlined in table 6. In general, size-class 1 consists mostly of canopy trees, size-class 2 of the subcanopy layer, size-class 3 of both subcanopy and lowest layer trees, and size-class 4 entirely of lowest layer trees. Species density data for each size-class in each plot was considered as a separate entity and is represented on the scatter diagram. 5-metre distance intervals were used for this analysis.

The axes on the scatter diagram appear to largely represent gradations of the two principal tree species, Beech and Sugar Maple. When interpreted as such, however, the scales are not absolute. Sugar Maple is represented by the vertical axis (with highest values below axis 2) and Beech by the horizontal axis (with highest values to the right of axis 3). Arrows on the diagram connect only size-classes 1 and 4 for each plot as it was not possible to legibly outline complete trajectories.

¹ The majority of T2 trees in this size class are found in the control section from 0-15 metres where the density of this layer (and Beech in particular) is very high.



No consistent pattern in size-class trajectories is apparent except for a general increase in the importance of Sugar Maple with decreasing diameter size (i.e. downward trend on the vertical axis) starting at size-class 3¹ but most noticeable at size-class 4.

A comparison of the ordination results for trail and control data suggest two possible changes in successional trends induced by the trail opening: (1) the suppression of both Beech and Sugar Maple in the smallest size-class in the trail edge plot (separated from other members of size-class 4 by axis 3)¹, and (2) the exaggeration of a trend toward the dominance of Sugar Maple in trail plots 2 and 3. These trends will be examined in the discussion section along with relevant findings for the shrub and ground layers.

1

Apart from the low densities of Maple and Beech, the compositional distinctiveness of the trail edge plots (i.e. the important edge species component in size class 4) is not represented on the diagram. As noted earlier, the similarity measure used for the PCA (Gower coefficient) tends to emphasize abundances of the most dominant species. This characteristic is an advantage in this instance since the long term trends of the major species is of interest.

DISCUSSION

In order to put the study results into perspective, the discussion begins with a comparison of findings with previously published work. An overview of edge microenvironment follows. The project results are then considered in relation to the past in a reconstruction of the probable development sequence since the opening of the trail, and in relation to the future in a projection of present forest development trends. When results have been considered in relation to the past and future, certain theoretical implications are addressed (reciprocal replacement, continuity / discontinuity, community stability). To end the discussion, management implications of the results are briefly considered.

COMPARISON OF RESULTS WITH PREVIOUS FINDINGS

Differences in study objectives, approaches and assumptions preclude a definitive comparison of findings with previously published work. In addition to these factors, differences in study location, community type, and in edge age, orientation, and maintenance in many cases limit the validity of comparisons. The comparison is structured under the following sub-headings: impact distance, edge delimitation, species abundance/size,

species richness, species composition, structural adaptation, and variability.

Impact Distance

The impact distance of 10-15 metres identified in this study falls within the range of 2-30 metres found in the literature for the width of forest edges. Principal factors influencing impact distance appear to be land use, corridor width, aspect, latitude, topography, and community type.

In their work directed toward eliminating edge-effect bias in forest sampling, Finney and Palca (1947) cite one crown width (2.5-5 m in young stands; 12-18.5 m in old stands) as an approximation of edge depth. Gysel (1951) and Wales (1972) studied advancing or unstabilized edges on north and south aspects. Gysel found edge width ranges of 2-10 metres but noted great variability in the width and distinctiveness of edge communities. Wales found depths of 10 and 20 metres on north and south edges respectively, and concluded that although microclimatic differences resulting from edge orientation were important, the overriding influence on edge width was land use history (i.e. edge maintenance/abandonment). Ranney et al (1981) found similar edge widths to those of the current study (10-15 metres) for north, south, and east edges; however, on west edges they observed a 30-metre or greater depth. They also cited land use factors to account for these differences. Dale and Weaver (1974), studying impact effects of hiking/riding trail corridors on Rocky Mountain forests found effects only to 1-2 metres of the trail edge. The width of these trails, however, did not exceed

2.5 metres¹. Ranney (1977) notes that latitude influences edge dimensions because of its effects on solar angle and accordingly on the amount of solar radiation received and the depth to which solar radiation penetrates. These factors are also influenced by topography. Community type is additionally considered to affect edge width; edges in spruce-fir forests, for example, are narrower than in northern deciduous forests (Horn 1971; Ranney 1978).

Edge Delimitation

Edges were delimited according to different characteristics in the studies reviewed. In the current investigation, the range of trail influence appeared to vary with structural layer and variable measured (see table 7). Contrary to other findings (Ranney et al. 1981), a vegetation discontinuity was found in the groundlayer from 5-10 metres, and a less marked discontinuity in the lower shrub layer from 15-20 metres². Although effects were most marked to 10 metres, 15 metres represents the inward extent of elevated values for species density, cover, and richness in the lower shrub layer; it also represents the inner extent of high variability for these parameters which tended to stabilize inwards from 15 metres. Impact distance for these variables appeared to be less in the other structural layers. Elevated values were found up to 10 metres from the edge in the upper shrub and subcanopy layers and up to 5 metres in the ground and lowest tree layers. Structural adaptation effects were most

¹ 13-16 m in the present study.

² See p. 123 for a discussion of these discontinuities.

evident to 10 metres.

Ranney et al. (1981) found no abrupt discontinuity that could be used to separate edge from interior. They found that continuous decreases in species richness, density, and basal area, and the variability of these values stabilized inwards of 10-15 metres. In the ground and shrub layers, however, they observed high density values only in the first few metres. Wales (1972) found that the inner margins of the unstabilized edges that he studied corresponded to the position of the original forest/field edges. These margins were characterized by tree densities comparable to the interior but by a significantly higher basal area. Canopy trees at these margins exhibited characteristics of edge trees (e.g. lower branching on stems, with branches extending towards the exterior). These margins also represented the inner limits of high numbers of values significantly different from the interior for tree density and shrub-herb cover.

Species Abundance/Size

A reduction in the average size of the dominant biota is a characteristic of most stressed communities, regardless of stress type (Rapport et al. 1985). Classic studies illustrating this response along a gradient of stress intensity are those of gamma-ray radiation exposure (Woodwell and Whittaker 1968) and smelter sulphur dioxide emissions (Gorham and Gordon 1960; Gordon and Gorham 1963; Luzon 1971; Freedman and Hutchinson 1979). Although the stress in the current study is non-toxic and can be considered of the positive or 'subsidy' variety (Odum et al.

1979), the findings clearly indicate a dramatic increase in density and cover in the smaller size classes adjacent to the trail edge (figs 10-11). In the studies reviewed, however, with the exception of Cole (1978), although species abundance was found to be consistently high in edges and to decrease toward the interior, the structural layers in which these characteristics were most marked varied. Edge age (or elapsed time since edge initiation) appears to be the main differentiating factor here.

In the present study (edge age 14 years), increases in density and cover were most dramatic in the ground and shrub layers, and some of these effects extended to the lower tree layer. No density effects were evident in the canopy or subcanopy layers. In addition, except for slightly higher values (within the control range) in the subcanopy layer from 5-10 metres¹, basal area was not significantly affected in the edge zone. In contrast, Ranney et al (1981) who studied edges primarily within the age range of 40-100 years found less distinct trends for the ground and shrub layers, yet marked trends for the density and basal area of trees. These differences appear reasonable when edge age is considered. Tree density effects could not be reflected above the lower tree layer within the 14 years since trail opening of the current study. Furthermore, since basal area is partly dependent on density, large increases would not be expected for the limited sample size. In older edges, however, some of these effects would be expected in canopy and subcanopy trees that became established

¹Also highest cover values in study area for this layer.

or were released at the time of edge initiation. In addition, the lateral extension of canopy crowns (Trimble and Tyron, 1966) as well as the dense growth of small trees would reduce light intensities closer to the edge so that shrub and groundlayer responses would tend to be restricted to a narrow margin of the trail edge. These effects are consistent with the findings of Ranney et al.

In a beech-maple woodland in southern Michigan, Gysel (1951) observed the frequency and cover of groundlayer species to be much greater in border areas than the interior; the density and frequency of saplings (>1 m; <10 cm dbh) to be much greater; and the density and frequency of larger size classes to be not much different. Wales (1972) found increased density and basal area in edge zones in an oak-hickory forest in New Jersey. With the exception of basal area, these findings are consistent with those of the present study.

Revel et al (1984; Dougherty et al. 1986) found tree cover adjacent to seismic lines ¹ in a Lodgepole Pine-Black Spruce forest in southwestern Alberta to be slightly greater than in control plots, shrub cover to be noticeably greater, and herb cover to be about the same. Using a comparative growth index based on diameter ², they determined that the radial increment growth rate of all ages of the two dominant tree species adjacent to seismic lines was 33-45% greater than that of

¹ Plots extending 0-5 metres from the edge.

² CGI = (post-seismic line-cutting increment/pre-seismic line-cutting increment) x 100.

interior control trees. Growth rates were greatest when temperature, light, and site moisture conditions were not extreme and when stand density was high. In the present study, elevated mean tree diameter from 0-10 metres was noted in the subcanopy layer¹, and in the lowest tree layer for Sugar Maple². Contrary to other investigations, Cole (1978) found a decrease in groundlayer cover immediately adjacent to, and two metres from the edge, of hiking trails in the northern Rocky Mountains of Oregon. This decrease was attributed primarily to trampling stress.

Species Composition

Consistent with the stress-response synthesis by Rapport et al. (1985), changes in species composition in the current study, and in those studies reviewed, indicate a retrogression of the vegetation community to an earlier successional stage. Although effects were less marked in the seismic line study by Revel et al. (1984), all other studies reviewed found a significant difference in species composition at forest edges when compared with the interior. Under stress, the most responsive species are necessarily those specialized for, and limited by, the niche parameters modified (Hurd et al. 1971). Changes in species

¹ Values were within control range.

² Apart from the small sample set on which these measurements were based, mean diameter is not a sensitive measure of impact as it does not take into consideration local site conditions, tree age, or individual growth rates of trees. The CGI used by Revel et al. overcomes these difficulties. Although tree cores were taken for all Beech trees >10cm dbh, time limitations did not permit an analysis of these cores. In any event, sample size would have limited generalizations from such an analysis.

composition at forest edges therefore reflect the decline or elimination of shade-tolerant mesic species, an increase in less shade-tolerant species, and the invasion of opportunistic species more tolerant of environmental extremes. Significant factors influencing species composition at forest edges appear to be edge orientation, edge maintenance form, edge age, and corridor width.

In the current study, shade-intolerant 'edge' species were confined to a zone within 8 metres of the trail margin. Of the 66 species found within the study area, 36% were found only at the edge, and 30% were absent from the edge. Comparable figures in Gysel's (1951) study are 61 species, 31% and 3%. The order of magnitude of difference in the last figure (i.e. interior species not found at the edge) is probably primarily due to the difference in edge maintenance and edge age for the two studies. Gysel studied advancing edges of varying age, and noted that the original border trees had developed wider and longer crowns with low overhanging side branches (up to 9 metres) which caused shading of the ground surface and the accumulation of a litter layer. A dense growth of subcanopy trees and saplings had developed at the outer edge of this overhang, further reducing light intensities. This environment inhibited the growth of shade-intolerant species which were mainly restricted to the shrub community beyond the extent of the upper tree canopies. The border area was therefore quite conducive to the growth of interior species up to this outer zone. In the current study, structural adaptation of canopy trees was far less advanced; in

0 addition, the edge was maintained mid-way between the stem and canopy dripline. As a result, exposure (to insolation, wind etc.) was much higher in the edge zone and created a much more hostile environment for interior species.

In a floristic study of an oak-hickory forest in New Jersey, Frei and Fairbrothers (1963) identified 312 species of vascular plants of which 22% were found only in edge zones, and 43% were absent from edge zones. For the purposes of their study, however, an edge was defined as "a strip of land approximately 4 feet wide extending from the last visible furrow of cultivated land where it could be seen adjoining the Forest". Thus defined, the edge zone was restricted to the outer margin of that considered in the current study, and was accordingly even more likely to be inhospitable to interior species.

Studying advancing north and south edges of the same forest in New Jersey, Wales (1972) noted species segregation within and between edges. He found species characterized by shade intolerance and good vegetative reproduction to be most prevalent at edges, with a greater incidence of intolerant xeric species on south edges. Ranney et al. (1981) studied edges at all four cardinal directions, and also found the incidence of tolerant species to vary with aspect as well as with distance from the edge. Their findings showed shade-intolerant xeric species to be most prevalent along south and west edges, and those of intermediate tolerance to be favoured along north and east edges. The absence of a notable complement of xeric tolerant species in the current study (SSW exposure) can be related to the diverse topography of the area and the resultant shading and sheltering

effects by adjacent and opposite slopes, as well as by canopy trees on the opposite side of the trail. The greater importance of the less shade-tolerant White Birch in the more exposed unit 3 (compared with the greater abundance of Yellow Birch in units 1 and 2) seems to support this supposition. Consistent with the findings of the current study, all investigations in beech-maple communities found a decrease in the importance of Beech towards the edge. Most studies also found a similar although less pronounced distributional pattern for Sugar Maple. Elevated values for this species in a secondary buffer zone interior to the edge (i.e. 5-15 metres in present study) were not observed in other investigations. Data presented by Ranney (1978) clearly demonstrates the absence of this effect.

Species Richness

A reduction in species diversity is one of the most widespread responses of ecosystems to stress according to the synthesis by Rapport et al. (1985). The authors do, however, note a few exceptions to this general rule, quoting two instances of terrestrial physical restructuring that resulted in higher species diversity of birds. The current study as well as the edge studies reviewed can be added to this list of exceptions. In fact, this high diversity response is a component of the 'edge effect'¹. This response may also be related to the 'subsidy' effect of some types of stress at low levels of impact noted by Odum et al. (1979).

¹

See introduction pp. 8-9.

The pattern of species richness in the current study and in the studies reviewed largely parallels that outlined in the previous section for species abundance. Consistently high in edges, species richness decreased toward the interior. Variations among studies in the structural layers in which these characteristics were most marked¹ can similarly be related to edge age.

Only one of the studies reviewed showed a weak response for these characteristic trends. Revel et al. (1984) found a modest variation in mean species numbers from edge (34) to interior plots (28), and noted that shrub and herb species richness at the edge only marginally exceeded control values. In addition to age differences (10-30 years versus 14 years), these quantitative divergences from the current study may be partly attributable to corridor width (5-8 m versus 13-16 m) and to community type.

Structural Adaptation

Horn (1971) found that variations in incident light affect the growth form and the distribution of structural support in trees. Notable adaptation effects were observed by other authors (Gysel 1951; Trimble and Tyron 1966; Wales 1971). Because of the relatively young age of the ski trail corridor in the present study, structural adaptation effects, although evident, were less marked. If the results are not spurious, however, effects on canopy trees appear to extend a surprising distance into the forest (10-20 m).

¹ Highest in the current study in the ground, shrub and lowest tree layers.

Variability

Variability appears to be characteristic of edge vegetation and has been related by individual authors to land use and to light intensity. Topography is suggested by the current study as a third influencing factor.

Gysel (1951) observed high variability in the width and distinctiveness of border communities and in the structure and composition of edges within the same woodlot and between different woodlots. Variations in lower strata cover appeared to correlate with available light. Wales (1972)—also noted considerable variation with distance from the edge and between sample plots, particularly for shrub and herb species. Ranney et al. (1981) found the outer portions of edges to be extremely variable and noted a decline in variability from 0-15 metres from the edge. They, in fact, used variability to assist in the delineation of edge width. In their study, variability in edges appeared particularly high for tree and sapling (T1-T3) density, basal area, and species richness. High compositional variability was found even within edges of similar aspect. Ranney et al. inferred that much of this variability resulted from differing land use histories of the edges studied.

In the current study, considerable variability was noted between replicate plots for density, cover, and species richness in the shrub and lower tree layers. This variability extended to 15 metres in the shrub layers and to 5 metres in the lowest tree layer (Tables 7-8).

Unit 3 showed the most dramatic edge response, with edge

plot density and cover values in the upper shrub and lowest tree layers significantly exceeding those for the other two units. Yet the density and cover of the lower shrub layer were actually higher in units 1 and 2. A number of factors may have contributed to an initial stronger and subsequent reduced response in unit 3. At the time of trail opening, additional sidelighting contributed by the upper part of the trail (fig. 3) may have increased light intensity and provided an additional stimulus to growth in unit 3 resulting in high density and cover of the ground and lower shrub layers (present upper shrub and lower tree layers). At the same time, the unit's position at the base of a steep rise would have increased exposure to wind and downdrafts from the upper trail section. The high relative importance of the shade-intolerant White Birch in unit 3 (compared to the more tolerant Yellow Birch in the other two units) would appear to support altered microclimatic conditions of this nature. Initial dense growth of these layers, however, would have quickly reduced the sidelighting advantage of unit 3. The overhead canopy would have further contributed to lower light intensities. In addition to lower S2 density and cover values, factors supporting this hypothetical development history are the significantly lower importance of intolerant shrub species in this layer in unit 3, and reduced current light levels (fig. 5).

Variability interior to the edge plot appears to be directly related to this differential outer edge response. S2 cover values in unit 3 are significantly reduced from 5-10 metres, but density and cover values are comparable to control values from 10-15 metres. Values in units 1 and 2, on the other hand are

elevated to 15 metres. It accordingly appears that the buffering effect of high edge plot density and cover has effectively reduced the current distance of trail impact by 5 metres in unit 3 by restoring interior conditions at a much faster rate than in units 1 and 2¹. The proposed mechanisms for this effect (i.e. increased exposure and sidelighting resulting from trail layout with respect to topography) would suggest topography as an additional factor influencing edge depth and variability.

EDGE MICROENVIRONMENT

Forest edges reflect steep microclimatic gradients between the extremes of open land and forest interior (Wales 1972). At edges, light intensity, wind flow patterns, and the temperature and moisture of the soil and air can differ considerably from the interior forest.

Solar radiation appears to be the most important microclimatic variable influencing forest edge (Ranney 1977). Radiation intensity, the proportions of direct and diffuse radiation, and the depth to which solar radiation penetrates a forest edge depend on factors such as solar angle², edge aspect

¹
The interpretation of faster recovery (as opposed to a shorter initial impact distance) is supported by a high groundlayer density in unit 3 from 10-15 m of the trail edge (exceeding values for units 1 and 2 by 74% and 41% respectively). This higher groundlayer density cannot be explained by current (lower) light intensity values. It is likely, therefore, that this layer contains suppressed seedlings which, in units 1 and 2 would have succeeded to the S2 layer.

²
Solar angle, in turn, depends on latitude, time of year, and time of day (Ranney 1977).

(Wales 1967, 1972; Swift and Knoerr 1973; Holland and Steyn 1975; Ranney et al. 1981), topography (Swift and Knoerr 1973; Holland and Steyn 1975), cloudiness (Geiger 1975), the reflectivity of the ground surface (Lykowski 1970; Colwell 1974), and the density, height, and composition of the edge (Geiger 1975; Ranney 1977). Within the zone of radiation penetration, light intensity and summer daytime temperatures of both air and soil are higher than in the forest interior (Geiger 1975; Ranney 1977). Increased light and temperature stimulate vegetation growth and result in increased evapotranspiration and soil moisture loss. Lacking the protective influence of the interior forest, forest edges also experience higher wind velocity and air circulation, and greater diurnal and seasonal temperature variations (Geiger 1975; Ranney 1977).

Precipitation interception, snow accumulation, and runoff patterns at the edge also differ from the forest interior (Geiger 1975; Ranney 1977). A study of snow accumulation and ablation rates in forest openings of sizes varying from 1/4 to 6 tree heights in diameter (Golding and Swanson 1978) suggests high precipitation input and retention in openings three quarters to one tree height in diameter (i.e. comparable to ski trail width). All openings, in fact, had higher values than those of forest interiors. However, a number of factors tend to reduce the soil moisture status at the trail edge. Firstly, the sloping land surfaces of the trail and adjacent areas facilitate runoff.

¹ Shading by opposite and adjacent slopes, as well as slope inclination interior to the edge.

Secondly, increased evapotranspiration resulting from elevated light and temperature tend to deplete soil moisture. Higher wind velocity and air circulation at edges additionally increase evapotranspiration and reduce soil moisture and humidity (Geiger 1975; Ranney 1977). Lower soil moisture levels extending up to 5 metres into the adjacent forest were noted by Revel et al (1984) on northern edges (southern aspect) of E-W seismic lines. Lower soil moisture at forest edges was also measured by Oosting and Kramer (1946).

Overall, forest edges tend to experience more xeric conditions and greater temperature extremes and fluctuations than forest interiors and are accordingly areas of greater environmental stress (Ranney 1977).

Although this study was confined to the measurement of trail impact effects on adjacent vegetation, an approximation of the most important microclimatic variable affecting forest edges was considered desirable, and light intensity was used as a surrogate for solar radiation. It is probable that trail section light intensity values slightly exceeded control section values even before the trail was cleared. Higher present-day values 30 metres from the trail edge and beyond the range of trail impact effects on the vegetation would appear to support this conclusion. Following trail opening, the original light intensity gradient would have been reversed by sidelighting, probably from 0-15 or 20 metres. Beyond this distance, (1) the present-day gradient begins to parallel the control trend, and (2) no vegetation effects that could be attributed to trail

0 impact were noted. In contrast to the discontinuous nature of the present gradient (fig. 5), the light intensity slope at trail initiation would have decreased relatively continuously from 0-15 or 20 metres of the trail edge¹.

VEGETATION DEVELOPMENT FOLLOWING TRAIL OPENING

In the more extreme microenvironment created by the trail opening, sensitive interior species declined and in some cases disappeared, and fast-growing shade-intolerant species became established adjacent to the trail. In this high-light environment, the existing shrub layers and the new ground layer grew vigorously. In time, a dense buffer zone of shade intolerant tree and shrub species became established in the shrub layers that would eventually reduce interior light intensities. Within the 14-year period following trail opening some fast-growing edge species grew to the height of the lowest tree layer. This edge zone is currently characterized by high species richness, density and cover values in the ground, shrub, and lowest tree layers; by the importance of shrub and herb species; by the absence of many interior species; and by the high relative importance of edge species.

Interior to this zone, toward the range limit of edge species, and in intermediate light intensities, a secondary buffer zone of Sugar Maple became established. Growth of this species was particularly vigorous in terms of density and cover from 5-15 metres, as presently exemplified in the shrub and

¹ See pp. 123-124 for discussion of continuity/discontinuity of microclimatic and vegetation gradients.

lowest tree layers (fig. 8; table 7). An apparently less successful competitor in these conditions, Beech¹ became suppressed to a distance of 15 metres from the trail edge. Low values in the shrub and T3 layers reflect this suppression.

The rapid growth of these two buffer zones may have resulted in considerably reduced light levels at the ground from 15-20 metres of the trail edge. The low density and cover values in the S2 layer (lowest in the trail section) may be relicts of these lowered values² (figs. 10-11).

Continued shading from edge species in the flourishing outer buffer zone and increasing cover of the subcanopy tree layers eventually led to a dramatic drop in light intensity at ground level closer to the trail. Present-day low light intensities from 5-10 metres of the edge (fig. 5) result from this shading and are reflected by very low density, species

¹ Although the specific mechanisms are not clear, environmental requirements for seedling growth may have favoured the establishment of Sugar Maple over Beech in this zone. Beech seedlings require warmth, humus and shade for rapid growth and are susceptible to drying. Sugar Maple is more competitive in the open (Frothingham 1915), and although comparative growth rates are not readily available, statistics provided by Fowells (1965) suggest that Sugar Maple has a faster growth rate than Beech for at least 25 years following establishment.

² An alternative explanation for these low values may be site factors: two of the three replicate plots had steep slopes with very irregular microrelief. On the other hand, the third plot with gentle slopes and only slightly irregular microrelief had comparable density values and the lowest cover values. A number of fallen tree stems were, however, recorded in this plot. A site factor explanation would appear to be supported by the fact that the S2 layer discontinuity is echoed by low density and cover values from 15-20 metres in the G1, T3, and T2 layers, effects that could not be attributed to trail impact or to present-day light intensity values (lowest 20-25 metres). The discontinuity is also not evident on the transect profiles of the CA first axes for the shrub layers (fig. 27).

richness, and cover values in the groundlayer. This reduction in light levels interior to the edge must be a relatively recent development as the dense S2 layer, initiated at a time of higher light intensity, is unlikely to be more than 7 years old¹.

Trees that were established before the opening of the trail were not insensitive to the changing microenvironment. In the lowest tree layer, Sugar Maple increased in diameter adjacent to the trail and in cover from 0-15 metres. Subcanopy trees close to the trail increased in mean diameter, and those from 5-10 metres increased in cover. All layers of trees responded to increased light intensities by growing toward the new light source. Present stem inclination and longest branch orientation toward the edge reflect this behaviour. Although these effects were most evident in the plots adjacent to the trail, possible effects were noted up to 20 metres in the canopy layer.

FUTURE FOREST DEVELOPMENT

As long as the trail is maintained in its present position, the first five metres of the edge will probably equilibrate at a younger successional age than the interior forest because of differing environmental conditions. An analysis of species composition by structural layer suggests that an initial White Birch-Sugar Maple association will yield to a White Birch, Yellow Birch and Sugar Maple community; this community should eventually give way to a Yellow Birch-Sugar Maple forest with an admixture

¹
1.5-5.5 years for the Sugar Maple component judging by growth rates for this species (Fowells 1965).

of Beech¹. A significant number of interior species will be permanently absent from this edge zone (currently 30% of all species found within the study area). On the other hand, a component of shade-intolerant species should persist close to the edge. Although the present range of edge species extends to 8 metres of the trail edge, it is expected that reduced light intensities resulting from growth of the vegetation itself will result in a reduction of the effective edge width.

From 5-15 metres of the trail edge, Sugar Maple will likely succeed Beech as the dominant species for the foreseeable future. Both the diameter size-class ordination of trees (fig. 33) and an analysis of species importance by structural layer (fig. 34; table 7) indicate this future dominance for Sugar Maple. The exceptionally high values for this species in the ground, shrub,² and lower tree layers and the less dramatic but evident suppression of Beech in the shrub and lowest tree layers are probable responses to the trail opening. The trend toward Sugar Maple dominance does not preclude the re-establishment of Beech in the canopy layer in the long term. The microenvironmental conditions that induced the strong growth response in Sugar Maple are being modified by the dense growth of the vegetation itself. Conditions favourable to the competitive re-establishment of

¹ The persistence of Beech in the edge zone is uncertain. In addition to its competitive disadvantage in terms of light intolerance, Beech is susceptible to sunscald on account of its thin bark. It is also highly susceptible to sap-rotting fungi that enter through sunscald and other wounds that heal comparatively slowly (Fowells 1965).

² High relative and absolute values in the ground and shrub layers; high relative values in the lower tree layer.

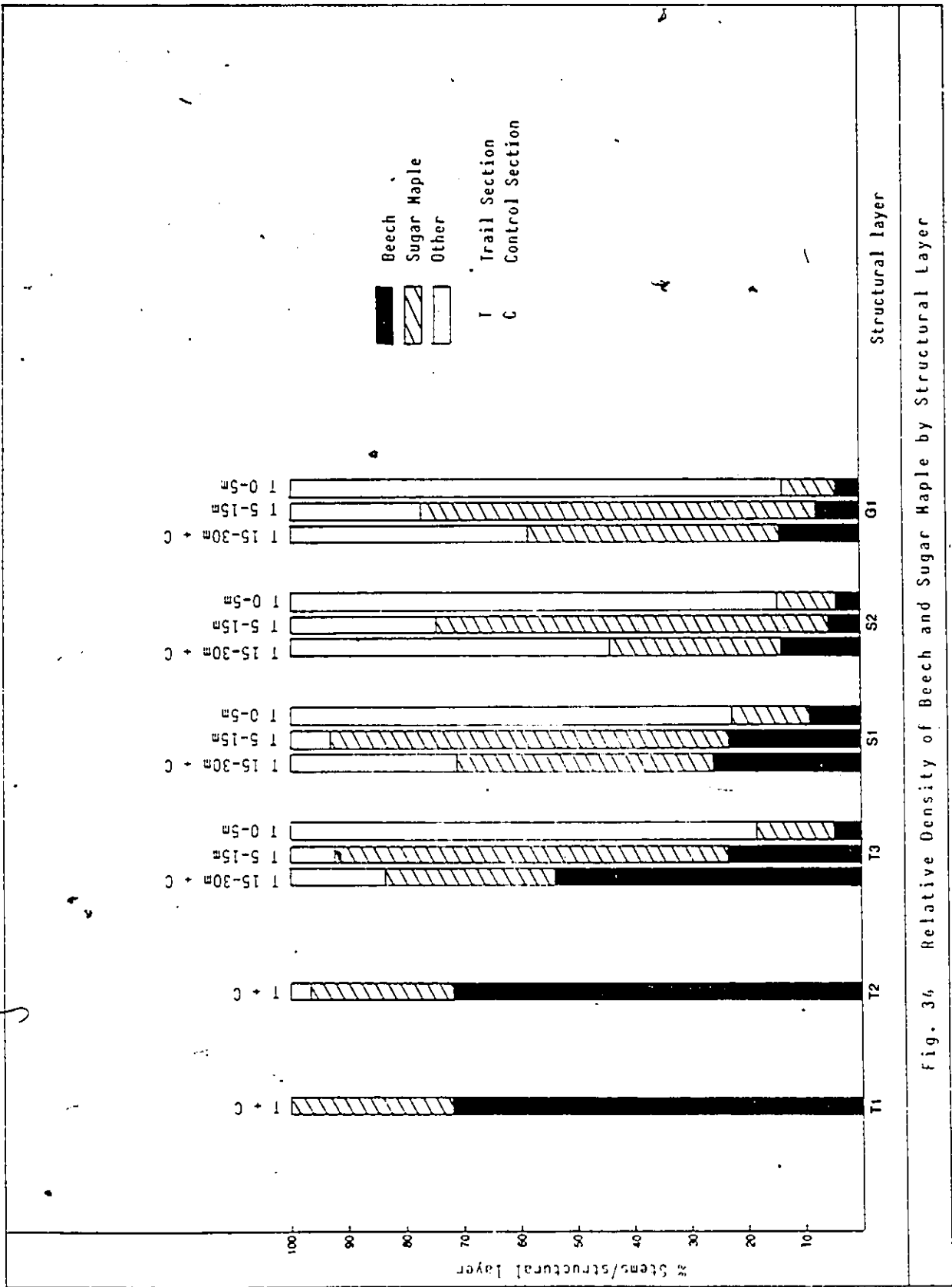


Fig. 34 Relative Density of Beech and Sugar Maple by Structural Layer

Beech may accordingly be restored. Possible evidence of this recovery is the fact that in the groundlayer Beech density and frequency exceed comparable control values beyond 10 metres of the trail edge.

Beyond 15 metres of the trail edge, and in the control area, future canopy dominance is less certain but will probably be by Beech for some time to come. The interior forest appears to be in a state of relative equilibrium at a comparatively advanced successional stage¹. Precluding a major disturbance, future development, uninterrupted by the presence of the trail should be primarily restricted to the process of tree-by-tree replacement by advanced reproduction in canopy gaps created by fallen trees. Apart from its dominant and occasionally co-dominant position throughout the subcanopy tree layers in these areas, Beech grows faster than Sugar Maple, upon release, in the diameter size range

¹
Evidence used to support this conclusion is as follows:

1. The codominant species, Beech and Sugar Maple, are shade-tolerant climax species;
2. The all-age population structure of the dominant species shows a proportion of stems in the subcanopy layers > the canopy layer;
3. The 24 m height of one edge Beech tree that was measured (36.6 cm dbh vs. largest in area 49 cm dbh) is at the top of the average height range for that species (Fowell's 1965);
4. The age of canopy trees is probably in the order of 100-200 years; the largest Sugar Maple tree with a diameter of 61 cm may be more than 250 years old (Frothingham 1915; Morey 1936);
5. The maple-beech community is considered the climax community of the region (Lafond and Ladouceur 1968) and appears to be the most widespread in the area above 250 m where site conditions are not extreme (fig. 2).

above 5 cm (Fox 1977)¹. Its chances of succeeding to the canopy layer are accordingly very high in spite of a general trend toward increasing Sugar Maple importance with decreasing diameter size that was noted in the size-class ordination of trees. Sugar Maple is considerably more important than Beech in the shrub and ground layers in these interior areas (fig. 34), a likely indication of canopy dominance for this species in the more distant future. Lower mortality for Beech with increasing age (Forcier 1975)² could in time reduce this gap, however, and in some instances lead to shared dominance. The fact that the current relationship is in some areas more equivocal for frequency than for density would support this possibility.

THEORETICAL IMPLICATIONS OF FINDINGS

Reciprocal Replacement

The coexistence, in a climax ecosystem, of canopy species with apparently similar site requirements appears inconsistent with the competitive exclusion principle (Forcier 1975). This principle predicts the ultimate demise of one species when two species compete for the same limiting resources. Such coexistence accordingly implies some differences in the factors limiting the two species (Levin 1970). Although site requirements for mature trees of two or more species may be

1

Based on studies in New Hampshire and Pennsylvania.

2

A survivorship table for Beech and Sugar Maple growing under closed canopy (Forcier 1975) shows a lower mortality rate for Beech with increasing age (with the gap becoming particularly noticeable after 5 years) and an overall Beech/Sugar Maple survivorship ratio of 2:1 over the first 10 years of growth.

similar, niche variables for these species may differ considerably in their early developmental stages. Canopy influence is one factor that could cause microenvironmental changes that might be experienced differentially by two species in the developmental stages. If one species is more competitive under the canopy of another species than its own, species alternation or reciprocal replacement (Woods 1979) could provide a mechanism for the persistence of both species in the canopy layer.

A number of studies have suggested the reciprocal replacement of the codominant species in a beech-maple forest (Forcier 1975; Fox 1977; Woods 1979; Runkle 1981). In a number of forest types dominated by two species, Fox (1977) found the reciprocal relationship to be strongest in a beech-maple association; he also found the relationship to be most marked in monospecific patches of either species. The studies cited (with the exception of Forcier) found Sugar Maple saplings¹ associated with Beech canopy and the converse. Forcier studied species replacement in a Beech-Sugar Maple-Yellow Birch climax forest in New Hampshire, and found Sugar Maple saplings associated with Yellow Birch canopy, and Beech saplings associated with Sugar Maple canopy; neither Birch nor Sugar Maple saplings appeared associated with a Beech canopy. Forcier hypothesized a cyclic Yellow Birch-Sugar Maple-Beech succession initiated by endogenous disturbance and based on the differing reproductive

1

The definition of "sapling" varied considerably as follows: >0.5 m height, <2 cm dbh (Forcier); 5-33 cm dbh (Fox); >2 m height, <12.5 cm dbh (Woods); >1 m height, <25 cm dbh (Runkle).

strategies of the three species that ensured their simultaneous persistence.

In view of these findings in beech-maple communities, and in particular, monospecific patches, results of the present study were examined for evidence of species alternation and for potential effects of trail impact on such a replacement process. Considering regeneration of the S1 and S2 shrub layers (Forcier's definition of sapling), it is apparent that Sugar Maple is of greatest importance, regardless of canopy species (fig. 22). As Beech is the dominant canopy species throughout most of the study area (except control plots 0-10 m) it could be concluded that the reciprocal relationship appears to hold when Beech is the dominant canopy species. Although this outcome appears most certain in trail section plots from 5-15 m (as discussed earlier and primarily attributed to trail impact effects), mortality rates could affect the final outcome in the remaining plots where Sugar Maple dominance is less pronounced. Whether or not complete species alternation eventually takes place, there is no doubt that Sugar Maple will be of increasing importance in the canopy layer in the more distant future. There is also little doubt that some additional factor (i.e. trail impact) has emphatically reinforced this trend from 5-15 metres of the trail edge.

On investigating species alternation and the maintenance of codominance in a beech-maple forest in Michigan, Woods (1979) found high mortality under conspecific canopy in saplings between two and four metres in height (S1 layer). Fox (1977) also

concluded that events responsible for species alternation took place before the lower size limit of his sapling range (5 cm dbh). Results of the present study are consistent with these findings and indicate that, of the layers in which these observations were recorded (S2-T1), mortality, disease and dead or broken leaders were highest in the upper shrub and lower tree layers. In view of these findings, prediction of future species dominance might appear more reliable when based on existing relationships in the subcanopy tree layers. (The reciprocal relationships established by Fox, Woods, and Runkle were also based on these larger size classes although class limits differed¹.) When only subcanopy trees >2.5 cm dbh are considered as potential successors to the canopy layer, the reciprocal replacement hypothesis, at least for the proximate future, holds only for plots from 5-15 metres of the trail edge. Beech saplings, thus defined, are dominant or co-dominant in all plots other than 5-15 metres in the trail section, regardless of canopy species (principally Beech). As the importance of Sugar Maple from 5-15 metres of the trail edge is of note only in the lowest of the tree layers, the relationship in this case appears to be attributable to the trail influence rather than to natural species alternation.

In summary, although the reciprocal replacement hypothesis has limited application for the near future (i.e. when subcanopy tree layer regeneration is considered alone), Sugar Maple replacement of, or codominance with Beech appears a good

¹ Runkle also included most of the shrub layer (see note 1, p. 120).

possibility in the long term, when the species composition of the ground and shrub layers is considered. Although the converse relationship is not evident in plots currently under Sugar Maple canopy dominance, the limited size of these areas would preclude¹ the definitive establishment of such a relationship in any case. Canopy influence is considered to be of limited importance in the apparent pronounced species alternation from 5-15 metres of the trail edge. The high importance of Sugar Maple in these areas is considered to be the result of trail impact, and the same result² would be anticipated under Maple canopy dominance.

Continuity/Discontinuity

Vegetation discontinuities are generally regarded as adaptive responses to environmental discontinuities (either natural or induced by disturbance). Such a discontinuity is implicit in the definition of the induced, abrupt edge of a ski trail corridor, and is perpetuated by trail maintenance. Based on the assumption that the microclimatic gradients imposed at the forest edge at trail initiation were relatively continuous from edge to interior, continuity of impact effects on the vegetation within this transition zone might be expected. It is interesting to note, however, how the buffering effect of the vegetation response has reinforced the abruptness of the transition between

1

It is interesting to note in support of the reciprocal replacement hypothesis that of the ten dead Sugar Maple stems found in the upper shrub and lowest tree layer in the study area, nine occurred under Sugar Maple canopy dominance.

2

One replicate plot from 5-10 metres of the trail edge under Maple canopy dominance showed the same effect.

edge and interior and has essentially produced vegetation and microclimatic discontinuities in a formerly continuous microclimatic gradient (figs. 5, 9-11). In the groundlayer, for example, although a relatively steep transition zone between the dense species-rich edge and the less dense and diverse interior might be predicted (as is evident in the shrub layers), the drop below interior values immediately behind the edge plots might not be anticipated. If not caused by site conditions¹, the less dramatic but evident discontinuity in the lower shrub layer from 15-20 metres of the edge may be a relict of the same origin. The groundlayer discontinuity will likely persist as long as the trail is maintained and the outer buffer zone remains intact. If the lower shrub discontinuity is a relict of the same origin, it will probably disappear over time as original conditions are restored.

Community Stability

As stated in the introduction, two components of relative stability can be used to define the response of a forest ecosystem to stress: resistance, the ability of a system to resist displacement from its initial state when subject to perturbation (Webster et al. 1975; Vitousek et al. 1981), and resilience, the ability of a system to return to a reference state following a disturbance or stress period (Webster et al. 1975). Since this study was concerned with the response of a forest community to stress induced by an open corridor, the principal findings (table 7) are indicative of the degree of

¹

See note 2, p. 114.

deflection from the initial state, or the resistance component of stability, measured in terms of vegetation structure and species composition. The first axes of ordination diagrams (e.g. figs. 15-16, 25-26) are graphic representations of the extent of this displacement.

The second component of relative stability--resilience--is more difficult to assess in the context of the present study as the concept implies removal of the source of stress or disturbance; yet, as long as the trail edge is maintained in its present position, the disturbance source will remain. In spite of this definitional problem, the results do suggest a remarkable capacity of the vegetation community to neutralize the stress and to restore initial conditions through the buffering effect of the dense zones noted (outer, shade-intolerant species; inner, Sugar Maple). As internal microclimatic conditions are restored by this vegetation response, the community is in turn adjusting to these changes. The effective width of the significantly altered edge community can accordingly be expected to diminish through time. Close to the edge, however, disturbance effects exceed the resilience threshold¹ of the community, and characteristics will remain permanently altered in the outer few metres of the forest as long as the edge is maintained². Although the original community will be restored interior to this zone, a long-term shift in the dominant species (i.e. from Beech to Sugar Maple)

¹ Amplitude (Westman 1978).

² Ranney et al. (1981) hypothesize a potential state of equilibrium for forest edges comparable to Clement's (1916) disclimax.

appears likely within 15 metres of the trail edge.

The ability of the beech-maple forest to buffer corridor disturbance would suggest considerable inherent resilience to this type of stress. Many authors have suggested that an ecosystem's ability to contend with specific stresses is partly related to its evolutionary history (Lugo 1978; Rapport et al. 1984). Evolutionary adaptation to stresses of a similar nature or within the same range of magnitude, duration, frequency, and spatial extent appear to confer on a system the ability to assimilate such stresses without degeneration to a permanently altered state or to total system disintegration (Woodwell 1970; Boesch and Rosenberg 1981). Corridor construction would appear to fall well within the range of variation of natural disturbances experienced by this forest community, namely, openings created by fire, wind, and ice damage, and by the senescence of canopy trees. The same response mechanisms appear to be activated in gaps or openings created by these disturbances: the rapid growth of residual vegetation within the opening (Bray 1956); lateral encroachment from the periphery (Trimble and Tryon 1966); and the appearance and shift of competitive advantages to new species dependent on openings for their persistence (Marks 1974). In time these openings disappear and the forest is restored to the natural range of variation of its initial state. Corridor maintenance, however, sustains the disturbance and counteracts these restorative efforts at the trail edge.

Both resistance and resilience concepts of relative

stability are defined in terms of a reference state (i.e. deflection from and recovery to this state). In the context of the current study, this state is defined by structural and species compositional characteristics of the vegetation, within the range of variation of control samples. It should be borne in mind, however, that value judgements are inherent in the definition of this reference state (Hill 1975; O'Neill and Reichle 1979). From a holistic ecosystem perspective, the restoration of overall functional characteristics of a system such as nutrient and energy flows could be considered sufficient to denote recovery. If a system retains its ability to absorb CO_2 , release O_2 , and process wastes, its functional integrity could be considered intact and changes in species composition disregarded as irrelevant. From resource management and recreationist perspectives, on the other hand, the ecosystem can be viewed as a support system for valued species; from an environmentalist or conservationist point of view, the preservation of the constancy of relationships and of existing species are of paramount importance. These latter viewpoints would accordingly require the incorporation of species composition into a definition of stability.

MANAGEMENT IMPLICATIONS OF FINDINGS

It is apparent from the results of this study that fragmentation by open corridors could have long term effects on the species composition of adjacent forests. These changes could extend to at least 15 metres of the trail edge. Although the beech-maple forest community at Mont-Ste-Marie appears to have

the resilience to restore interior microclimatic and community characteristics inwards of approximately 5 metres, effects on species dominance (i.e. replacement of Beech by Sugar Maple) can be expected to 15 metres. The outer 5 metres of the trail edge is likely to remain in a permanently altered state of younger successional age as long as the trail is maintained. It follows that the denser the network of corridors and the greater the resultant forest fragmentation, the more widespread these impact effects are likely to be.

Studies of forest islands in Wisconsin and New Jersey indicate that a minimum threshold size of 2-3 hectares is required to maintain interior forest conditions and accordingly the species adapted to this environment (Forman 1976; Levenson 1976; Ranney et al. 1981). This minimum critical size would be larger if the dense edge vegetation were absent (Forman 1976). Findings by Levenson (1976) suggest that a forest island width of over 100 metres would be required to permanently sustain Beech populations and about 15 metres to sustain Sugar Maple. Judging from the results of the current study, permanent alteration of the forest would occur if the trails were positioned 30 metres or less from one another. Beyond this distance, a certain minimum size of unimpacted forest would be required to sustain sensitive interior species. Although the complete absence of certain interior species from the trail section, and the appearance of others between 15 and 30 metres of the trail edge might result from fortuitious events (e.g. the unavailability of propagules or

¹
At the western edge of its range in Wisconsin.

0 suitable microsites), it is likely that some of these absences are related to trail impact. It might therefore be a conservative estimate to suggest a minimum placement distance of 60 metres between trails. This additional distance would appear particularly warranted if these trails were cleared at the same time, as the edge buffer zones would be absent. Although this minimum distance is generally currently exceeded except near trail intersections, a plan for future trail development close to the study area (fig. 3) reveals that considerably less than this minimum distance will be adhered to. Should this proposal be implemented¹, permanent alteration of the forest community can be expected to result in an 'all edge' environment prevailing in some of the forest islands that will be created.

Echoing the earlier discussion on perspectives and value judgements², the seriousness of these impacts would have to be interpreted in the light of management objectives in the area. The primary concern of management may be the maintenance of adjacent vegetation (regardless of structure or species composition) in order to maintain slope stability, reduce runoff and soil erosion, and to reduce wind velocity that might otherwise remove snow from the trails. The preservation of interior plant species, and of the wildlife species that depend on these interior habitats, may not be of concern or of high priority. If such is the case, the vegetation community could be

¹ In view of a recent change in ownership of the Mont-St-Marie ski area (summer, 1986), the status of these plans is uncertain.

² See p. 127.

viewed as highly resilient and the specific changes as unimportant, even though these changes might be viewed with some concern from the perspective of the forest or wildlife manager or the environmentalist. On the other hand, species characteristics that could influence the attainment of management objectives for the area (e.g. windfirmness, longevity, susceptibility to insect infestations and disease etc.) would also have to be considered, whether or not the preservation of these species per se was a concern.

Other factors that should be considered¹ by area managers in assessing potential impacts, and that have been held constant in the current study, are vegetation community type, successional age, edge aspect and edge maintenance (Ranney et al. 1981), and corridor width. A review of the literature and a comparison of results reveals, for example, that edge width (impact distance) appears to be less in some coniferous than deciduous forests (Horn 1971; Ranney 1978); community age at impact affects the type and extent of community transformation as well as the time requirements and potential for recovery; species composition of the edge community appears to be strongly related to edge aspect, with a greater component of xeric tolerant and shade intolerant species occurring on edges of south and west orientations (Wales 1972; Ranney et al. 1981)²; edge maintenance type influences impact distance³ (Wales, 1972) and the position of edge

¹ Maintenance form (e.g. canopy base, canopy dripline), and type (e.g. stabilized/maintained, advancing).

² This effect can however be modified by shading in topographically diverse areas as evidenced in the present study.

0 maintenance affects the rate of edge closure (i.e. slowest for edges maintained at stem base (Ranney 1978)); disturbance and impact effects appear to increase with trail width (Dale and Weaver 1974; Revel¹ et al. 1984) .

An additional factor that should be considered by area managers--the influence of topography on vegetation response and recovery--was identified in the current study. The mechanism of this influence is indirect, through effects of topography on solar radiation and on exposure to wind and temperature extremes. Topography would also influence drainage and soil moisture availability.

¹ In view of the apparent relationship between the intensity of vegetation response to impact, and recovery time (see discussion pp. 109-110), the recovery process may take longer on narrow trails.

SUMMARY AND CONCLUSIONS

Purpose

The purpose of this study was to investigate the impact effects of alpine ski trail corridors on the adjacent vegetation at Mont-Ste-Marie, Quebec. Specific objectives were to measure impact effects in terms of structural and species compositional changes to the adjacent vegetation; to measure the spatial variation of impact effects in terms of distance from the trail edge; and to consider implications of impact effects on future forest development.

Results

Results of the study indicate that the distance of impact effects, and the structural and species compositional characteristics that change, vary with structural layer.

Generalized findings are as follows:

- o Impact distance of approximately 10-15 metres;
- o Community retrogression or the return to an earlier successional stage of forest development characterized by changes in species composition: a decline in importance and the elimination of many "interior species" adjacent to the trail; the appearance of and high relative

Since the distance of impact effects was studied by structural layer, spatial variation was actually measured in two dimensions -- vertical as well as horizontal.

abundance of a considerable number of shade-intolerant 'edge' species from 0-8 metres of the trail edge; an increase in the importance of shrub and herb species from 0-8 metres of the trail edge.

- o A reduction in the average size of the dominant species as a result of increases in density and cover in the ground, shrub, and lowest tree layers for a distance ranging from 5 to 15 metres of the trail edge.
- o The development of two distinct buffer zones as a consequence of these increases in density and cover (outer--0-5 m--dominated by shade-intolerant species; inner--5-15 m--dominated by Sugar Maple).
- o Increases in species diversity (richness) in the ground, shrub, and lowest tree layers within 5 to 15 metres of the trail edge.
- o Increases in variability of density, cover, and species richness in the ground, shrub, and lowest tree layers within 5 to 15 metres of the trail edge.
- o Structural adaptation of trees to at least 10 metres of the trail edge.
- o The 66 species found within the study area were grouped according to distributional pattern as edge (36%), intermediate (17%), or interior species (47%). By definition, no edge species were found beyond 8 metres of the trail edge. 20 (65%) interior species were not found within 8 metres of the trail edge. Intermediate species were more common at the edge but were also found in the interior.

Future implications of an age (size) class analysis of these impact effects are:

- o A change in canopy dominance from Beech to Sugar Maple from 5-15 metres of the trail edge;
- o The maintenance of the outer edge zone (0-5 m) in a permanently altered state of 'arrested' successional development.

Some unique findings of this study are:

- o The appearance of a secondary buffer zone of Sugar Maple interior to the outer zone of predominantly shade-intolerant species. In addition to contributing to the restoration of the interior microenvironment and subsequent community characteristics, this impact response is likely to effect the replacement of Beech by

Sugar Maple as the future canopy dominant for a distance of 15 metres from the trail edge.

- o The transformation of continuous microclimatic and vegetation gradients into discontinuous gradients by the vegetation response to impact. Contrary to other findings (Ranney et al. 1981), not all gradients of observed variables were continuous from edge to interior. A discontinuity in the light intensity gradient between 5 and 10 metres of the trail edge resulted from shading by the dense outer zone. This discontinuity was echoed by all measured vegetation characteristics in the groundlayer. A further vegetation discontinuity appeared in the lower shrub layer from 15 to 20 metres of the trail edge and may be a relict of the same origin.
- o The intensity of the initial vegetation response to disturbance may affect the rate of restoration of impacted forest. A high intensity response may result in interior vegetation recovery at a faster rate than a low intensity response. Increased exposure and sidelighting appear to enhance the intensity of response. There may therefore not be a simple relationship between trail width and impact effects (i.e. reduced impact on narrower trails).
- o The effect of edge aspect on species composition is moderated by topography and by shading by canopy trees on the opposite side of the trail.
- o Trail layout with respect to topography can considerably influence the variability of the vegetation response.

Comparison of Results with Previous Findings

In the context of the stress-response framework developed by Rapport et al. (1985), trail clearance would be considered a¹ terrestrial physical restructuring stress. Two of the three characteristic responses to this stress type noted by these authors and relevant to this investigation are supported by the study results: system retrogression and a reduction in the average size of dominant biota. Contrary to the general tendency cited by these authors, however, species diversity increased

¹
See table 1.

rather than decreased in the zone of corridor disturbance. This increased diversity is nevertheless consistent with the findings of other vegetation studies of edges or ecotones between forested and non-forested land.

With the exception of the unique results indicated, most of the study results are consistent with the findings of these other forest edge studies; differences can generally be related to differing community and site variables such as community type, edge age, orientation, and maintenance. It therefore appears that the findings of these studies are applicable to open corridor situations although the effects of additional variables such as corridor width and topography need to be considered.

Implications of Findings for Community Stability

The response of the beech-maple forest community to corridor disturbance was considered in this investigation in relation to two components of relative stability: resistance and resilience. The principal findings of the study can be considered as measures of the resistance of the community (i.e. ability to resist displacement) to the stress imposed by the ski trail. The ordination diagrams can be considered as graphic representations of the extent of this displacement.

The ability of the community to buffer corridor disturbance suggests considerable inherent resilience (i.e. ability to recover) to this type of stress. Nevertheless, the threshold of community resilience to this stress is exceeded close to the trail edge, and community characteristics will remain permanently altered in this outer zone, provided that the edge is maintained.

A long term shift in dominant species from Beech to Sugar Maple from 5-15 metres of the trail edge is an additional result of corridor impact that could be considered as a measure of community resilience to this type of stress.

Both resistance and resilience concepts of stability are defined in terms of a reference state (i.e. deflection from and recovery to this state). In the context of the current study, this state was defined by structural and species compositional characteristics of the vegetation, within the range of variation of control samples. The definition of this reference state can, however, vary considerably according to the perspective of the observer. It can range from the maintenance of overall functional characteristics of an ecosystem, such as nutrient and energy flows, with a disregard of specific changes, to the preservation of the constancy of existing relationships and species.

Management Implications of Findings

It is apparent from the results of this study that fragmentation by open corridors could have long-term effects on the species composition of adjacent forests. The denser the network of corridors and the greater the resultant forest fragmentation, the more widespread these impact effects are likely to be. The study results suggest a minimum placement distance of 60 metres between trails in the Beech-Maple community at Mont-Ste-Marie. It should be borne in mind, however, that such a figure is provisional, being based on a relatively small sample area, and should be confirmed by further studies before being broadly applied. Although this distance is, in most cases,

0 currently exceeded except near trail intersections, a plan for future trail development at Mont-Ste-Marie reveals that considerably less than this minimum distance may be adhered to. Should this proposal be implemented, permanent alteration of the forest community can be expected to result in an "all edge" environment prevailing in some of the forest islands that will be created. The seriousness of these impacts would have to be interpreted in the context of management objectives in the area.

Other factors that should be considered by area managers in assessing the potential impact of trail placement are vegetation community type, successional age, edge aspect, topography, trail width, and edge maintenance form and type.

Relevance of Findings

The results of this study are of general relevance not only to ski area operators but to all those concerned with the environmental impact of open corridors, including power transmission line rights-of-way, oil and gas pipeline corridors, seismic survey lines, roads and hiking trails. Impact effects at Mont-Ste-Marie appear primarily due to changes in microsite caused by corridor opening. However, supplementary stresses such as trampling, herbicides, and pollutants affect some of these other corridor types and would have an additive effect on community change.

Findings of this study should also be of interest to forest and wildlife resource managers and recreationists concerned with the maintenance of forest communities as support systems for certain species, and to environmentalists concerned with the

preservation of forest ecosystems and their constituent species for their intrinsic value.

Recommendations for Further Research

It would be useful to direct further research efforts to the investigation of response to corridor impact in different forest communities and to monitor edge recovery over time in the same community type. Time constraints involved in the latter could be overcome by observing edge response characteristics of one community type for differing corridor ages. It would be of particular interest to discover whether the long term replacement of one climax species by another is a common response beyond the immediate edge zone.

In view of the uncertain relationship and the lack of comparable studies investigating corridor width and community response, a contribution in this area would be of considerable value also. Forest vegetation may be more resistant to the disturbance effects of narrow corridors (i.e. exhibit fewer changes) yet less resilient (i.e. take longer to recover).

Further studies of the radial increment growth of trees adjacent to open corridors such as that by Revel et al. (1984) are also recommended. The comparative growth index derived by these authors would be an appropriate tool in studies of this kind.

The application of the relative stability concepts of resistance and resilience helps to clarify vegetation response characteristics and accordingly appears particularly relevant to studies of corridor disturbance. In planning the route of a

corridor, for example, it is of evident interest to know which of a variety of potential routes would cause least impact on the adjacent vegetation. In an assessment of this kind, knowledge of which community types would resist change to the greatest extent, which community types would recover most quickly, and what specific changes would characterize a community's resistance and resilience responses would appear particularly helpful.

Analytical tools used in this study that would also be recommended for other investigations of this nature are graphic arrays and transect profiles of correspondence analysis ordinations of both samples and species, and scaled structural diagrams. All three provided dramatic visual representations of the degree and extent of corridor impact. The correspondence analysis diagrams could also be used in a quantitative comparison of impact effects on different community types or on the same vegetation community over time.

LITERATURE CITED

Anderson, J.P., and Egler, F.E. 1984. Man-created stable low vegetation under a roadside utility line, Norfolk, Connecticut. Phytologia 55(6): 345-60.

Austin, M.P. 1977. Use of ordination and other multivariate descriptive methods to study succession. Vegetatio 35(3): 165-75.

Baidarin, V.V. 1983. Winter recreation and subniveal plant development. Soviet Journal of Ecology 13(5): 287-91.

Barick, F.B. 1945. Environmental analysis of forest edges in relation to wildlife. Transactions of the Tenth North American Wildlife Conference, 126-36.

_____. 1950. The edge effect of the lesser vegetation of certain Adirondack forest types with particular reference to deer and grouse. Roosevelt Wildlife Bulletin 9(1).

Barrett, G.W. 1981. Stress ecology: an integrative approach. In Stress Effects on Natural Ecosystems, ed. G.W. Barrett and R. Rosenberg, 3-12. Chichester: John Wiley and Sons.

Bates, G.H. 1935. The vegetation of footpaths, sidewalks, cart-tracks and gateways. Journal of Ecology 23(2):420-27.

_____. 1937. The vegetation of wayside and hedgerow. J. Ecology 25:467-81.

Bayfield, N.G. 1971. Some effects of walking and skiing at Cairngorm. In The Scientific Management of Animal and Plant Communities for Conservation, ed. E. Duffey and A.S. Watts, 469-85. 11th Symposium of the British Ecological Society, University of East Anglia, Norwich, July 1970.

Boesch, D.F., and Rosenberg, R. 1981. Response to stress in marine benthic communities. In Stress Effects on Natural Ecosystems, ed. G.W. Barrett and R. Rosenberg, 179-200. Chichester: John Wiley and Sons.

Boss, T.R. 1974. Vegetation study of a powerline right-of-way, Whatcom County. M.A. Thesis, Western Washington State College.

Bostock, H.S. 1970. Physiographic subdivisions of Canada. In Geology and Economic Minerals of Canada, ed. R.J.W. Douglas. Economic Geology Report No. 1. Ottawa: Department of Energy, Mines and Resources, Geological Survey of Canada.

Braun-Blanquet, J. 1932. Plant Sociology. Transl. G.D. Fuller and H.S. Conrad. New York: McGraw-Hill.

Bray, J.R. 1956. Gap phase replacement in a maple-basswood forest. Ecology, 37(3):598-600.

Bruner, M.C. 1977. Vegetation of forest island edges. M.Sc. Thesis, University of Wisconsin-Milwaukee.

Burgess, R.L., and Sharpe, D.M. 1981. Forest Island Dynamics in Man-Dominated Landscapes. New York: Springer-Verlag.

Canada, Energy, Mines and Resources Canada, Geological Survey of Canada. 1968. Tectonic Map of Canada. Map no. 1251A. Scale 1:5 000 000. Prepared by the Tectonic Map of Canada Committee, Chairman C.H.S. Stockwell. Ottawa.

_____, Surveys and Mapping Branch. 1975. Aerial photograph A31014-69. Scale 1:36 000. Ottawa.

_____, Surveys and Mapping Branch. 1976. Low, Québec. Topographic map 31G/13. Scale 1:50 000. Ottawa.

_____, Geographical Services Division. Forthcoming. Climatic Regions: Köppen Climatic Classification. Map. Scale 1:7 500 000. The National Atlas of Canada, 5th Edition. Ottawa.

Canada, Environment Canada, Atmospheric Environment Service. 1982a. Canadian Climatic Normals 1951-1980--Bright Sunshine/ Normales climatiques au Canada 1951-1980--Insolation effective. Volume 7. Downsview, Ontario.

_____. 1982b. Canadian Climate Normals 1951-1980--Degree-Days / Normales climatiques au Canada 1951-1980--Degrés-jours. Volume 4. Downsview, Ontario.

_____. 1982c. Canadian Climatic Normals 1951-1980--Frost/ Normales climatiques au Canada 1951-1980--Gel. Volume 6. Downsview, Ontario.

_____. n.d. Canadian Climate Normals 1951-1980--Temperature and Precipitation, Quebec / Normales climatiques au Canada 1951-1980--Températures et précipitations, Québec. Downsview, Ontario.

Canada Expert Committee on Soil Survey. 1983. The Canada Soil Information System (CANSIS) Manual for Describing Soils in the Field, ed. J.H. Day. Ottawa: Agriculture Canada, Research Branch.

Canada Soil Survey Committee (CANSIS). 1978. The Canadian System of Soil Classification. Publication 1646. Ottawa: Canada Department of Agriculture, Research Branch.

Clements, F.E. 1916. Plant Succession. Pub. No. 242. Washington: Carnegie Institute.

Cole, D.N. 1978. Estimating the susceptibility of wildland vegetation to trailside alteration. Journal of Applied Ecology 15:281-86.

Colwell, J.E. 1974. Vegetation canopy reflectance. Remote Sensing of Environment 3:175-83.

Daget, P., and Godron, M. 1974. Vocabulaire d'Ecologie. Paris: Hachette.

Dale, D., and Weaver, T. 1974. Trampling effects on vegetation of the trail corridors of north Rocky Mountain forests. Journal of Applied Ecology 11(2): 767-72.

Dansereau, P. 1943. L'érablière laurentienne I. Valeur d'indice des espèces. Canadian Journal of Research 21:66-93.

_____. 1946. L'érablière laurentienne II. Les successions et leurs indicateurs. Canadian Journal of Research 23(6):235-91.

Dore, W.G. 1967. Floristic inventory of Mont Ste. Marie, Gatineau County, Quebec. Ottawa: Department of Agriculture, Plant Research Institute.

Dougherty, T.D. et al. 1986. Retroactive assessment of changes in tree growth as a result of seismic line cutting using a comparative growth index. The Operational Geographer 10:8-12.

Enright, N.J. 1982. Recognition of successional pathways in forest communities using size-class ordination. Vegetatio 48:133-40.

Finney, D.J., and Palca, H. 1947. The elimination of bias due to edge effects in forest sampling. Forestry 21(1):31-47.

Forcier, L.K. 1975. Productive strategies and the co-occurrence of climax tree species. Science 189:808-10.

Forman, R.T.T. 1976. Effect of woodlot size on selected components. Unpublished manuscript quoted by Ranney et al. 1981.

_____. 1981. Interaction among landscape elements: a core of landscape ecology. In Perspectives in Landscape Ecology, 35-48. Proc. Int. Cong. Neth. Soc. Landscape Ecol., Veldhoven, 1981. Wageningen: Pudoc.

_____. 1983. Corridors in a landscape: their ecological structure and function. Ekologia (CSSR) 2(4):375-87.

Forman, R.T.T., and Godron, M. 1981. Patches and structural components for a landscape ecology. BioScience 31(10):733-40.

Fosberg, F. 1967. Definition quoted in: Daget, P., and Godron, M. 1974. Vocabulaire d'Ecologie. Paris: Hachette.

Fowells, H.A. 1965. Sylvics of Forest Trees of the United States. Agricultural Handbook No. 271. Washington: United States Department of Agriculture, Forest Service.

Fox, J.F. 1977. Alternation and coexistence of tree species. The American Naturalist 111(977):69-89.

Freedman, B., and Hutchinson, T.C. 1980. Long-term effects of smelter pollution at Sudbury, Ontario, on forest community composition. Canadian Journal of Botany 58:2123-40.

Frei, K.R. and Fairbrothers, D.E. 1963. Floristic study of the William L. Hutcheson Memorial Forest (New Jersey). Bulletin of the Torrey Botanical Club 90:338-55.

Frenkel, R.E. 1970. Ruderal Vegetation Along Some California Roadsides. Berkley: University of California Press.

_____. 1974. Floristic changes along Everitt Memorial Highway, Mount Shasta, California. The Wasmann Journal of Biology 32(1): 105-36.

Frothingham, E.H. 1915. The Northern Hardwood Forest: Its Composition, Growth, and Management. Bulletin No. 285. Washington, D.C.: United States Department of Agriculture.

Gauch, H.G. Jr. 1982. Multivariate Analysis in Community Ecology. Cambridge: Cambridge University Press.

Geiger, R. 1961. The Climate near the Ground. Translated by Scripta Technica, Inc. Cambridge, Mass: Harvard University Press, 1965.

Ghiselin, J. 1977. Analyzing ecotones to predict productivity. Environmental Management 1(3):235-38.

Gleason, H.A. 1952. The New Britten and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. New York: Hafner.

Godron, M., and Forman, R.T.T. 1983. Landscape modification and changing ecological characteristics. In Disturbance and Ecosystems, ed. H.A. Mooney and M. Godron, 13-28. Berlin: Springer-Verlag.

Goff, R.G., and Zedler, P.H. 1972. Derivation of species succession vectors. The American Naturalist 87(2): 397-412.

Goldsmith, F.B. and Harrison, C.M. 1976. Description and analysis of vegetation. In Methods in Plant Ecology, ed. S.B. Chapman, 85-155. Oxford: Blackwell Scientific Publications.

Golding, D.L., and Swanson, R.H. 1978. Snow accumulation and melt in small forest openings in Alberta. Canadian Journal of Forest Research 8:380-88.

Goodall, D.W. 1973. Numerical classification. In Handbook of Vegetation Science V Classification and Ordination of Vegetation, ed. R. Tuxen, 577-615. The Hague: Junk.

Gordon, A.G., and Gorham, E. 1963. Ecological aspects of air pollution from an iron-sintering plant at Wawa, Ontario. Canadian Journal of Botany 41:1063-78.

Gorham, E., and Gordon, A.G. 1960. Some effects of smelter pollution northeast of Falconbridge, Ontario. Canadian Journal of Botany 38:307-12.

Grandtner, M.M. 1966. La Végétation forestière du Québec méridional. Québec: Les Presses de l'Université Laval.

Gregory, S. 1978. Statistical Methods and the Geographer. Fourth Edition. London: Longman.

Greig-Smith, P. 1983. Quantitative Plant Ecology. 3rd ed. Los Angeles: University of California Press.

Guthrie, J.E., and Dugle, J.R. 1983. Gamma-ray irradiation of a boreal forest ecosystem: the field irradiator-gamma (FIG) facility and research programs. The Canadian Field Naturalist 97:120-28.

Gysel, L.W. 1951. Borders and openings of beech-maple woodlands in southern Michigan. Journal of Forestry 49:13-19.

Hessing, M.B. et al. 1982. Early secondary succession of a pinyon-juniper woodland in a northern Arizona powerline corridor. The Southwestern Naturalist 27(1):1-9.

Hill, A.R. 1975. Ecosystem stability in relation to stresses caused by human activities. Canadian Geographer 19(3): 206-220.

Hill, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. Journal of Ecology 61:237-49.

_____. 1974. Correspondence analysis: a neglected multivariate method. Applied Statistics 23(3): 340-54.

Hill, M.O., and Gauch, H.G. Jr. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47-58.

Hoffer, H. 1981. (The influence of skiing tourism to alpine silicat-soil-herbage exemplified by the Gurgler Heide (Oetzal, Tyrol) and observations on the phenology of the curvuletum). Ber. Naturwiss-Med. Ver. Innsbruck 68:31-56. (Abstract in English.)

Holland, P.G., and Steyn, D.C. 1975. Vegetational responses to latitudinal variations in slope angle and aspect. Journal of Biogeography (1975)2:179-83.

Horn, H.S. 1971. Adaptive Geometry of Trees. Princeton, New Jersey: Princeton University Press.

Hosie, R.C. 1969. Native Trees of Canada. Ottawa: Department of the Environment, Canadian Forestry Service.

Hurd, L.E. et al. 1971. Stability and diversity at three trophic levels in terrestrial successional ecosystems. Science 173:1134-6.

Johnson, H.B. et al. 1975. Productivity, diversity and stability relationships in Mojave Desert roadside vegetation. Bulletin of the Torrey Botanical Club 102(3):106-115.

Jones, R.K. et al. 1983. Field Guide to Forest Ecosystem Classification for the Claybelt, Site Region 3E. Toronto: Ontario Ministry of Natural Resources in association with Agriculture Canada and Environment Canada.

Kenting Earth Sciences. 1973. Unpublished topographic map of Mont-Ste-Marie area, Sheet #7. Scale 1:2 400. Ottawa.

Kershaw, K. 1964. Definition quoted in: Daget, P. and Godron, 1974. Vocabulaire d'Ecologie. Paris:Hachette.

Lafond, A., and Ladouceur, G. 1968. Les forêts, les climax et les régions biogéographiques du bassin de la Rivière Outouais, Québec. Le Naturaliste canadien 95:317-66.

Lajoie, P. 1962. Soil Survey of Gatineau and Pontiac Counties, Quebec. Ottawa: Canada Department of Agriculture, Research Branch in association with the Quebec Department of Agriculture, and McGill University, MacDonald College.

Legendre, L., and Legendre, P. 1983. Numerical Ecology. New York: Elsevier.

Leopold, A. 1933. Game Management. New York: Charles Scribner's Sons.

Levenson, J.B. 1976. Forested woodlots as biogeographic islands in an urban-agricultural matrix. Ph. D. Dissertation, University of Wisconsin-Milwaukee.

Levin, S.A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. American Naturalist 104:413-23.

Linzon, S.N. 1971. Economic effects of sulfur dioxide on forest growth. Journal of the Air Pollution Control Association 21(2): 81-86.

Ludwig, J.A. et al. 1977. An evaluation of transmission line construction on pinion-juniper woodland and grassland communities in New Mexico. Journal of Environmental Management 5:127-37.

Lykowski, B. 1970. Reflection of solar radiation by vegetation. Ekologia Polska 8:211-23.

Marie-Victorin, Frère. 1964. Flore laurentienne. Montréal: Presses de l'Université de Montréal.

Marks, P.L. 1974. The role of Pin Cherry (Prunus pensylvanica L.) in the maintenance of stability in northern hardwood ecosystems. Ecological Monographs 44:73-88.

Ministère des Terres et Forêts, Service de l'inventaire forestier. 1974. Petite Flore forestière du Québec. Éditeur officiel du Québec.

Morey, H.F. 1936. Age-size relationships of Hearts Content, a virgin forest in northwestern Pennsylvania. Ecology 17(2):251-57.

Munsell Color Company. 1954. Munsell Soil Color Charts. Baltimore, Maryland.

Nakashizuka, T. 1983. Regeneration process of climax beech forests III Structure and development processes of sapling populations in different aged gaps. Japanese Journal of Ecology. 33:409-18.

Niering, W.A. 1958. Principles of sound right-of-way management. Economoc Botany 12:140-44.

Niering, W.A., and Goodwin, R.H. 1974. Creation of relatively stable shrublands with herbicides: arresting succession on rights-of-way and pastureland. Ecology 55(4):784-95.

Noy-Meir, I.; Walker, D.; and Williams, W.T. 1975. Data transformations in ecological ordination II On the meaning of data standardization. Journal of Ecology 63:779-800.

Noy-Meir, I., and Whittaker, R.H. 1977. Continuous multivariate methods in community analysis: some problems and developments. Vegetatio 33(2/3):79-98.

Odum, E.P. et al. 1979. Perturbation theory and the subsidy-stress gradient. Bioscience 29(6):349-52.

O'Neill, R.V., and Reichle, D.E. 1979. Dimensions of ecosystem theory. In Forests: Fresh Perspectives from Ecosystem Analysis, ed. R.H. Waring. Proceedings of the 40th Annual Biology Colloquium. Corvallis, Oregon: Oregon State University Press.

Oosting, H.J., and Kramer, P.J. 1946. Water and light in relation to pine reproduction. Ecology 27:47-53.

Patton, D.R. 1975. A diversity index for quantifying habitat "edge". Wildlife Society Bulletin 3(4):171-73.

Peterman, R.M. 1980. Influence of ecosystem structure and perturbation history on recovery processes. In Recovery Processes in Damaged Ecosystems, ed. J. Cairns Jr., 125-39. Ann Arbor, Michigan: Ann Arbor Science Publishers.

Peters, J. E. 1972. The ecological implications of trail use, Cypress Hills, Alberta. M. A. Thesis, University of Alberta.

Phipps, M. 1974. Forest Communities; Overburden. Maps, Scale 1:8,400. In: Annex to Report on Ecological Study of Mont Ste. Marie Area, 1974. Department of Geography and Regional Planning, University of Ottawa.

Pielou, E.C. 1984. The Interpretation of Ecological Data. New York: John Wiley and Sons.

Quebec Department of Natural Resources. 1950. Région de Denholm-Hinks/Denholm-Hinks Area. Map 830. Scale 1" to 1 mile. Preliminary Report 235.

Ranney, J.W. 1977. Forest island edges: their structure, development, and importance to regional forest ecosystem dynamics. EDFB/IBP-77/1. Oak Ridge, Tenn: Oak Ridge National Laboratory.

_____. 1978. Edges of forest islands: structure, composition, and importance to regional forest dynamics. Ph. D. Dissertation, University of Tennessee, Knoxville.

Ranney, J.W.; Bruner, M.C.; and Levenson, J.B. 1981. The importance of edge in the structure and dynamics of forest islands. In Forest Island Dynamics in Man-Dominated Landscapes, ed. R.L. Burgess and D.M. Sharpe, 67-95. New York: Springer-Verlag.

Rapport et al. 1985. Ecosystem behaviour under stress. The American Naturalist 125(5):617-40.

Revel, R.D.; Dougherty, T.D.; and Downing, D.J. 1984. Forest Growth and Revegetation along Seismic Lines. Calgary: University of Calgary Press.

Rowe, J.S. 1972. Forest Regions of Canada. Publication No. 1300. Ottawa: Department of the Environment, Canadian Forestry Service.

Runkle, J.R. 1979. Gap phase dynamics in climax mesic forests. Ph. D. Dissertation. Cornell University, Ithica, New York.

_____. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology 62(4):1041-51.

_____. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology 63(5): 1533-46.

_____. 1984. Development of woody vegetation in treefall gaps in a beech-sugar maple forest. Holarctic Ecology 7(2):157-64.

Swift, L.W., and Knoerr, K.R. 1973. Estimating solar radiation on mountain slopes. Agricultural Meteorology 12:329-36.

Thomas, J.W. et al. 1979. Edges. In Wildlife Habitats in Managed Forests: the Blue Mountains of Oregon and Washington. Agriculture Handbook No. 553, U.S. Department of Agriculture, Forest Service.

Thompson, M.M. 1970. Standard time and time zones in Canada. Journal of the Royal Astronomical Society of Canada 64:129-62.

Trimble, G.R. Jr., and Tryon, E.H. 1966. Crown encroachment into openings cut in Appalachian hardwood stands. Journal of Forestry 64:104-8.

Vasek, F.C. et al. 1975. Effects of pipeline construction on creosote bush scrub vegetation of the Mojave Desert. Madróno 23:1-13.

Vitousek, P.M. et al. 1981. Nitrogen cycling and loss following forest perturbation: the components of response. In Stress Effects on Natural Ecosystems ed. G.W. Barrett and R. Rosenberg, 115-27. Chichester: John Wiley and Sons.

Vogl, R.J. 1977. Fire: a destructive menace or a natural process? In Recovery and Restoration of Damaged Ecosystems, ed. J. Cairns and K.L. Dickson, 261-89. Charlottesville: University Press of Virginia.

_____. 1980. The ecological factors that produce perturbation-dependent ecosystems. In Recovery Processes in Damaged Ecosystems, ed. J. Cairns Jr., 63-94. Ann Arbor, Michigan: Ann Arbor Science Publishers.

Wales, B.A. 1967. Climate, microclimate and vegetation relationships on north and south forest boundaries in New Jersey. William L. Hutcheson Memorial Forest Bulletin 2(3):1-57.

_____. 1972. Vegetation analysis of north and south edges in a mature oak-hickory forest. Ecological Monographs 42:451-71.

Webster, J.R. et al. 1975. Nutrient recycling and the stability of ecosystems. In Mineral Cycling in South-Eastern Ecosystems, ed. F.G. Howell et al. Springfield: Energy Research and Development Administration, Technical Info. Center.

Westman, W.E. 1978. Measuring the inertia and resilience of ecosystems. BioScience 28(11):705-710.

Whitney, G.G., and Runkle, J.R. 1981. Edge versus age effects in the development of a beech-maple forest. Oikos 37:377-81.

Williams, W.T.; Lambert, J. M.; and Lance, G.W. 1966. Multivariate methods in plant ecology V Similarity analyses and information analyses. Journal of Ecology 54:427-55.

Woods, K.D. 1979. Reciprocal replacement and the maintenance of codominance in a beech-maple forest. Oikos 33:31-39.

Woods, K.D., and Whittaker, R.H. 1981. Canopy-understory interaction and the internal dynamics of mature hardwood and hemlock-hardwood forests. In Forest Succession: Concepts and Application. New York: Springer-Verlag.

Woodwell, G.M. 1970. Effects of pollution on the structure and physiology of ecosystems. Science 168:429-433.

Woodwell, G.M., and Whittaker, R.H. 1968. Effects of chronic gamma irradiation on plant communities. Quarterly Review of Biology 43:42-55.

APPENDIX I

DERIVED VARIABLES

Density, the number of individuals per unit area, is expressed as the number of stems per plot. Relative density is the density of a species as a percentage of the total density of all species. Deviation from theoretical density for a species was calculated as follows:

The theoretical density for a species (T) was first calculated according to probability theory as:

$$T = \frac{d_1 d_2}{d_3}$$

where d_1 = total density for a sample
 d_2 = total density for a species in the sample area
 d_3 = total density for all species in the sample area

The theoretical density was then subtracted from the actual density to obtain the deviation from theoretical density (D1):

$$D_1 = d_1 - T$$

In order to reduce the range of values between samples and between species, for the purposes of graphic portrayal, deviation values were standardized by species totals to obtain deviation scores (D_2):

$$D_2 = \frac{D_1}{d_2} \times 100$$

Frequency, defined as the chance of finding a species in a particular area in a particular trial sample (Chapman 1976), reflects the spatial distribution of individuals as well as their density. Species frequency per plot was calculated as the number of subplots within which a species occurred (stem location).

Cover is defined as the proportion of ground occupied by a perpendicular projection of the aerial parts of individuals of a species (Goldsmith and Harrison 1976). Testing indicated that relatively accurate percentage cover values per plot could be derived for the ground and lower shrub layers by the averaging of

class midpoint values (table 4) for the five subplots and replicates. Cover estimates were accordingly obtained by this method for these layers. The upper shrub layer was generally too sparse for accurate estimates to be obtained from class midpoints. This method also proved unsatisfactory for tree layer estimates which were carried out on a plot rather than subplot basis. For these reasons, percentage cover values were obtained directly in the field for the tree and upper shrub layers by the conversion of aerial cover estimates. Relative cover is the cover of a species as a percentage of the total cover for all species.

Diversity was measured as species richness or variety, the number of different species that occurred in each sample.

Basal area, the area occupied by the cross-section of stems at 1.3 metres above the ground (Goldsmith and Harrison 1976), was calculated for the three tree layers from diameter at breast height (dbh) measurements ($A = \pi r^2$) and was expressed as cm^2 per (5×10 m) plot. dbh measurements were derived from recorded circumference at breast height (cbh) values ($C = 2\pi r$). Mean tree diameter was calculated by the averaging of sample replicate values.

APPENDIX II

MULTIVARIATE TECHNIQUES

Correspondence analysis (CA) is a doubly-standardized¹ form of non-centred eigenvector analysis (Noy-Meir and Whittaker 1977) that simultaneously ordinales both samples and species (Hill 1973). The first axis CA ordination scores have the property of maximizing the correlation of samples and species (Gauch 1982). Apart from the significant advantage of simultaneous ordination of both samples and species, CA ordination diagrams display relatively low curvilinear distortion² (Noy-Meir and Whittaker 1977). This property arises partly from the simultaneous double standardization of the technique (Noy-Meir and Whittaker 1977) which also has the effect of emphasizing the distinctiveness of samples in terms of their species composition (Noy-Meir et al. 1975). Unlike other ordination techniques, CA ordination scores are not derived from a secondary matrix of sample similarities or distances (Hill and Gauch 1980).

Principal component analysis (PCA) is an eigenvector method of analysis that ordinales one set of variables (e.g. samples or species). The technique concentrates the variance of sample/species values into relatively few axes (Gauch 1982). A non-centred form of PCA was used in this analysis to ordinate samples. Non-centred PCA can usefully portray discontinuities in compositional variation which are not well represented by centred PCA (Noy-Meir and Whittaker 1977). The similarity measure used to derive the secondary matrices that were ordinated by PCA was the Gower coefficient. This coefficient is a similarity measure standardized by species abundance range. It is essentially a

1

By sample and species.

2

Most ordination techniques assume a linear relationship between axes and species variables. Because the relationships between species abundances and environmental variables are non-linear, however, a curvilinear distortion of ordinations often hinders the interpretation of axes in terms of environmental gradients (Noy-Meir and Whittaker 1977).

normalized distance subtracted from unity to produce a similarity measure (Legendre and Legendre 1983). An advantage of this coefficient is its capacity to eliminate from the calculations incidences of species absence. For the purposes of this analysis, double absences of a species (i.e. from both samples being compared) were eliminated. The standardization by species achieved by this coefficient tends to equalize the weights of species so that those that are most abundant do not completely dominate the results.

Information analysis is an hierarchical¹, agglomerative², polythetic³ classification technique that is based on a measure of the diversity or information content of a frequency or probability distribution, rather than on a conventional measure of similarity and derived similarity matrix (Legendre and Legendre 1983). Each sample has a certain information content which is based on its species composition; the more similar a pair of samples, the smaller the increase in diversity or information when the two samples are combined. The technique accordingly operates by combining samples which, upon fusion, result in the smallest increase in information. The version of information analysis available for use employed a single linkage (nearest neighbour) clustering strategy⁴.

¹ Groups of similar entities (classes) are arranged in a hierarchy (Cauch 1982).

² Individuals are progressively fused into groups of increasing size until the entire population is fused into a single group (Greig-Smith 1983)

³ Classification is based on a number of different attributes taken into account simultaneously (Goodall 1973). In the case of this analysis, the entire species composition of samples was considered.

⁴ Grouping at each stage is based on a single pair of samples, each belonging to a different group, whose fusion results in the smallest increase in information.

APPENDIX III

MULTIVARIATE ANALYSIS: INPUT DATA AND NUMERICAL RESULTS

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LIST OF SPECIES AND IDENTIFICATION NUMBERS

Identification Number	Species
S01	<u>Fagus grandifolia</u>
S02	<u>Acer saccharum</u>
S03	<u>Ostrya virginiana</u>
S04	<u>Tilia americana</u>
S05	<u>Abies balsamea</u>
S06	<u>Acer rubrum</u>
S07	<u>Quercus rubra</u>
S08	<u>Betula alleghaniensis</u>
S09	<u>Betula papyrifera</u>
S10	<u>Amelanchier sp.</u>
S11	<u>Prunus virginiana</u>
S12	<u>Prunus pensylvanica</u>
S13	<u>Populus tremuloides</u>
S14	<u>Salix sp.</u>
S15	<u>Acer pensylvanicum</u>
S16	<u>Acer spicatum</u>
S17	<u>Corylus cornuta</u>
S18	<u>Viburnum alnifolium</u>
S19	<u>Lonicera canadensis</u>
S20	<u>Diervilla Lonicera</u>
S21	<u>Sambucus pubens</u>
S22	<u>Cornus alternifolia</u>
S23	<u>Cornus rugosa</u>
S24	<u>Apocynum androsaemifolium</u>
S25	<u>Aralia racemosa</u>
S26	<u>Rubus allegheniensis</u>
S27	<u>Rubus odoratus</u>
S28	<u>Rubus idaeus</u>
S29	<u>Ribes triste</u>
S30	<u>Actaea pachypoda</u>
S31	<u>Ozmorhiza Claytonii</u>
S32	<u>Streptopus roseus</u>
S33	<u>Polygonatum pubescens</u>
S34	<u>Smilacina racemosa</u>
S35	<u>Maianthemum canadensis</u>
S36	<u>Medeola virginiana</u>
S37	<u>Trientalis borealis</u>
S37	<u>Clintonia borealis</u>
S38	<u>Mitella Diphylla</u>
S39	<u>Epifagus virginiana</u>
S40	<u>Trillium grandiflorum</u>
S41	<u>Clintonia borealis</u>
S42	<u>Pyrola sp.</u>
S43	<u>Prenanthes sp.</u>
S44	<u>Prenanthes sp.</u>
S45	<u>Epipactis Helleborine</u>
S46	<u>Impatiens capensis</u>
S47	<u>Polygonum cilinode</u>
S48	<u>Aster acuminatus</u>
S49	<u>Aster macrophyllus</u>

S50 Viola pallens
S51 Viola incognita
S52 Viola sp.
S53 Tiarella cordifolia
S54 Vicia cracca
S55 Hieracium aurantiacum
S56 Leontodon sp.
S57 Medicago sativa
S58 Cirsium arvense
S59 Onoclea sensibilis
S60 Dryopteris marginalis
S61 Equisetum sp.
S62 Grass/Sedge
S63 Unidentified

NOMBRE DE FACTEURS A EXTRAIRE . 2

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72 58C00 CORRESPONDENCE ANALYSIS HDENCR
(A3,10F8.3)

T01	-1.830	0.254	-0.131	-0.084	0.130
C01	0.488	0.563	0.343	0.043	-0.072
T02	-0.493	0.322	0.221	-0.106	-0.022
C02	0.484	0.584	0.450	0.155	-0.000
T03	0.447	0.675	0.446	0.185	-0.050
C03	0.485	0.637	0.449	0.621	0.243
T04	0.477	0.508	0.288	-0.001	0.104
C04	0.538	0.628	0.367	0.901	0.574
T05	0.289	0.343	0.134	-0.332	-0.117
C05	0.508	0.304	0.111	0.122	0.129
T06	0.375	0.384	0.172	-0.291	-0.299
C06	0.379	-0.934	0.254	-0.113	0.431
T07	0.469	0.246	-0.611	-0.383	-0.182
C07	0.187	-0.726	0.127	-0.110	0.272
T08	0.495	-0.006	-0.418	-0.358	-0.139
C08	0.355	-0.633	0.185	-0.080	0.245
T09	0.484	-0.057	-0.481	-0.402	-0.287
C09	0.237	-0.448	0.122	-0.076	-0.085
T10	0.528	0.039	-1.237	0.402	0.008
C10	-0.590	-0.784	0.299	0.495	-0.571
S01	0.319	-0.095	-0.154	-0.432	-0.099
S02	0.386	0.362	0.208	0.167	-0.003
S03	0.302	0.803	0.800	1.503	0.236
S04	0.362	0.672	0.325	-1.106	-0.464
S05	0.445	-1.239	0.449	-0.265	-0.975
S06	0.409	-0.374	-0.689	0.197	-0.276
S07	0.579	0.644	-0.498	0.296	-0.386
S08	0.156	-0.586	-0.336	-0.342	-1.515
S09	-2.294	0.438	-0.318	-0.278	0.517
S10	0.261	-1.136	0.344	-0.143	0.019
S11	-0.740	-1.533	0.725	1.650	-2.268
S12	-2.294	0.498	-0.318	-0.278	0.517
S13	0.457	-1.308	-0.507	-0.550	0.088
S16	0.103	-0.112	0.444	0.391	-0.667
S17	0.587	0.994	0.698	-0.004	0.411
S18	0.526	-0.386	-0.272	-0.126	0.636
S19	0.614	0.583	-0.700	1.071	0.687
S20	-2.164	0.427	-0.287	-0.277	0.478
S25	0.136	0.090	0.593	0.353	-1.063
S28	-0.618	0.630	0.537	-0.355	-0.887
S28	-2.222	0.511	-0.282	-0.265	0.496
S30	0.382	0.872	0.325	-1.108	-0.464
S31	0.470	0.713	0.418	-0.968	-1.187
S32	0.393	-0.592	0.431	-0.311	0.005
S33	0.491	0.438	-0.286	0.569	-0.292
S34	0.470	0.713	0.418	-0.968	-1.187
S35	0.117	-1.390	0.452	0.136	0.283
S36	0.551	-0.238	-1.395	-0.466	0.127
S37	0.496	0.253	0.278	-0.433	0.088
S38	0.609	1.246	1.090	2.068	0.588
S39	0.648	0.936	-0.179	2.033	1.135
S40	0.297	-0.878	0.297	-0.252	-0.260
S41	-0.740	-1.533	0.725	1.650	-2.268
S42	-0.740	-1.533	0.725	1.650	-2.268
S43	0.862	0.077	-3.603	1.339	0.031
S44	0.662	0.077	-3.603	1.339	0.031
S45	-0.867	0.918	0.382	0.169	0.159
S46	-2.294	0.496	-0.318	-0.278	0.517
S47	-0.394	-1.315	-0.582	1.016	-1.599
S48	-1.560	0.044	-0.280	0.319	-0.067
S49	-1.960	0.302	-0.432	-0.276	0.497
S50	-1.567	-0.323	0.116	0.449	-0.579
S51	-2.294	0.496	-0.318	-0.278	0.517
S52	-2.294	0.496	-0.318	-0.278	0.517
S53	-1.937	0.525	-0.136	-0.245	0.388
S54	0.470	0.713	0.418	-0.968	-1.187
S55	-2.294	0.496	-0.318	-0.278	0.517
S56</					

	1	2	3	4	5
VALUE	5.6363924E 02	0.2311784106	0.17841472 02	0.8013304E-01	0.5341882E-01
TEST	5.356279E 04	0.2542361 04	0.17841472 02	0.1427354E 04	0.5341882E-01
POURCENTAGE	42.33	17.37	11.30	11.30	4.22

LOWER COEFFICIENT OF GROUND LAYER SPECIES DENSITY (all species)

***** CALC. OF GOWER COEFFICIENTS 20 PLOTS X 52 GROUND SPEC.															
T01	1.000	0.212	0.273	0.176	0.209	0.211	0.195	0.211	0.228	0.294	0.164	0.251	0.169	0.222	0.224
C01	0.194	0.189	0.229	0.100	0.269	0.269	0.269	0.269	0.269	0.269	0.269	0.269	0.269	0.269	0.269
T02	0.212	1.000	0.654	0.624	0.578	0.578	0.578	0.578	0.578	0.578	0.578	0.578	0.578	0.578	0.578
C02	0.273	0.502	0.572	0.320	0.450	0.450	0.450	0.450	0.450	0.450	0.450	0.450	0.450	0.450	0.450
T03	0.176	0.624	0.578	1.000	0.512	0.512	0.512	0.512	0.512	0.512	0.512	0.512	0.512	0.512	0.512
C03	0.209	0.578	0.578	0.588	0.512	0.512	0.512	0.512	0.512	0.512	0.512	0.512	0.512	0.512	0.512
T04	0.211	0.585	0.608	0.504	0.599	0.599	0.599	0.599	0.599	0.599	0.599	0.599	0.599	0.599	0.599
C04	0.481	0.408	0.517	0.367	0.419	0.419	0.419	0.419	0.419	0.419	0.419	0.419	0.419	0.419	0.419
T05	0.195	0.617	0.617	0.546	0.536	0.536	0.536	0.536	0.536	0.536	0.536	0.536	0.536	0.536	0.536
C05	0.497	0.484	0.530	0.364	0.416	0.416	0.416	0.416	0.416	0.416	0.416	0.416	0.416	0.416	0.416
T06	0.211	0.570	0.645	0.512	0.492	0.492	0.492	0.492	0.492	0.492	0.492	0.492	0.492	0.492	0.492
C06	0.224	0.557	0.557	0.508	0.508	0.508	0.508	0.508	0.508	0.508	0.508	0.508	0.508	0.508	0.508
T07	0.524	1.000	0.557	0.508	0.508	0.508	0.508	0.508	0.508	0.508	0.508	0.508	0.508	0.508	0.508
C07	0.596	0.557	1.000	0.468	0.468	0.468	0.468	0.468	0.468	0.468	0.468	0.468	0.468	0.468	0.468
T08	0.467	0.506	0.468	0.501	0.423	0.423	0.423	0.423	0.423	0.423	0.423	0.423	0.423	0.423	0.423
C08	0.615	0.658	0.739	0.625	0.625	0.625	0.625	0.625	0.625	0.625	0.625	0.625	0.625	0.625	0.625
T09	0.432	0.415	0.423	0.480	0.480	0.480	0.480	0.480	0.480	0.480	0.480	0.480	0.480	0.480	0.480
C09	0.453	0.815	0.528	0.561	0.561	0.561	0.561	0.561	0.561	0.561	0.561	0.561	0.561	0.561	0.561
T10	0.460	0.526	0.484	0.628	0.628	0.628	0.628	0.628	0.628	0.628	0.628	0.628	0.628	0.628	0.628
C10	0.479	0.535	0.534	0.606	0.629	0.629	0.629	0.629	0.629	0.629	0.629	0.629	0.629	0.629	0.629
T11	0.536	0.572	0.484	0.538	0.596	0.596	0.596	0.596	0.596	0.596	0.596	0.596	0.596	0.596	0.596
C11	0.481	0.497	0.498	0.588	0.611	0.611	0.611	0.611	0.611	0.611	0.611	0.611	0.611	0.611	0.611
T12	0.408	0.484	0.487	0.564	0.601	0.601	0.601	0.601	0.601	0.601	0.601	0.601	0.601	0.601	0.601
C12	0.517	0.530	0.591	0.559	0.623	0.623	0.623	0.623	0.623	0.623	0.623	0.623	0.623	0.623	0.623
T13	0.367	0.364	0.373	0.346	0.471	0.471	0.471	0.471	0.471	0.471	0.471	0.471	0.471	0.471	0.471
C13	0.419	0.416	0.463	0.423	0.507	0.507	0.507	0.507	0.507	0.507	0.507	0.507	0.507	0.507	0.507
T14	0.511	0.443	0.542	0.517	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

GOWER COEFFICIENT OF GROUND LAYER SPECIES DENSITY (herb species)

	CALC.	OF GOWER COEFFICIENTS	20 PLOTS X 31 HERB	SPEC.
T01	1.330	0.146	0.144	0.144
C01	0.105	0.160	0.148	0.148
T02	0.146	0.160	0.148	0.148
C02	0.144	0.160	0.148	0.148
T03	0.146	0.160	0.148	0.148
C03	0.144	0.160	0.148	0.148
T04	0.146	0.160	0.148	0.148
C04	0.144	0.160	0.148	0.148
T05	0.146	0.160	0.148	0.148
C05	0.144	0.160	0.148	0.148
T06	0.146	0.160	0.148	0.148
C06	0.144	0.160	0.148	0.148
T07	0.146	0.160	0.148	0.148
C07	0.144	0.160	0.148	0.148
T08	0.146	0.160	0.148	0.148
C08	0.144	0.160	0.148	0.148
T09	0.146	0.160	0.148	0.148
C09	0.144	0.160	0.148	0.148
T10	0.146	0.160	0.148	0.148
C10	0.144	0.160	0.148	0.148

75 58C00 CORRESPONDENCE ANALYSIS CORNERB
(A3,10F8.3)

T01	-2.092	0.386	-0.126	-0.050	-0.004
C01	0.211	0.200	0.060	0.164	-0.004
T02	-0.722	-1.693	1.041	0.052	-0.637
C02	0.213	0.143	0.211	0.360	-0.002
T03	-0.245	0.242	0.371	0.092	0.654
C03	0.170	0.074	0.439	-0.254	0.397
T04	0.226	0.266	0.420	0.032	-0.032
C04	0.403	0.487	1.128	-0.983	0.328
T05	0.288	0.006	0.414	0.024	0.072
C05	0.379	0.220	0.120	0.125	-0.108
T06	0.204	0.145	0.259	1.439	0.322
C06	0.402	-0.053	-0.433	-0.098	-0.407
T07	0.225	0.073	0.018	0.222	0.160
C07	0.315	-0.053	-0.328	0.024	-0.307
T08	0.374	0.241	0.107	0.018	-0.033
C08	0.259	-0.017	-0.454	-0.014	-0.452
T09	0.366	0.065	-0.188	0.055	0.010
C09	-0.004	-0.221	-0.537	-0.093	-0.051
T10	0.430	0.441	0.136	-0.329	-0.237
C10	0.077	-0.774	-0.519	-0.286	0.918
S01	0.175	0.099	0.073	0.158	0.029
S02	0.117	0.064	0.242	0.034	0.090
S03	0.062	-0.849	1.159	-0.738	0.492
S04	0.411	0.012	0.958	0.062	0.199
S05	0.370	-0.038	-1.050	-0.017	-1.243
S06	0.338	0.007	0.369	0.018	0.069
S07	0.403	0.543	0.467	1.277	0.077
S08	0.316	-0.791	-0.816	-0.301	1.278
S09	-2.984	0.863	-0.278	-0.130	-0.012
S10	0.133	-0.666	-1.186	-0.346	0.196
S11	0.111	-1.728	-1.201	-0.745	2.523
S12	-2.984	0.863	-0.278	-0.130	-0.012
S15	0.352	0.107	0.060	0.050	-0.045
S16	0.049	-0.977	0.048	0.058	0.383
S17	0.323	0.595	0.972	0.083	-0.087
S18	0.491	0.407	0.258	0.345	-0.407
S19	0.460	0.599	1.040	-0.984	0.182
S20	-2.239	0.523	-0.519	-0.158	-0.044
S25	0.075	-0.342	-0.100	0.024	1.587
S26	-1.030	-3.781	2.410	0.161	-1.751
S28	-2.458	0.311	0.147	-0.056	-0.004
S30	0.411	0.012	0.958	0.052	0.199
S31	0.290	0.324	0.599	3.749	0.885
S32	0.262	-0.224	0.010	0.260	-0.125
S33	0.286	0.158	0.230	-0.273	0.776
S34	0.290	0.324	0.599	3.749	0.885
S35	0.329	-0.338	0.778	-0.145	-0.540
S36	0.439	0.205	-0.395	-0.312	-0.477
S37	0.420	0.191	-0.149	0.334	-0.344
S38	0.242	0.165	1.017	-0.680	1.089
S39	0.520	0.813	1.574	-1.562	0.474
S40	-0.006	-0.494	-1.243	-0.242	-0.141
S41	0.111	-1.728	-1.201	-0.745	2.523
S42	0.111	-1.728	-1.201	-0.745	2.523
S43	0.613	0.988	0.315	-0.857	-0.650
S44	0.613	0.988	0.315	-0.857	-0.650
S45	-1.595	0.702	0.291	0.055	0.892
S46	-2.984	0.863	-0.278	-0.130	-0.012
S47	0.072	-1.317	-1.215	-0.578	-0.635
S48	-0.390	-0.531	-0.169	0.049	0.047
S49	-1.401	0.298	-0.712	-0.135	-0.250
S50	-1.795	-0.576	-0.045	-0.199	-0.121
S51	-2.484	0.663	-0.278	-0.130	-0.012
S52	-1.030	-3.781	2.410	0.161	-1.751
S53	-2.202	-0.995	0.797	-0.013	-0.701
S54	0.290	0.324	0.599	3.749	0.885</

	1	2	3	4	5
VAL JP PCPRI	0.0119451 CC	0.0044122 CC	0.1872732 CC	0.1477431 CC	0.3321278 CC
TEST = 0.9902242 CC	0.0056078 CC	0.0073042 CC	0.0009927 CC	0.0000000 CC	0.3321278 CC
PCQCNTAGL	27.27	11.13	10.37	1.18	7.98

DIMENSION	1	2	EN	ENSEMBLE	Species
DIMENSION	10	10	10	10	20
DIMENSION	10	10	10	10	20

NUMBER OF FACTORS A LAYOFF IS

[illegible]

48 SUBDD CORRESPONDENCE ANALYSIS SDENCR
(A3,10F6.3)

T01	-1.443	-0.227	-0.043	0.024	0.015
C01	0.417	0.725	0.136	0.656	0.648
T02	-0.468	0.379	0.059	-0.062	-0.058
C02	0.416	0.847	0.267	0.314	0.227
T03	0.138	0.831	-0.058	-0.341	-0.020
C03	0.447	0.887	0.054	0.448	0.150
T04	0.419	0.974	-0.029	-0.377	-0.049
C04	0.510	0.664	0.045	0.265	0.424
T05	0.478	0.451	0.044	-0.209	-0.161
C05	0.571	0.048	-0.038	0.411	0.327
T06	0.596	-0.131	-0.176	-0.205	-0.038
C06	0.710	-0.522	-0.275	0.064	0.157
T07	0.650	-0.256	-0.183	-0.164	-0.004
C07	0.705	-0.490	-0.223	0.074	0.234
T08	0.737	-0.636	-0.279	-0.113	-0.017
C08	0.618	-0.008	-0.138	0.177	-0.187
T09	0.757	-0.704	-0.334	-0.210	0.007
C09	0.497	-0.134	-0.116	0.665	-0.724
T10	0.783	-0.843	-0.351	-0.091	-0.053
C10	0.538	-0.619	-0.528	-0.150	-0.037
S01	0.335	0.210	0.181	0.532	0.213
S02	0.342	0.820	-0.026	-0.134	-0.027
S03	0.422	0.213	0.489	1.194	-1.541
S04	0.355	0.230	0.467	0.294	0.556
S05	0.707	-0.030	-0.257	0.044	-0.307
S06	0.709	-0.270	-0.157	1.316	-1.875
S08	-1.417	-0.180	-0.042	0.092	-0.028
S09	-1.606	-0.338	-0.072	0.071	-0.044
S10	0.736	-0.310	-0.267	0.893	-1.969
S11	0.832	-1.167	0.286	-0.612	0.181
S12	-1.686	-0.428	-0.089	0.098	0.072
S13	-1.686	-0.428	-0.089	0.098	0.072
S14	-1.686	-0.428	-0.089	0.098	0.072
S15	0.753	-0.719	-0.209	-0.072	-0.009
S16	-0.178	-0.179	1.243	0.024	-0.512
S17	0.648	0.243	0.776	0.984	1.197
S18	0.681	0.314	0.372	0.088	0.224
S19	0.754	-0.440	-0.358	-0.083	-0.217
S20	-1.568	-0.296	-0.076	0.033	0.044
S21	-0.844	-0.173	-0.163	-0.280	-0.326
S22	-0.874	0.626	0.836	-0.534	-0.279
S23	-1.230	0.029	-0.004	-0.043	-0.069
S24	-1.505	-0.237	-0.053	0.039	0.013
S25	-1.467	-0.199	-0.046	0.028	0.002
S26	-1.508	-0.236	-0.064	0.017	0.025
S27	-1.524	-0.249	-0.076	-0.001	0.043
S28	-1.286	-0.008	-0.042	-0.099	-0.023
S29	-1.686	-0.428	-0.089	0.098	0.072

Axis 1 2 3 4 5

[illegible]

(2X.AA-9A-1SE8-3>101-15F3) C-023-7360 X 24 = 400 SEC.

[illegible]

GOWER COEFFICIENT OF SHRUB LAYER SPECIES DENSITY (shrub species)

	GOWER COEFFICIENTS 20 PLOTS X 12 SHRUB SPEC.											
12X, 44, 4X, 15F, 3, 21, 13X, 15F, 31)	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
T01	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
C01	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
T02	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
C02	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
T03	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
C03	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
T04	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
C04	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
T05	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
C05	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
T06	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
C06	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
T07	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
C07	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
T08	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
C08	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
T09	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
C09	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
T10	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075
C10	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075	0.075

GOWER COEFFICIENT OF SHRUB LAYER SPECIES DENSITY (tree species)

	GOWER COEFFICIENTS 20 PLOTS X 16 TREE SPEC.									
	1.000	0.263	0.373	0.388	0.400	0.408	0.408	0.334	0.341	0.337
T01	0.263	1.000	0.373	0.388	0.400	0.408	0.408	0.334	0.341	0.337
C01	0.373	0.373	1.000	0.388	0.400	0.408	0.408	0.334	0.341	0.337
T02	0.388	0.388	0.388	1.000	0.400	0.408	0.408	0.334	0.341	0.337
C02	0.400	0.400	0.400	0.400	1.000	0.408	0.408	0.334	0.341	0.337
T03	0.408	0.408	0.408	0.408	0.408	1.000	0.408	0.334	0.341	0.337
C03	0.408	0.408	0.408	0.408	0.408	0.408	1.000	0.334	0.341	0.337
T04	0.334	0.334	0.334	0.334	0.334	0.334	0.334	1.000	0.341	0.337
C04	0.341	0.341	0.341	0.341	0.341	0.341	0.341	0.341	1.000	0.337
T05	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	1.000
C05	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337
T06	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337
C06	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337
T07	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337
C07	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337
T08	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337
C08	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337
T09	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337
C09	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337
T10	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337
C10	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337	0.337

SHRUB LAYER FREQUENCY BY SPECIES AND BY PLOT (3-metre intervals)

CORRESPONDENCE ANALYSIS CORRESPONDANCE

DIMENSION JJ 1 24 ENSEMBLE 24 Species

DIMENSION JJ 2 24 NE ENSEMBLE 24 Plots

NOMBRE DE FACTEURS A EXTRAIRE 5

MATRICE CORRESPONDANCE

Plot	T01	C01	T02	C02	T03	C03	T04	C04	T05	C05	T06	C06	T07	C07	T08	C08	T09	C09	T10	C10
Species	501	502	503	504	505	506	507	508	509	510	511	512	513	514	515	516	517	518	519	520
501	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
502	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
503	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
504	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
505	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
506	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
507	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
508	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
509	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
510	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
511	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
512	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
513	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
514	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
515	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
516	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
517	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
518	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
519	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
520	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
521	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
522	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
523	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
524	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
525	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
526	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
527	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
528	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

BETA

	1	2	3	4	5
VALUE PROPE	0.563492E 00	0.1267828E 00	0.9022818E 01	0.1246732E 01	9.9793352E -01
TEST	0.320851E 00	0.2485037E 00	0.1730378E 00	0.1389675E 00	0.9793352E -01
PERCENTAGE	50.17	11.28	1.08	7.32	5.17

Tree Species

173

8 Species
12 Plots (5-metre intervals)
4 Size-Classes

[illegible]

OWER COEFFICIENT OF TREE LAYER DENSITY

48 10 000 OOWER COEFFICIENT 48 PLOTS X 8 SP. MATRICE A

T11	0.820	-0.198	0.171	-0.089	-0.181	0.040	0.116	-0.010	0.038	0.054
T12	0.900	-0.284	-0.202	-0.047	-0.027	0.132	-0.032	-0.020	0.060	-0.119
T13	0.800	0.068	-0.183	0.076	0.112	0.017	-0.023	0.031	0.028	0.018
T14	0.500	-0.055	-0.171	0.634	-0.190	-0.262	-0.032	-0.073	0.414	-0.136
C11	0.934	-0.031	-0.226	-0.034	0.194	-0.066	-0.074	-0.055	-0.007	-0.050
C12	0.919	-0.255	-0.030	-0.380	-0.136	0.118	0.366	-0.045	0.049	-0.021
C13	0.514	0.721	0.058	0.040	-0.174	0.153	-0.192	0.109	0.082	-0.121
C14	0.632	0.226	0.078	0.097	0.077	-0.162	0.630	0.148	-0.043	-0.185
T21	0.820	-0.198	0.171	-0.089	-0.181	0.040	0.116	-0.010	0.038	0.054
T22	0.891	0.250	0.104	-0.065	0.104	-0.165	0.051	0.017	0.056	-0.024
T23	0.846	-0.210	-0.159	-0.013	0.035	0.013	-0.091	0.044	-0.017	-0.005
T24	0.818	0.473	-0.352	-0.155	-0.325	-0.102	-0.041	-0.070	-0.141	0.185
C21	0.794	0.226	-0.343	-0.208	0.101	-0.118	0.014	0.027	0.201	0.116
C22	0.946	-0.210	-0.159	-0.013	0.035	0.013	-0.091	0.044	-0.017	-0.005
C23	0.808	0.167	0.232	0.016	0.189	-0.109	-0.391	-0.046	-0.008	-0.086
C24	0.870	0.576	0.024	-0.068	-0.292	0.078	-0.146	0.021	0.039	-0.160
T31	0.919	-0.255	-0.030	-0.080	-0.136	0.118	0.066	-0.045	0.049	-0.021
T32	0.958	-0.170	-0.037	-0.036	-0.036	0.008	-0.025	0.027	-0.041	0.034
T33	0.849	0.116	-0.296	-0.160	0.201	-0.108	0.032	0.038	0.180	0.047
T34	0.739	0.465	-0.144	-0.116	-0.312	-0.011	0.048	-0.095	-0.103	0.053
C31	0.958	-0.122	0.110	-0.030	-0.033	-0.026	0.015	0.052	-0.041	0.036
C32	0.934	0.116	-0.167	-0.025	0.148	-0.134	-0.027	-0.036	-0.022	-0.035
C33	0.808	0.167	0.232	0.010	0.189	-0.109	-0.391	-0.040	-0.008	-0.086
C34	0.637	0.389	0.082	0.211	0.093	0.430	0.071	0.258	0.188	-0.071
T41	0.867	-0.027	0.400	0.034	-0.004	-0.068	-0.079	0.019	0.062	0.032
T42	0.825	-0.138	-0.144	0.814	-0.179	-0.032	-0.035	-0.151	-0.272	-0.172
T43	0.946	-0.062	0.234	-0.005	-0.012	-0.054	-0.042	0.063	-0.032	0.010
T44	0.958	0.059	-0.195	0.029	0.088	-0.037	-0.020	-0.048	-0.080	-0.037
C41	0.934	-0.031	-0.226	-0.034	0.194	-0.066	-0.074	-0.055	-0.007	-0.050
C42	0.803	-0.111	0.328	-0.025	-0.090	-0.046	0.025	0.014	0.021	0.087
C43	0.900	-0.284	-0.202	-0.047	-0.027	0.132	-0.032	-0.020	0.060	-0.119
C44	0.581	0.262	0.195	0.204	0.334	0.421	0.089	-0.302	-0.025	0.246
T51	0.858	-0.122	0.110	-0.030	-0.033	-0.028	0.015	0.052	-0.041	0.036
T52	0.946	-0.210	-0.159	-0.013	0.035	0.013	-0.091	0.044	-0.017	-0.005
T53	0.946	-0.062	0.234	-0.005	-0.012	-0.054	-0.042	0.063	-0.032	0.010
T54	0.862	0.040	0.130	0.043	-0.060	-0.015	-0.002	0.144	-0.055	-0.005
C51	0.900	-0.111	0.328	-0.025	-0.090	-0.046	0.025	0.014	0.021	0.087
C52	0.803	-0.223	-0.132	-0.041	0.042	0.048	-0.091	0.074	-0.031	0.018
C53	0.884	0.092	-0.110	0.011	0.031	-0.030	0.033	-0.065	-0.076	-0.013
C54	0.853	0.370	0.006	-0.033	-0.046	-0.005	0.103	-0.075	-0.014	0.047
T61	0.887	-0.027	0.400	0.034	-0.004	-0.068	-0.079	0.019	0.062	0.032
T62	0.919	-0.255	-0.030	-0.080	-0.136	0.118	0.066	-0.045	0.049	-0.021
T63	0.908	0.167	0.232	0.010	0.189	-0.109	-0.091	-0.040	-0.008	-0.086
T64	0.828	0.126	-0.119	0.034	0.065	0.049	0.086	-0.135	-0.109	0.065
C61	0.900	-0.284	-0.202	-0.047	-0.027	0.132	-0.032	-0.020	0.060	-0.119
C62	0.920	-0.136	0.171	-0.069	-0.161	0.040	0.116	-0.010	0.038	0.054
C63	0.887	-0.016	-0.212	0.232	0.079	0.030	-0.057	0.509	-0.223	0.223
C64	0.920	0.093	-0.203	0.052	0.115	0.043	0.036	-0.116	-0.093	0.040

COVER COEFFICIENT 40 PLOTS X 4 SP.

ANALYSE FACTORIELLE EN COMPOSANTES PRINCIPALES

PRINCIPAL COMPONENT ANALYSIS OF TREE LAYER SPECIES DENSITY

PAGE 1	VAL. PH.	2.818	1.934	1.126	0.995	0.744	0.644	0.587	6.516	0.388
P. CENT.	74.545	5.885	4.029	2.303	2.073	1.549	1.358	1.223	1.071	0.828
P.C. CUM.	74.545	80.411	84.440	86.743	88.816	90.365	91.714	92.937	94.008	94.837
1-T11	3.822	-0.196	0.171	-0.288	-0.161	0.040	0.116	-0.010	0.038	0.054
2-T12	3.822	-0.244	-0.202	-0.347	-0.027	0.132	-0.132	-0.020	0.080	-0.119
3-T13	0.912	0.068	-0.163	0.026	0.112	0.017	-0.023	0.001	0.028	0.018
4-T14	2.509	-0.045	-0.171	0.634	-0.190	-0.242	-0.032	-0.073	0.414	0.138
5-C11	3.834	-0.031	-0.224	-0.034	0.194	-0.066	-0.074	-0.055	-0.007	-0.050
6-C12	0.919	-0.255	-0.030	-0.080	-0.136	0.118	0.088	-0.045	0.049	-0.021
7-C13	0.914	0.721	0.038	0.040	-0.174	0.153	-0.182	0.109	0.042	-0.121
8-C14	1.832	0.226	-0.078	0.087	0.077	-0.182	0.430	0.148	-0.045	-0.169
9-T21	3.822	-0.196	0.171	-0.288	-0.161	0.040	0.116	-0.010	0.038	0.054
10-T22	3.822	0.250	0.109	-0.365	0.104	-0.165	0.051	0.017	0.058	-0.024
11-T23	3.848	-0.210	-0.129	-0.012	0.039	0.013	-0.081	0.044	-0.017	-0.005
12-T24	3.616	0.475	-0.352	-0.155	-0.325	-0.102	-0.041	-0.078	-0.141	0.185
13-C21	0.794	0.226	-0.343	-0.226	0.101	-0.116	0.014	0.027	0.201	0.116
14-C12	3.848	-0.210	-0.158	-0.013	0.035	0.013	-0.081	0.044	-0.017	-0.005
15-C23	3.808	0.167	0.232	0.616	0.198	-0.108	-0.081	-0.040	-0.008	-0.088
16-C24	3.672	0.978	0.024	-0.069	-0.292	0.078	-0.149	0.021	0.039	-0.180
17-T31	0.919	-0.255	-0.030	-0.080	-0.136	0.118	0.088	-0.045	0.049	-0.021
18-T32	3.958	-0.170	-0.037	-0.036	-0.036	0.028	-0.025	0.027	-0.041	0.034
19-T33	3.848	0.118	-0.288	-0.180	0.201	-0.108	0.032	0.038	0.180	0.047
20-T34	0.733	0.485	-0.144	-0.116	-0.312	-0.011	0.048	-0.085	-0.103	0.053
21-C31	3.958	-0.172	0.110	-0.030	-0.053	-0.028	0.015	0.032	-0.041	0.038
22-C32	0.834	0.116	0.187	-0.025	0.148	-0.134	-0.027	-0.038	-0.022	-0.039
23-C33	0.808	0.167	0.232	0.010	0.189	-0.108	-0.081	-0.040	-0.008	-0.088

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PAGE	2									
VAL-PR.	38.762	2.018	1.934	1.138	0.995	0.764	0.646	0.587	6.514	0.398
P-CENT.	74.545	5.886	4.529	2.303	2.075	1.549	1.358	1.323	1.071	0.328
P.C-CUM.	74.545	80.411	84.446	88.743	93.038	90.365	91.714	92.937	94.008	94.937
2A-C34	3.857	C.349	3.382	6.711	0.693	0.430	0.071	8.258	5.188	-0.071
2B-T41	3.867	-C.077	6.460	3.034	-0.004	-0.088	-0.078	0.018	0.002	0.032
26-T42	0.625	-0.136	-0.144	3.614	-0.179	-0.832	-0.035	-0.191	-0.272	-0.178
27-T43	0.946	-0.042	0.234	-0.005	-0.012	-0.054	-0.042	0.063	-0.032	0.010
28-T44	0.656	0.079	-0.185	3.028	0.084	-0.037	-0.020	-0.046	-0.069	-0.037
28-C41	3.934	-C.031	-0.226	-0.034	0.184	-0.088	-0.074	-0.055	-0.007	-0.058
3C-C42	0.913	-0.111	0.328	-0.025	-0.086	-0.048	0.029	0.014	0.021	0.067
3I-C43	0.850	-0.274	-0.262	-0.047	-0.027	0.132	-0.032	-0.028	0.060	-0.119
3Z-C44	0.581	0.282	0.185	0.224	0.334	0.421	0.068	-0.302	-0.029	0.248
3J-T51	0.958	-0.122	0.110	-0.030	-0.053	-0.026	0.015	0.092	-0.041	0.038
34-T52	0.946	-0.210	-0.159	-0.113	0.035	0.013	-0.001	0.044	-0.017	-0.005
3Y-T53	0.946	-0.082	3.234	-0.009	-0.012	-0.054	-0.042	0.083	-0.032	0.010
3E-T54	3.952	0.041	3.156	0.043	-0.066	-0.019	-0.002	0.044	-0.035	-0.005
37-C51	0.943	-0.111	0.328	-0.025	-0.086	-0.048	0.025	0.014	0.021	0.067
38-C52	0.863	-0.223	-0.132	-0.041	0.045	0.044	-0.001	0.074	-0.031	0.018
38-C53	0.964	0.092	-0.110	0.011	0.038	-0.030	0.030	-0.085	-0.078	-0.013
40-C54	0.853	0.370	0.606	-0.333	-0.048	-0.009	0.103	-0.075	-0.014	0.047
41-T61	0.867	-0.027	0.400	0.034	-0.034	-0.088	-0.078	0.018	0.002	0.032
42-T62	0.918	-0.255	-0.036	-0.080	-0.138	0.118	0.018	-0.045	0.048	-0.021
43-T63	0.908	0.187	0.232	0.010	0.188	-0.109	-0.001	-0.040	-0.000	-0.088
46-T64	0.829	-0.126	-0.118	0.034	0.385	0.049	0.086	-0.139	-0.109	0.088
49-C61	0.900	-0.284	-0.202	-0.047	-0.027	0.132	-0.032	-0.020	0.080	-0.118
48-C62	0.920	-0.186	3.171	-0.169	-0.161	0.040	0.118	-0.010	0.038	0.054
47-C63	0.887	-0.016	-0.212	0.232	0.078	0.630	-0.057	0.308	-0.223	0.223
48-C64	0.920	0.083	-0.263	0.052	0.115	0.043	0.038	-0.118	-0.003	0.046

APPENDIX IV

SPECIES LIST

The 66 species found within the study area are grouped according to distributional pattern as edge (24), intermediate (11), or interior species (31). The definitions used for this division are as follows:

Edge species: species that were sampled exclusively in the trail section from 0-8 metres.

Intermediate species: species that were sampled with greatest abundance in the trail section from 0-8 metres but were also present elsewhere in the trail and/or control sections.

Interior species: species that were sampled exclusively or with greatest abundance in interior plots.

This classification is based entirely on observed distributional patterns of species. Because of the limited number of sample sites, the limited occurrence of some species, and the natural variability of site conditions, the classification of a few species may be anomalous. Known anomalies of this type are identified in footnotes.

The listing also indicates the structural layer(s) in which each species was sampled and the limit of distribution for edge species. Nomenclature is based primarily on Marie-Victorin (1964) and secondarily on Gleason (1952), with common names for tree species derived from Hosie (1969). Plant identification was also based on these three sources as well as on Ministère des Terres et Forêts (1974). Parentheses indicate that the occurrence of a species is rare in a particular section or structural layer (1-4 plants).

Species	Common Name	Observed Limit of Distribution (metres from trail edge)	Structural Layer					
			G1	S2	S1	T3	T2	T1
EDGE SPECIES								
Tree Species								
<i>Betula papyrifera</i> Marsh.	White Birch	6	(x)	x	x	x		
<i>Populus tremuloides</i> Michx.	Trembling Aspen	2		(x)				
<i>Prunus pennsylvanica</i> L.f.	Pin Cherry	3	(x)	(x)	x			
<i>Salix</i> sp.	Willow	3		x	x	x		
Shrub Species								
<i>Apocynum androsaemifolium</i> L.	Spreading Dogbane	4		x				
<i>Cornus rugosa</i> Lam.	Roundleaf Dogwood	6			(x)	(x)		
<i>Rubus allegheniensis</i> Porter	Allegheny Blackberry	8	(x)	x	x			
<i>Rubus idaeus</i> L.	Raspberry	8	x	x				
<i>Rubus odoratus</i> L.	Flowering Raspberry	7		x				
<i>Ribes coccineum</i> Pallas	American Red Currant	2		(x)				
Herb Species								
<i>Anaphalis margaritacea</i> (L.) Benth. + Hook.	Life-everlasting	1		x				
<i>Cicuta lutea</i> L.	Lutetian Enchanter's Nightshade	1		(x)				
<i>Cirsium arvense</i> (L.) Scop.	Canada Thistle	1	(x)					
<i>Epipactis helleborine</i> (L.) Grantz	Hellebore-like Epipactis	8	(x)					
<i>Equisetum</i> sp.	Horehound	3		x				
<i>Hieracium aurantiacum</i> L.	Orange Hawkweed	1		x				
<i>Impatiens capensis</i> Moench	Cape Touch-me-not	1	(x)					
<i>Leontodon</i> sp.	Dandelion	5	(x)					
<i>Medicago sativa</i> L.	Alfalfa	1	(x)					
<i>Onoclea sensibilis</i> L.	Sensitive Fern	3	x					
<i>Solidago</i> sp.	Goldenrod	5		x				
<i>Thymus sordidus</i> L.	Coolwort	5	x					
<i>Viola incognita</i> Brainerd	Large-leaved White Violet	3	x					
<i>Viola</i> sp.	Violet	5	(x)					

Species	Common Name	Section		Structural Layer						
		Trail	Control	G1	S2	S1	T3	T2	T1	
INTERMEDIATE SPECIES										
Tree Species										
<i>Betula alleghaniensis</i> Britton	Yellow Birch	x	(x)	(x)	x	x	(x)	(x)		
<i>Acer spicatum</i> Lam. ¹	Mountain Maple	x	x	x	x	x				
<i>Cornus alternifolia</i> L.f.	Alternate-leaved Dogwood	x	(x)	x	x					
Shrub Species										
<i>Aralia racemosa</i> L.	Indian Root	x	(x)	(x)	x					
<i>Dicorylla loniceris</i> Mill. ²	Bush Honeysuckle	x	(x)	x	x					
<i>Sambucus pubens</i> Michx. ³	Red-berried Elder	x			x					
Herb Species										
<i>Aster acuminatus</i> Michx.	Acuminate Aster	x	x	x	x					
<i>Aster macrophyllus</i> L.	Large-leaved Aster	x	(x)	x						
<i>Polygonum ciliolobum</i> Michx.	Fringed Bindweed	x	(x)	(x)	x					
<i>Viola pallens</i> (Banks) Brainerd	Northern White Violet	x	x	x						
<i>Dryopteris marginalis</i> (L.) A. Gray	Evergreen Shield-Fern	x	x	x	x					

¹This species was almost as abundant at the back of the control section as from 0-8 m in the trail section. Beyond the trail edge plots, it tended to occur on rocky ledges and other well-drained sites of shallow soil.

²Except for one occurrence in the groundlayer at the back of the control section this species occurred exclusively in the trail section from 0-8 metres. According to Dansereau (1943) it is generally found in open places.

³This species occurred with very low abundance in the trail section to 17 metres of the trail margin. According to Dansereau (1943) it is generally found in open places.

Species	Common Name	Section		Structural Layer					
		Trail	Control	G1	S2	S1	T3	T2	T1
INTERIOR SPECIES									
Tree Species									
<i>Abies balsamea</i> (L.) Mill.	*Balsam Fir	(x)	(x)	(x)	(x)				
<i>Acer pennsylvanicum</i> L.	Striped Maple	x	x	x	x	x	x		
<i>Acer rubrum</i> L.	Red Maple	x	x	x	x				
<i>Acer saccharum</i> Marsh.	Sugar Maple	x	x	x	x	x	x	x	x
<i>Amelanchier</i> sp.	*Serviceberry	(x)	x	x	x				
<i>Fagus grandifolia</i> Ehrh.	American Beech	x	x	x	x	x	x	x	x
<i>Ostrya virginiana</i> (Mill.) K. Koch	Ironwood	x	x	x	x	(x)	(x)	(x)	
<i>Prunus virginiana</i> L.	*Choke Cherry		x	x	x	(x)			
<i>Quercus rubra</i> L.	*Red Oak	(x)	(x)	(x)					
<i>Tilia americana</i> L.	Linden (Basswood)	x	x	(x)	x	(x)	(x)		
Shrub Species									
<i>Corylus cornuta</i> Marsh.	*Beaked Hazlenut	(x)	x	(x)	x	x			
<i>Lonicera canadensis</i> Bartr.	*American Fly-Honey-suckle	x	x	x	x				
<i>Viburnum alnifolium</i> Marsh.	Mooneyberry	x	x	x	x	x			
Herb Species									
<i>Actaea pachypoda</i> Ell.	Thick-pediced Baneberry	(x)		(x)					
<i>Clintonia borealis</i> (Ait.) Raf.	*Yellow Clintonia		(x)	(x)					
<i>Epifagus virginiana</i> (L.) Bart.	*Beechdrops	x	x	x					
<i>Lycopus uniflorus</i> Michx.	*Northern Bugle-weed	(x)		x					
<i>Maianthemum canadense</i> Desf.	Wild Lily-of-the-valley	(x)	x	x					
<i>Medeola virginiana</i> L.	*Indian Cucumber-root	x	x	x					
<i>Mitella diphylla</i> L.	*Two-leaved Mitrewort		(x)	(x)					
<i>Oxypetala claytonii</i> (Michx.) Clarke	*Hairy Sweet-Cicely	(x)		(x)					
<i>Prenanthes</i> sp.	*White Lettuce	x		x					
<i>Prenanthes</i> sp.	*White Lettuce	x		x					
<i>Prenanthes altissima</i> L.	Tall White Lettuce	(x)	(x)		x				
<i>Polygonatum pubescens</i> (Wild.) Pursh	*Hairy Solomon's Seal	x	x	x					
<i>Pyrola</i> sp.	*Wintergreen		(x)	(x)					
<i>Saxifraga racemosa</i> (L.) Desf.	*False Solomon's Seal	(x)		(x)					
<i>Streptopus roseus</i> Michx.	Pink Streptopus	x	x	x					
<i>Trientalis borealis</i> Raf.	*Star-flower	x	x	x					
<i>Trillium grandiflorum</i> (Michx.) Salisb.	*Large-flowered Trillium		(x)	(x)					
	*Unidentified	(x)		(x)					

*Species not found within 8 metres of trail edge

¹This species occurred with low abundance in the upper control section (only two occurrences in upper trail section). According to Dansereau (1943) this species is generally found in open places.

²Found only in unit 5 at back of the control section. This species is also generally found in open places (Dansereau 1943).