VEGETATION, ENVIRONMENT, AND DISTURBANCE IN THE UPLAND FORESTED LANDSCAPE OF ALGONQUIN PARK, ONTARIO

by

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Vegetation, Environment, and Disturbance in the Upland Forested Landscape of Algonquin Park, Ontario

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ABSTRACT

The major purpose of this thesis is to examine the two conflicting models that provide an explanation for the influence of environment on upland forest vegetation composition in the Great Lakes-St. Lawrence Forest Region. First, using modern fire records and forest resource inventory maps, an index to fire incidence was developed. Results of the Chi-squared test and t test showed that fire incidence for each species differed significantly from at least two others. This index was then used to quantify fire impact on each stand sampled. The second and third studies examined the relationship between environmental factors, including fire, and upland forest vegetation of the (1) overstory and (2) understory vegetation using ordination methods including detrended correspondence analysis and canonical correlation analysis. Results indicated that the major influence on forest overstory composition is a fire-soil moisture complex gradient in which (1) the two influences are inversely related and (2) fire has the greatest impact. The tolerant hardwood stands, dominated by *Acer saccharum*, *Betual lutea*, and *Tsuga canadensis*, occur mainly at the low fire-high moisture end of the gradient, the pine stands, dominated by *Pinus strobus*, *Pinus resinosa*, and *Pinus banksiana*, occur mainly at the high fire-low moisture end, and the intolerant hardwood stands, dominated by *Populus* spp., *Betula papyrifera*, and *Quercus rubra*, occur at an intermediate position along the gradient. Results also indicated that a light-fire complex gradient exerted the major influence on understory vegetation composition where (1) fire and light are directly related, and

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(2) light is regarded as the more important influence. Understory species were classified into one of three growth strategy categories. The "stress tolerators/avoiders", dominated by trees, ferns and Lycopods (e.g., *Acer saccharum*, *Dryopteris spinulosa*, and *Lycopodium obscurum*), can tolerate light stress but not fire. The "ruderals/endurers", dominated by shrubs and summer herbs (e.g., *Corylus cornuta* and *Aralia nudicaulis*), can tolerate fire but not light stress. The "generalists", dominated by all major growth forms including trees, shrubs, and summer herbs (e.g., *Acer rubrum*, *Viburnum alnifolium*, and *Trientalis borealis*) are successful across a wide range of fire and light intensities. It is probable that fire suppression in Algonquin Park has changed and will continue to change the composition of the upland vegetation

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Recognition of the ecosystem concept by the scientific community in the late 19th Century emphasized the need to focus on relationships between and among organisms, their assemblages, and their environment. Early investigations which focussed on the influence of environment upon the composition of biota identified climate, in the form of temperature (Merriam, 1894) and the ratio of precipitation to evaporation (Tanseay, 1905), as the primary determinants of animal and plant community composition. Later, Thornthwaite (1948) analyzed temperature and precipitation records to determine water availability which was then shown to be correlated with the regional distributions of major types of vegetation.

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ABSTRACT

The major purpose of this thesis is to examine the two conflicting models that provide an explanation for the influence of environment on upland forest vegetation composition in the Great Lakes-St. Lawrence Forest Region. One model focusses on soil moisture as the primary determinant of vegetation composition whereas the other focusses on fire as the primary determinant. Three studies were conducted. For the first study, an index to fire incidence was developed using modern fire records and forest resource inventory maps. Results of the Chi-squared test and t-test showed that fire incidence for each tree species differed significantly from at least two other species. This index was then used to determine the probability of fire incidence for each stand sampled. The second and third studies examined the relationship between environmental factors, including fire, and upland forest vegetation of the (1) overstory and (2) understory using ordination methods, including detrended correspondence analysis and canonical correlation analysis. Results indicated that the major influence on forest overstory composition is a fire-soil moisture complex gradient in which (1) the two influences are inversely related and (2) fire has greatest impact. The tolerant hardwood stands, dominated by *Acer saccharum*, *Betula lutea*, and *Tsuga canadensis*, occur mainly at the low fire-high moisture end of the gradient, the pines, dominated by *Pinus strobus*, *Pinus resinosa*, and *Pinus banksiana*, occur mainly at the high fire-low moisture end, and the intolerant hardwood stands, dominated by *Populus* spp., *Betula papyrifera*, and *Quercus rubra*, occur at an intermediate position along the gradient. Results also indicated that a light-fire complex gradient exerted the major influence on understory vegetation composition where (1) fire and light are directly related, and (2) light is regarded as the more important influence. Understory species were classified into one of three growth strategy categories. The "stress tolerators/avoiders", dominated by trees, ferns and Lycopods (e.g. *Acer saccharum*, *Dryopteris spinulosa*, and *Lycopodium obscurum*), can tolerate low light stress but not fire. The "ruderals/endurers", dominated by shrubs and summer herbs (e.g. *Corylus cornuta* and *Aralia nudicaulis*), can tolerate fire but not low light stress. The "generalists", dominated by all major growth forms including trees, shrubs and summer herbs (e.g. *Acer rubrum*, *Viburnum alnifolium*, and *Trientalis borealis*) are successful across a wide range of fire and light intensities. It is probable that fire suppression in Algonquin Park has changed and will continue to change the composition of the upland vegetation.

CHAPTER 1 - INTRODUCTION

"Natural communities provide the research subjects through which evolution and the function of the living world may be understood, and a standard by which the behavior of ecosystems altered by man can be interpreted" (Whittaker, 1975; pg. 371). We are, however, rapidly losing our opportunity to develop this understanding and to accurately interpret human influence upon the behavior of forested ecosystems throughout the world. This is principally because we have failed to protect many ecosystems from human alteration and because, in those cases where protection is impossible, we have failed to monitor the impacts of our influence.

One such case is Algonquin Park, Ontario. Although it is one of North America's oldest and most well-known parks, it was only recently that small portions of it were designated for protection from human influence (Ontario Ministry of Natural Resources, 1974). The major forms of human influence in the park include timber harvesting, fire suppression, acid deposition, and recreation (Martin, 1959; Pimlott et al., 1969; Ontario Ministry of Natural Resources, 1974; Cwynar, 1977; Cwynar, 1978; Brown, 1980), none of which is currently being monitored for the purpose of conserving the forest resources of the park. The future integrity of Algonquin is dependent upon successful conservation of these forest resources.

To accurately assess alterations due to human activity, one must have a sound concept of the structure and function of the undisturbed or mature ecosystem (Bormann et al., 1974). The first step in developing such a concept for forested ecosystems is to discover the compositional variation in the dominant ecosystem component, the primary producers or the green plants (Carleton, 1984; Weins, 1984). The variation within the dependent variable (vegetation composition) is "ultimately controlled by two sets of independent variables: physical environmental parameters and other species" (Diamond, 1986; pg. 3). Because environmental factors, including resource availability, are more fundamental to the description of species habitat than the effects of other species (Billings, 1952; Daubenmire, 1974; Price et al., 1984), the majority of forest community studies have focussed on the former.

Since Whittaker's (1956) seminal work in the Great Smoky Mountains, many studies have demonstrated the importance of environmental factors in explaining forest composition within various regions of North America. These include studies within the Boreal Region (Damman, 1964; Drew and Sharks, 1965; Jeglum, 1974; Dyrness and Grigal, 1979; Carleton and Maycock, 1980; Carleton, 1982; Corns, 1983; Viereck et al., 1983; Yarie, 1983), the Great Lakes Region (Curtis, 1959; Maycock and Curtis, 1960; Lopoukhine, 1974; Pastor et al., 1982; Pregitzer et al., 1983; Boerner 1984, Whitney 1986), the northern Appalachian Mountains (Holway and Scott, 1969; Bormann et al., 1970; Siccama, 1974; Whitney and Moeller, 1982), the central Appalachian Mountains (McIntosh, 1972; Keever, 1973; Collins and Pickett, 1982), the southern Appalachian Mountains (Mowbry and Oosting, 1968; Golden, 1981; Harmon et al., 1983;

Mansberg and Wentworth, 1984; Rheinhardt and Ware, 1984), the Atlantic Coastal Plains (Pella-Bianca and Olson, 1961; Nesom and Treiber, 1977; Marks and Harcomb, 1981; Jones and Gresham, 1985), the Rocky Mountains (Langenheim, 1962; Patten, 1963; Despain, 1973; Whittaker and Niering, 1975; Peet, 1981). and the Pacific Coast Mountains (Gardner, 1958; Whittaker, 1960; Waring and Major, 1964; Baily and Poulton, 1968; Waring, 1969; Wali and Krajina, 1973; Zobel et al., 1976; Moral, 1978; Vankat, 1982; Parker, 1982; Goldberg, 1982; Borchert and Hibberd, 1984).

Although descriptive, survey oriented scientific studies cannot demonstrate causation (Pianka, 1969), they are extremely useful for identifying and determining the relative importance of ecological relationships, for generating testable hypotheses (Gauch, 1982; Pielou, 1984), and for putting later more detailed studies into context. Quinn and Dunham (1983, pg. 603) state that:

> "In practice, the logic of ecological and evolutionary research differs from the Popperian model in being largely inductive...Generally, no single cause can be shown to account for all of the observed variation in patterns and processes in natural communities. The objective of investigation in cases of this sort is not to determine the single cause of a pattern, as no such cause exists, but rather to assign relative importances to the contributions of, and interactions between, a number of processes, all known or reasonably suspected of operating to some degree...It is certainly true that

> the history and sociology of actual scientific advances often correspond poorly to the process envisioned in the hypothetico-deductive model (Kuhn, 1970; Brush, 1974)."

Relative to the hypothetico-deductive methods of laboratory and field experimentation, the natural experimental or survey approach is most advantageous with regard to temporal scale, spatial scale, realism, and generality (Diamond, 1986). It is, however, the worst procedure with respect to regulation of independent variables and site matching.

For this study, the survey approach was used to examine two conflicting models that provide an explanation for the influence of environment upon forest composition within the Great Lakes-St. Lawrence (GLSL) Forest Region. This involved identification and description of vegetation composition and its variation within typical upland forests of Algonquin Park and examination of relationships between vegetation composition and environmental factors.

Three separate but related studies were conducted for this thesis. The first study involves the development of a method to quantify the incidence of fire in post-fire stands within which the evidence of fire no longer existed or was too scanty to utilize. This method was necessary in order to carry out the second and third studies. For the second study the relationship between environmental factors, including fire, and overstory vegetation was quantified. Because the understory of a temperate forest normally differs substantially from its overstory with regard to plant growth forms (herbs and shrubs versus mature trees) and life cycle stage of the trees (seedlings and saplings versus mature trees), the relationships between understory vegetation and environment were investigated separately from the relationships between overstory vegetation and environment for the third study.

CHAPTER 2 - LITERATURE REVIEW

In 1877 the need for modern science to recognize the concept of biota and environment as an integrated whole was stated by Mobius: "Science possesses, as yet, no word by which such a community of living things (oyster beds) may be designated; no word for a community where the sum of species and individuals, being mutually limited and selected under the average external conditions of life, have, by means of transmission continued in possession of a certain definite territory". To define this phenomenon, he proposed the term "biocoenosis". In western science, however, this concept has come to be known as the "ecosystem", originally coined by Tansley in 1935.

Recognition of the ecosystem concept by the scientific community in the late 19th Century emphasized the need to focus on relationships between and among organisms, their assemblages, and their environment. Early investigations which focussed on the influence of environment upon the composition of biota identified climate, in the form of temperature (Merriam, 1894) and the ratio of precipitation to evaporation (Tanseay, 1905), as the primary determinants of animal and plant community composition. Later, Thornthwaite (1948) analyzed temperature and precipitation records to determine water availability which was then shown to be correlated with the regional distributions of major types of vegetation.

For a number of years, the theory that moisture determined the distribution of vegetation types dominated descriptive forest ecosystem studies within the GLSL Forest Region. The broadest of these studies was carried out by Maycock and Curtis (1960) who sampled stands throughout the Great Lakes region. They explained the occurrence of species and community types using a moisture gradient as the dominant environmental influence. The dry end of their gradient was dominated mainly by white pine and red pine; the wet end was dominated mainly by sugar maple, yellow birch, and hemlock; and the intermediate portion of the gradient was dominated by red maple, white spruce, and white birch. Other studies which focussed on the forests of the GLSL Forest Region were more local in nature.

In a northern Minnesota study, Alway and McMiller (1933) showed that from high levels of site moisture to low levels, the following tree species were observed to dominate, respectively: maple-basswood, white pine, Norway spruce, and jack pine. Flaccus and Ohmann (1964) also presented data which were consistent with the moisture hypothesis. In addition to the types observed by Alway and McMiller (1933), Flaccus and Ohmann (1964) observed forests dominated by red pine, sugar maple-yellow birch, black spruce-tamarack, northern white cedar, and black ash occurring along a moisture gradient from low to high. In adjacent northern Wisconsin, Brown and Curtis (1952) found that, in addition to those observed by Flaccus and Ohmann (1964) and Alway and McMiller (1933), the patterns of forest communities dominated by hemlock, red oak, white birch, trembling aspen, and _Quercus ellipsoidalis_ were strongly influenced by soil moisture.

Very little work on the structural relationships between forest composition and environment has been conducted in the eastern portion of the GLSL Forest Region. One study indicated that the occurence of forest communities within Gatineau Park, Quebec is determined primarily by differences in site moisture conditions (Lopoukhine, 1974). Major species included sugar maple, American beech, and yellow birch at the moist end of the gradient, white and red pine at the dry end, and intermediate along the gradient were red oak and poplar. Adjacent to the eastern border of Algonquin Park, closer to the central portion of the GLSL Forest Region, Fraser (1954) also found that moisture was the major determinant of forest composition.

It was not until Hill´s (1959) and Anderson´s (1969) work within and around Algonquin Park, however, that moisture was perceived as a member of a complex environmental influence rather than the sole forest compositional determinant. In his forest ecosystem classification scheme Hills (1959) considered the influence of soils and disturbance as well as climate. The most important of these were texture, fire, logging, clearing, insects, diseases, browsing, and silvicultural treatments all of which were described as having variable influences upon forest succession based upon qualitative field assessment.

Although it was not noted by Hills (1959), fire is not only important in initiating forest succession, but it is integral to maintaining certain types of mature, or old-growth forest communities such as those dominated by white and red pine (Horton and Brown, 1960; Anderson 1969). Workers such as Stearns (1951), and Flaccus and Ohmann

(1964) mentioned the possible influence of fire, but generally dismissed it as relatively unimportant. Instead, the theory that fire plays an important role in determining forest composition in the GLSL Forest Region was pursued by a different group of researchers than those who focussed on moisture as the major influence upon forest composition.

These fire-based studies began in 1935 when Maissurow showed that natural regeneration of white pine in central Quebec was associated with the effects of fire. Drawing from observations in New England, Michigan, and Wisconsin, Cary (1936) also pointed out the importance of fire in the perpetuation of white pine. Later Maissurow (1941) found that abundant reproduction occurred in yellow birch, basswood, elm, hemlock and white pine stands as a result of surface fire, but that reproduction was very low in similarly affected sugar maple stands. He concluded that fire is a "beneficial and necessary factor in the perpetuation of [many] virgin forests" in the GLSL Forest Region.

Studies of the effects of recent fire stimulated further research into the historical incidence of fire and its relationship to forest composition both in Minnesota (Spurr, 1954; Heinselman, 1973; Swain, 1973) and central Ontario (Cwynar, 1977; 1978). The results of these historical studies confirmed that the presence of pine forests is due mainly to the effects of periodic fire. In addition, the presence of aspen was found to be significantly influenced by fire because of the tendency of aspen to sprout under conditions of increased temperature (Swain, 1973; Heinselman, 1973). Swain (1973) and Cwynar (1977, 1978) have determined that the average fire rotation for portions of the GLSL

Forest Region dominated by pine and poplar ranged from 60 to 80 years.

In addition to being influenced by environmental factors, forest community composition is affected by the process of ecological succession, also known as ecosystem development (Bormann and Likens, 1979b). Succession may be defined as a change in ecological community composition with time. In contrast to the classical succession model of community-by-community replacement, modern concepts suggest that "succession occcurs as the result of differential survival and growth of individual species that are adapted to grow best at different stages in the successional sequence" (Kimmins, 1987; pg. 410). Finegan (1984) states, however, that "Neither reductionist [(modern succession concepts)] nor holistic [(classical succession concepts)] theories of succession have produced models which explain field observations." He argues that a third, synthetic approach representing a combination of the two major successional theories should be sought.

Two primary studies of forest succession have been conducted in the Algonquin Region. Although these studies fit more with the classical theory of succession, they are valuable from a descriptive perspective. For the first study, Martin (1959) identified two major successional pathways in the forests of Algonquin. The hydrosere, a successional sequence that begins with the filling of open water and progresses to dry land, went from bog, to black spruce forest, to black spruce-white cedar forest and finally to a bottomland forest composed of balsam fir and alder.

The other successional pathway identified by Martin (1959) was a xerosere or a successional sequence occuring mainly on well-drained land areas. For the primary xerosere sequence, the progression was from balsam fir-white spruce forest, to white pine forest, to hardwood forest composed of sugar maple, yellow birch and hemlock. Secondary succession in the xerosere progressed from either a white birch-poplar forest or a jack pine forest, to a forest of either balsam fir-white spruce or white pine, to a subclimax of hardwoods and finally to a climax of hemlock. Climax here refers to the endpoint of successional development and subclimax refers to the stage immediately preceeding climax.

In contrast to Martin (1959), Hills (1959) recognized the variable affect of environmental gradients and disturbance on forest successional pathways in the Algonquin Region. He classified the environmental gradients at the first level based on climate using three broad classes: "normal ecoclimate", "hotter ecoclimate" and "colder ecoclimate". Within each broad climate class, six soil moisture classes were identified and various forms of disturbance such as fire, logging, clearing, insects, tree disease, browsing, planting, and silvicultural treatments were also considered. A total of 43 potential successional sequences that varied according to landform, temperature, soil moisture and disturbance were identified by Hills (1959) resulting in as many different climax communities. A total of 20 tree species occurred as dominants or co-dominants in these climax communities, 18 of which are common to Algonquin Park.

Hills' (1959) recognition that different successional sequences occur on different site types under different disturbance regimes was closer to the modern population oriented concept of forest succession than Martin's (1959) unidirectional, community-by-community replacement sequence.

CHAPTER 3 - STUDY AREA

INTRODUCTION

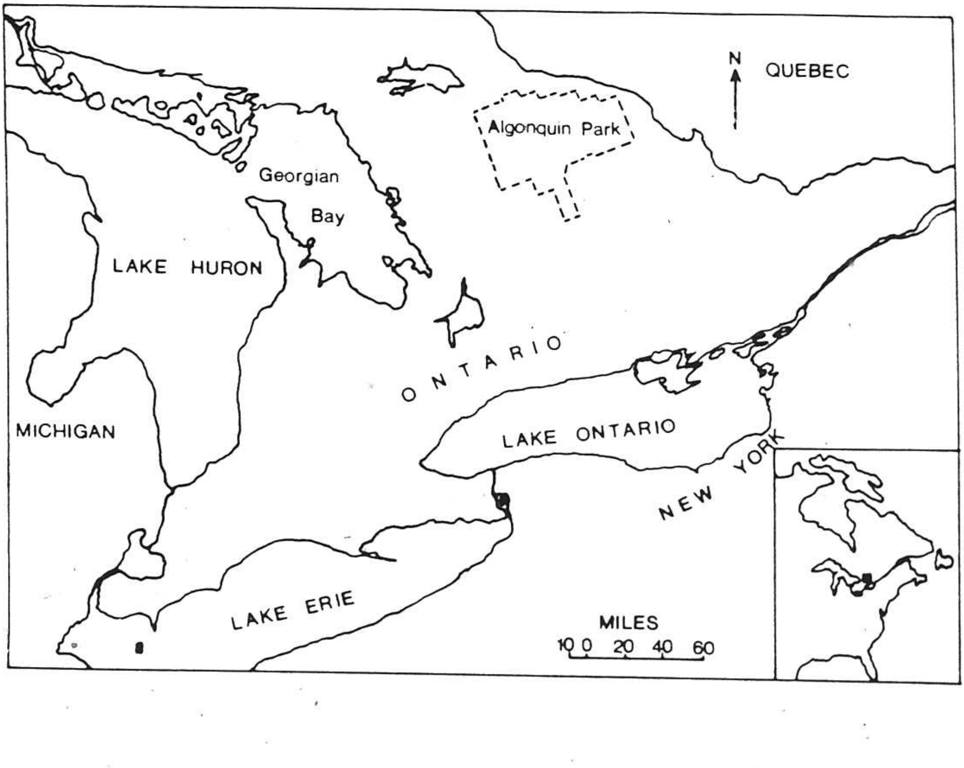
Algonquin Park is located in the northern part of southern Ontario and occupies approximately 770,000 ha (Figure 3-1). Two topographic systems predominate in the park - the Precambrian uplands in the west and the Ottawa lowlands in the east. The highest elevations, up to 580m, occur in the Precambrian uplands. Characteristic of these uplands are small, deep lakes scattered within a rolling, irregular topography. The Ottawa lowlands feature elevations ranging from 180 to 380 m with a more regular relief, a predominance of river systems and fewer lakes.

CLIMATE, GEOLOGY AND SOILS

Compared to adjacent areas, the park has lower temperatures and greater precipitation due to higher than average elevations. The average July air temperature is 19 degrees C and in January the air temperature averages -11.5 degrees C (Brown et al., 1980). Mean annual precipitation varies from 91 cm in the west to 66 cm in the east (Brown et al., 1980).

The bedrock underlying the park is part of the Canadian Shield known as the Grenville Structural Province and is dominated by granitic

FIGURE 3-1 - REGIONAL SETTING OF ALGONQUIN PARK



and biotite gneiss interspersed with intrusive dikes of amphibolites (Adams and Barlow, 1910; Hills, 1959). The soils of Algonquin are predominantly Dystric Brunisols although some Podsols do occur (Canada Soil Survey Committee, 1978). Within the Precambrian uplands, the soils have been derived mainly from glacial deposits of loose and compact till, and they range in depth from 0 to 3m with occasional depths over 10m in some areas. Sandy waterlain deposits do occur in narrow valleys. The Ottawa lowland soils are derived from the same parent material found in the uplands as well as from broad glacial outwash deposits of sand and gravel. These plains vary in texture from course gravel to fine sands with depths occasionally as great as 20m. All upland soils are generally coarse textured and acidic.

FOREST COVER

Pimlott et al. (1969) identified three major forest types in Algonquin Park that include the tolerant hardwoods, intolerant hardwoods, and pines. The tolerant hardwoods and intolerant hardwoods differ with respect to their tolerance to low levels of light. The western uplands of Algonquin Park are dominated by tolerant hardwoods including sugar maple (Acer saccharum Marsh.), yellow birch (Betula lutea Michx. f.), and hemlock (Tsuga canadensis (L.) Carr.). The eastern lowlands are dominated by both pines and intolerant hardwoods. The pines include white pine (Pinus strobus L.), red pine (Pinus resinosa Ait.), and jack pine (Pinus banksiana Lamb.). The intolerant hardwoods include trembling aspen (Populus tremuloides Michx.), large-toothed aspen (Populus grandidentata Michx.), white birch (Betula papyrifera Marsh.), and northern red oak (Quercus rubra L.).

There are a variety of similarities and differences between the forest composition in Algonquin and the forest composition in the other portions of the GLSL Forest Region. Lopoukhine's (1974) data from Gatineau Park, Quebec indicate that forest composition there differs from that in Algonquin mainly by the greater representation of black ash and red oak, the lesser dominance of yellow birch and jack pine, the association of red oak with sugar maple, and the association of hemlock with red and white pine. Sugar maple is the dominant forest type in both areas (Lopoukhine, 1974) and throughout southern Quebec (Lemeiux, 1963). Algonquin Park and the Gatineaus are also similar with regard to the common association of sugar maple with yellow birch and beech.

In the upper St. Lawrence River area, common upland tree species not found in Algonquin include white ash, shagbark hickory (Carya ovata (Mill.) K. Koch.), gray birch, butternut (Juglans cinerea L.), bitternut hickory (Carya cordiformis (Wang.) K. Koch.), and pitch pine (Pinus rigida Mill.) (Hirvonen and Woods, 1978a). Forest composition similarities include only Hirvonen and Woods' (1978a) poplar-birch association which was most similar to the poplar spp. community type identified within Algonquin.

The upland forests of Algonquin are also very similar to those which are found to the west, along the eastern shore of Lake Huron except that red oak, red maple, and beech are more abundant along the

Huron shore and poplar is much less abundant (Hirvonen and Woods, 1978b). In addition, white oak (Quercus alba L.), white ash (Fraxinus americana L.), and eastern red cedar (Juniperus virginiana L.) occur along Lake Huron's eastern shore but are absent from Algonquin.

Studies of upland forests further west in the Upper Peninsula of Michigan indicate that the majority of upland areas are dominated by sugar maple, yellow birch, and hemlock (Pregitzer and Barnes, 1984; Spies and Barnes, 1985). In addition, white pine, jack pine, red oak, black ash, and red maple occur throughout the upland forest communities. The common Algonquin species red pine, large-toothed aspen, and trembling aspen were not commonly found in northern Michigan.

The GLSL forests of northern Wisconsin differ from those of Algonquin mainly in terms of a greater importance of beech and jack pine, the lesser importance of large-tooth aspen, and the presence of a few common species which do not occur at all in Algonquin (Curtis, 1959). These include Hill's oak (Quercus ellipsoidalis E. J. Hill.) and white oak (Quercus alba L.).

The forests at the western extreme of the GLSL Forest Region in northeastern Minnesota are most dissimilar to those of Algonquin. The major difference is the absence of the tolerant hardwood community dominants including sugar maple, yellow birch, hemlock, and beech in Minnesota (Ohmann and Ream, 1971; Grigal and Ohmann, 1975). Red oak is of low importance in northeast Minnesota but occurs as a community dominant in Algonquin. The western GLSL forests have a greater proportion of boreal species including black spruce as an upland dominant.

FIRE

Palynological data from Barron Township on the east side of Algonquin Park indicate that, for the period 770 to 1270 A.D., the frequency of large fires was approximately once every 80 years (Cwynar, 1978). More recent fire history data for the pre-suppression period 1696 to 1920 indicate that the fire rotation in Barron Township is about 70 years (Cwynar, 1977). In other words, prior to human fire suppression, it took only approximately 70 years for fire to burn over 18,600 ha within Barron Township. Some areas may burn more than once, thus the entire township may not have burned within the 70 year rotation period.

Since 1921, fires have been suppressed in Algonquin Park. Using fire history data from Brown (1980, pg. 37) the fire rotation for Barron Township since suppression was calculated at 936 years, which represents a 13-fold decrease in the amount of forest burned in Barron Township for a 70-year period from 1921 to 1991. Because Barron Township is similar in forest composition to other townships on the east side of Algonquin it is probable that similar increases in fire rotation have taken place in these townships.

In addition to suppressing fires, humans affect the fire regime in Algonquin Park by igniting fires. Table 3-1 lists the causes of fires, their frequency, and area burned. Naturally-caused (lightning) fire for

TABLE 3-1 - THE CAUSES OF ALGONQUIN PARK FIRES AND AREA BURNED FOR 1973-1978 INCLUSIVE (from Brown, 1980, pg. 37)

CAUSE	FREQUENCY (6 years) Absolute	Percent	AREA BURNED (acres) Absolute	Percent
Lightning	68	22	431	47
Railway	16	5	321	35
Recreation	207	67	144	16
Resident	2	<1	<1	<1
Miscellaneous	6	2	3	<1
Industrial	3	1	1	<1
Incendiary	2	<1	2	<1
Unknown	6	2	5	<1

the period 1973 to 1978 inclusive made up the greatest percentage of the burned area. Railway fire ignition resulted in 35% of the burned area and recreation resulted in 16% of the area burned. Residential, industrial, and incendiary causes made up less than 1% each.

LOGGING

The location and nature of logging effects on forest ecosystems in Algonquin Park are unknown. However, a general review of the logging chronology in Algonquin Park is provided by Brown (1980). Cutting of white and red pine in Algonquin began about 1830 and peaked in 1864. Sawmilling, mainly of white and red pine, replaced the square timber trade in the late 1800's and by the 1930's other tree species were being cut. The harvesting of yellow birch, the first hardwood cut in Algonquin, peaked in the mid-1950's. Sugar maple harvesting began in 1945 and has expanded since then. In addition to coniferous pulpwood, the volume of low quality deciduous pulpwood has increased significantly in the last 15 years. All but the rare tree species in Algonquin are currently harvested.

Many silvicultural systems are used in the 75% of the park that is presently being logged. Variations of the selection method are applied in tolerant hardwood, hemlock, and balsam fir stands. The shelterwood method is used in white pine, black spruce, white cedar, hemlock, and tolerant hardwood stands. For red pine, white spruce, and red spruce stands the seed tree method is used. Lastly, clearcutting is applied in balsam fir, jack pine, poplar, and white birch stands.

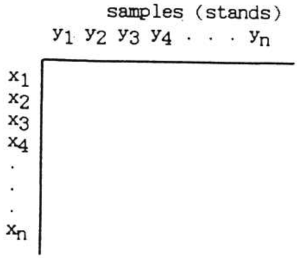
CHAPTER 4 - DESCRIPTION OF MULTIVARIATE METHODS

Data describing the structure of vegetation and environment within forested ecosystems are multivariate in nature. The vegetation structure for the study area was represented within a two-way data matrix which described species abundance for all sampled stands. The structure of the environment within these stands was also represented within a two-way data matrix which described the magnitude of a variety of environmental factors. Figure 1-1 shows the structure of a two-way data matrix which is the first step in data reduction and ordination. By reducing the complexity of these data it is possible to obtain interpretable results. A simple way to do this for vegetation data is to identify the distribution of species along an environmental gradient that is easily recognized and measured. This is called direct gradient analysis (Whittaker, 1948; 1967). Although this approach fulfills the objectives of summarizing and revealing the structure of multivariate data by using simple graphing procedures, it is generally not preferred over other methods because (1) the gradient is based on a single environmental factor when in fact there is usually a complex of environmental factors involved and (2) selection of the controlling environmental factor is subjective.

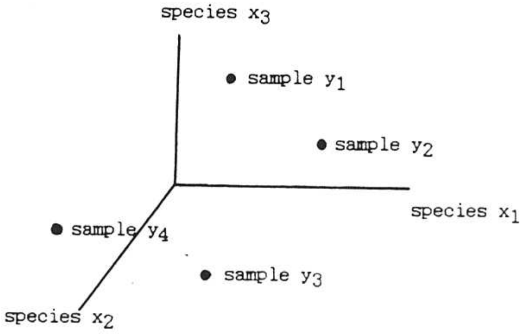
The alternative is indirect gradient analysis or ordination which is defined by Pielou (1984) as "a procedure for adapting a multidimensional swarm of data points in such a way that when it is

FIGURE 4-1 - DATA REDUCTION AND ORDINATION

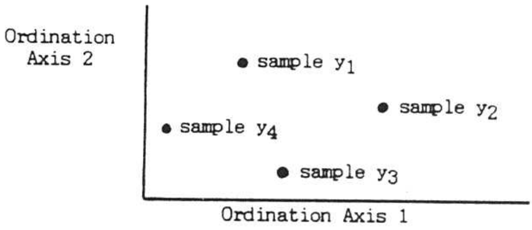
PART A - "Two-Way Data Matrix"



PART B - "Multi-dimensional Swarm of Data Points"



PART C - "Two-dimensional Ordination Plot"



projected onto a two[dimensional]-space any intrinsic pattern the swarm may possess becomes apparent." (see Figure 1-1, Parts B and C). The result is a graph in which similar samples are near each other and dissimilar samples are far apart. It differs from direct gradient analysis mainly in that all environmental influences can be objectively related to the biological data using the ordination results, however, this must be performed in a subsequent step.

Gittins (1979) states that there are three major advantages to ordinating vegetation for eventual analysis with environmental data. These include the following: (1) a sample represented by numerous species abundance values is reduced to a single value associated with each ordination axis which can then be assessed statistically as the dependent variable, (2) it renders the data more continuous, and (3) it transforms the vegetation data into more linear relationships to conform to the nature of the environmental data.

Of all the ordination methods currently available, Hill and Gauch (1980) have shown that detrended correspondence analysis (DCA) is at least as good as, and usually superior to, other ordination techniques. Therefore, DCA was chosen to ordinate the understory and overstory vegetation data collected for this study. DCA is based on the ordination technique reciprocal averaging (RA) (Hill, 1973) with the correction of its two main faults.

There are two ways to produce results using RA. First, RA can be thought of as a version of principal components analysis (PCA) that differs from it "in the way the data matrix is transformed before the eigenanalysis, and in the way in which the eigenvectors are transformed into scores after the eigenanalysis" (Pielou, 1984; pg. 177). The stand and species scores are calculated by RA as to maximize the correlation between them. The proof of this can be found in Anderberg (1973, pg. 215).

RA can also be done by reciprocal averaging. Pielou (1984) provides an outline of this procedure.

> First, arbitrary trial values are chosen for the species scores. Next, a first set of quadrat scores is computed from these species scores. Then a second set of species scores is computed from the first set of quadrat scores, then a second set of quadrat scores from the second set of species scores. And so on, back and forth reciprocally, until the vectors of scores maintain constant relative proportions.

During the process, RA scores are rescaled into a range of 0 to 100 in order to avoid a very small range. Between 20 and 100 iterations are normally required for convergence. However, the closer the first iteration scores are to the final scores, the fewer iterations are required. The amount of variation in the data accounted for by the first ordination axis (the first eigenvalue) is equal to the contraction in the range of species scores in one iteration after convergence. The second and consecutive axes are extracted using the same iterative method except for a correction for independence from the former axis or axes. Each new axis has an eigenvalue less than the one previous.

The two major faults of RA have been alleviated through the development of DCA. These faults include (1) the arch problem - successive axes may be geometric distortions of former axes, and (2) a given distance of separation between points (samples or species) in the ordination does not carry consistent meaning because the points at the first axis ends are compressed relative to those in the axis mid-section.

Both of the above weaknesses were remedied by Hill (1979). To correct the arch distortion problem of RA, detrending of its axes was implemented. This involved dividing axis 1 into a number of segments within which the axis 2 scores were adjusted to have an average of zero. This is done at each iteration until convergence is reached. At this point, final sample scores are determined without using detrending. Each successive axis is calculated by detrending sample scores with respect to all previous axes.

In order to ensure consistent meaning for distances between points in the ordination space, rescaling is undertaken. The objective of this is to (1) ensure that species turnover occurs at a random uniform rate along the species ordination axis and (2) that equal distances in the ordination correspond to equal distances in species composition. Rescaling was accomplished by assuring a constant within-sample standard deviation by contracting or expanding small segments of the sample ordination. This constant was set to 1 to achieve a standard scaling. Thus, instead of being scaled into a range of 0 to 100 as is done with RA, DCA is scaled in natural units. Detrending is applied to the second and higher axes and rescaling is applied to all axes.

The advantages of DCA over other ordination techniques include (1) species as well as sample ordinations (RA also provides this), (2) elimination of the arch problem, and (3) uniform axis scaling. The disadvantages of DCA include (1) coping with outliers and discontinuities - outliers must be removed, (2) interpretation of axes, (3) species ordinations are usually less satisfactory than stand ordinations, and (4) rather than a geometric process, detrending is empirical in nature.

The ordinated vegetation data in this study were correlated with environmental data using the multivariate technique called canonical correlation analysis (CCA) (Hotelling, 1936) which has been effectively applied and demonstrated by Gittins (1979, 1985). CCA is an eigenanalysis method designed to measure correlations between data sets (Pimentel, 1979). It is readily applicable to a samples scores-by-vegetation axes matrix of vegetational data and a samples-by-environmental measurements matrix of environmental data (Gauch, 1982). The correlations between the two sets of variables are examined by constructing two groups of linear compounds which are called canonical variates. Carleton (1984) states that "The variates may be conceived as a group of ordination axes derived from one set of variables (e.g. species in vegetation data) rotated, under certain constraints, to correlate maximally with a group of ordination axes derived from the other set of variables (e.g. environmental measurements at vegetation sample locations)." Intraset and interset correlations may be derived and their squared values indicate the proportion of variance explained by the corresponding canonical variate.

The value obtained by averaging the interset correlations for each canonical variate is termed the redundancy measure. This measure is equivalent to the R^2 criterion which is maximized in the techniques of multiple regression and multiple correlation problems (Cooley and Lohnes, 1971) and is synonymous with explained variance. The largest possible redundancy value is 1 which can only occur when canonical correlation is 1 and all the variance of a set is extracted. The larger the redundancy of sets, the greater is the relationship between the two.

The advantages of the use of CCA for elucidating vegetation-environment relationships include objectivity (Gauch, 1982) and consideration of environmental factors as interdependent and interrelated influences on vegetation as opposed to the straight regression approach which considers environmental factors as isolated, independent influences.

There are, however, three major problems associated with this technique which should be avoided (Carleton, 1984). First, linearity of data is assumed when, in fact, vegetation data are non-linear. To mitigate the effects of this problem, the vegetation variables were reduced and transformed from discontinuous, nonlinear data to continuous, linear form using the ordination technique of DCA. Second, spuriously high canonical correlations may arise from chance correlations between a single minor variable in each data set even though redundancy levels may be low. Therefore, emphasis should be placed on redundancy levels rather than canonical correlations. Third, small sample sizes can lead to a low sample:variance ratio which in turn can cause unreasonably high canonical correlations and/or insignificant redundancy levels.

CHAPTER 5 - AN INDEX TO FIRE INCIDENCE

INTRODUCTION

When assessing environmental influences on community structure and dynamics, it is necessary to consider the role of natural disturbance (Harmon et al., 1983; Sousa, 1984; Canham and Marks, 1985; Pickett and White, 1985). Naturally caused fire is often a very important influence on forest composition within the mixed forest region of eastern North America. The most suitable methods presently available for assessing the role of naturally caused fire in this region include (1) paleoecological analysis of lake sediments for influx of charcoal, aluminum, vanadium, varve thickness, and the charcoal/pollen ratio (Swain, 1973; Cwynar, 1978), (2) fire scar dating and mapping (Heinselman, 1973; Cwynar, 1977), (3) use of stand origin and age information from even-aged stands (Heinselman, 1973; Cwynar, 1977; Van Wagner, 1978), and (4) the use of historical documents and modern fire records (Spurr, 1954; Wein and Moore, 1977; Wein and Moore, 1979; Fahey and Reiners, 1981).

Paleoecological methods result in broad temporal and spatial generalizations which are usually based on evidence from one or a few sites and, therefore, are not capable of providing site specific fire measures for a series of individual stands distributed across a broad landscape. Fire scar evidence is most abundant and reliable on coniferous trees. Accurate aging of a stand which has resulted from a destructive crown fire requires the presence of even-aged stands. Because the mixed forest region of North America is populated by substantial amounts of uneven-aged deciduous forest, the use of fire scars and stand aging to study fire are not entirely suitable. Historical documents provide only very rough fire size and location estimates, while for modern fire records, the fire size data do not reflect the role of naturally caused fire because of the modifying influence of suppression.

The purpose of this study, therefore, was to develop a method of quantifying the occurrence of naturally caused (lightning caused) fires which (1) could be applied to both deciduous and coniferous dominated stands, (2) would not be subject to the confounding effect of fire suppression, and (3) could be calculated for any stand or community type sampled within the study area. Development of this method was based on testing the null hypothesis that fire incidence within pine, intolerant hardwood, and tolerant hardwood forest types does not differ significantly. Each forest type included a unique set of three species dominance types and fire incidence was defined as "one fire event taking place within a designated area during a designated time" (Romme, 1980; pg. 135).

METHODS

Fire records (Archives of Ontario, 1930-1979) for a 50 year period were analyzed to determine the location of 252 lightning caused fires within a two township wide and eight township long transect which traversed the 72 kilometer east-west width of Algonquin Park, Ontario (see Appendix I for fire information). To determine the species composition of the overstory vegetation at the fire sites, the method of Fahey and Reiners (1981) was used. This involved sampling the vegetation on Forest Resource Inventory (FRI) Maps (Ontario Ministry of Natural Resources; 1959, 1978) at the 252 fire locations using the latitude, longitude coordinates of each fire. Those fires which occurred during or before 1967 were located on the 1959 FRI maps and those occurring after 1967 were located on the 1978 FRI maps. The fire boundary locations obtained from these records, however, did not reflect the results of natural fire because of the modifying influence of fire suppression.

To minimize the influence of fire suppression, a standard FRI map area was sampled with a plot the shape and size of one lot by one concession (approximately 400m X 1000m) at each fire location. This plot configuration was used because it was the limiting resolution of fire location information provided in the fire records.

It was necessary to assume either that lightning strikes occurred randomly throughout the transect in Algonquin Park or that a greater number of lightning strikes occurred on the park's west side which is dominated by the tolerant hardwood forest where there is greater thunderstorm activity (Hills, 1959; Brown et al., 1980). In order to test the null hypothesis that forest types in

Algonquin Park do not differ in terms of fire incidence, the frequency distribution of the species dominance-types (Whittaker, 1973) within the 252 fire stricken plots was compared with the frequency distribution of the species dominance-types within 252 randomly chosen plots which were sampled from the same set of FRI maps. Species dominance-types were designated with the name of the most abundant overstory species within each plot. The chi-squared test of goodness of fit was used to compare these two distributions.

Following the comparison of observed versus expected results, fire incidence for the ten species dominance-types was examined for significant differences. To do this, a greater degree of accuracy for species abundances was required than that obtained from the chi-squared test. For each burn plot, therefore, a list of its tree species and their abundance (percent cover) was compiled. These data were summarized by species for all 252 burn plots in order to estimate each species' abundance within the total area burned over the 50 year period. The relative abundance of each species within the total area burned, expressed in decimal form, represented the probability that the species would be associated with fire in the transect area during a 50 year period.

The influence of unequal aerial coverages of the ten tree species resulted in higher burning probabilities for those species with relatively greater aerial coverage. In order to eliminate the influence of unequal species coverages so that probabilities would reflect only the association of the species with fire, the probabilities were expressed for a standard area. This was done by dividing the raw probability for each species by the number of ha within which that species was dominant throughout the entire transect to obtain the probability per unit area. The number of ha dominated by each species within the transect area was determined from a separate 15% systematic point sample of all forest stands designated on FRI maps for each of the 16 townships. This new value was called the fire incidence probability and was expressed as a function of the plot size (40 ha) and the time period represented by the data (50 years).

In order to test for differences between fire incidence probabilities of tree species and forest types, Sokal and Rohlfs' (1969) test for the equality of two percentages was used. A t-test was applied to the arcsine-transformed data which in turn were obtained by expressing probabilities as percentages.

RESULTS

Results of the chi-squared test of goodness of fit ($x^2=28.22$; $p<.005$) indicated that the frequency distribution of the species dominance-types within the burned area and the distribution of the species dominance-types within the randomly chosen plots were significantly different (see Table 5-1). The null hypothesis that forest types within the study area do not differ in terms of fire incidence was, therefore, rejected.

Table 5-2 provides a summary of species and forest type abundance

TABLE 5-1 - CHI-SQUARED CONTINGENCY TABLE COMPARING SPECIES DOMINANCE-TYPES IN FIRE-STRICKEN AREAS AND RANDOMLY CHOSEN AREAS (shows number of plots dominated by each species; $X^2=28.22$, $p<.005$)

	White Birch	Jack Pine	Red Pine	Yellow Birch	White Pine	Red Oak	Poplar	Hemlock	Sugar Maple	Others	Total
Randomly Chosen Areas	28	3	3	11	46	4	56	7	77	17	252
Fire Striken Areas	23	6	4	11	68	6	38	4	84	8	252

TABLE 5-2 - ABUNDANCE OF TREE SPECIES AND FOREST TYPES AND THEIR ASSOCIATED FIRE PROBABILITIES

		Abundance in Entire Transect Arca		* Abundance in Burned Areas	Raw Probability	Fire Incidence Probability (FIP) ($x\ 10^{-3}$) (40 ha/50 years)	Species with Significantly Different FIP (p< 05)
		Absolute (ha)	Relative (%)	Relative (%)			
	white birch (1)	13.525	4.1	9.7	097	287	4.5 6 7 8.9 10
	red pine (2)	8.247	2.5	4.8	048	233	6.7 8.9.10
	jack pine (3)	3.629	1.1	1.9	019	209	7.8 9.10
	yellow birch (4)	19.463	5.9	8.4	084	172	1.10
TREE	white pine (5)	58.058	17.6	22.7	227	156	1.10
SPECIES	red oak (6)	8.577	2.6	3.0	030	140	1 2.10
	poplar (7)	51.790	15.7	15.3	153	118	1.2.3
	hemlock (8)	15.504	4.7	4.1	041	106	1.2.3
	others (9)	46.512	14.1	12.3	123	106	1 2 3
	sugar maple (10)	104.570	31.7	17.8	178	068	1.2.3.4.5.6
	pines (11)	69.934	21.2	29.4	294	598	13
FOREST TYPES	intolerant hardwoods (12)	73.892	22.4	28.0	280	545	13
	tolerant hardwoods (13)	139.537	42.3	30.3	303	346	11.12

values and their associated fire probabilities. Sugar maple has the second highest raw probability (.178) of the ten species, however, in terms of fire incidence probability it is ranked lowest (.068 x 10^{-3}). This is due to its low dominance within the total area burned (17.8%) relative to its very high dominance within the entire transect area (31.7%), which results in a low probability on a per hectare basis. This contrasts with jack pine which has a much higher fire incidence probability ($.209 \times 10^{-3}$) than sugar maple in spite of its lower dominance than sugar maple in the total area burned (1.9%). Because of the lower dominance of jack pine within the entire transect area (1.1%) relative to its higher dominance in the total area burned its probability on a per hectare basis is higher than that of sugar maple. Results of the t-test indicate that although no one species fire incidence probability is significantly different from the rest, each species differs significantly from at least two others.

Using the addition rule of probability, the fire incidence probability for each forest type was calculated by summing the fire incidence probabilities for each of the three species which occurred within a forest type. The pines included red, jack, and white pine; the intolerant hardwoods included white birch, red oak and poplar; and the tolerant hardwoods included yellow birch, hemlock and sugar maple. Results of the t-test indicate that fire incidence probability for the pines ($.598 \times 10^{-3}$) and the intolerant hardwoods ($.545 \times 10^{-3}$) do not differ significantly, but that their fire incidence probabilities both differ significantly from the fire incidence probability for the tolerant hardwoods ($.346 \times 10^{-3}$).

DISCUSSION AND CONCLUSION

The results of this study indicate that fire incidence is significantly higher within both the pine forest and the intolerant hardwood forest compared to the tolerant hardwood forest. Results of this study also indicate that fire incidence for the ten overstory species in Algonquin Park differ significantly from one another, although no one overstory species differs significantly in terms of fire incidence from all others.

The major problem of using these historical data, however, was that both pre-fire and post-fire vegetation was sampled. Thus, it was impossible to separate species flammability which would be indicated by sampling pre-fire overstory vegetation from species regeneration strategy which could be, but is not necessarily, indicated by sampling post-fire overstory vegetation. For example, it is quite possible that the high fire incidence probabilities obtained for white and yellow birch resulted from sampling their early colonization of severely burned sites where the original overstory had been eliminated. Because the 1959 FRI maps were used to sample 29 years of previously burned vegetation, there was sufficient time for an early successional community of birch to develop following a fire which may have occurred early in this 29 year period. In this instance, the early successional birch community would be sampled rather than the community which was originally ignited.

Examining fire records and forest cover type maps in New Hampshire, Fahey and Reiners (1981) recognized this phenomenon with white birch. Maissurow (1941) found that yellow birch also exhibited early colonization characteristics on burned sites in the hardwood forests of northern Wisconsin. In cases where destructive crown fire did occur within the transect, it is likely that the birch and poplar species colonized the burned sites due to their r-selected regeneration strategy.

However, fires that destroy the forest overstory are rare within the North American temperate forest (Chandler et al., 1983). Therefore, it is probable that on most sites in Algonquin the dominant pre-fire forest overstory species survived fire and remained as the dominant overstory species on the site. Thus, it is likely that the majority of post-fire vegetation sampled represented the vegetation type ignited which in turn would indicate vegetation flammability.

The relationship between fire incidence and the flammability of vegetation has been discussed extensively in the literature (Mutch, 1970; Rundel, 1981; Snyder, 1984). The greater flammability of pine species than intolerant and tolerant hardwood species is due to a higher concentration of oils, waxes, and resins in the needles (Van Wagner, 1977; Rundel, 1981), a lower fuel moisture loading (Kourtz, 1967; Rowe and Scotter, 1973), a difference in stand structure featuring more fuel at intermediate heights and a more aerated litter layer (Van Wagner, 1971; Barden and Woods, 1974), and fewer natural firebreaks in areas of dominance. Intolerant hardwoods are more flammable than the tolerant hardwoods because of their lower leaf moisture content (Van Wagner, 1967) and a greater proportion of volatile chemical compounds in their leaves (Philpot, 1969).

Examination of pre-suppression fire rotations for forest types similar to those sampled in this study (Table 5-3) show that fire rotations for pines (22-80 years) and intolerant hardwoods (70-240 years) are much lower than fire rotations for tolerant hardwood forests (1200 years). It is not clear from the data in Table 5-3, however, whether fire rotation differs for pine and intolerant hardwood forests. Because fire suppression increases the fire rotation, forest type comparison for pre-suppression and suppression periods must be made independently. The suppression period data in Table 5-3 show similar relationships between fire rotations for the pine, intolerant hardwood, and tolerant hardwood forest types compared to the pre-suppression period. The obvious difference between the pre-suppression and suppression data is the much greater rotation period for forest types affected by fire suppression.

These fire rotation data support the findings that fire incidence is higher for the pine and intolerant hardwood forests compared to the tolerant hardwoods. A forest type with a high fire incidence is likely to burn more often than a forest type with a low fire incidence. The forest type that burns more frequently than another is likely to require less time to be completely burned over. Thus a forest type with a high fire incidence will most probably also have a low fire rotation.

The index to fire incidence can be determined for any stand within

TABLE 5-3 - FIRE ROTATIONS FOR SOME GREAT LAKES-ST. LAWRENCE FOREST TYPES

PRE-SUPPRESSION

Forest Type	Fire Rotation (yrs)	Location	Reference
Jack, Red, White Pine	22	Minnesota	Frissell (1973)
Jack Pine	60-70	Minnesota	Swain (1973)
Jack Pine	80	Michigan	Whitney (1986)
White Pine-Poplar	70	Ontario	Cwynar (1977)
White Pine-Poplar	80	Ontario	Cwynar (1978)
Pine, Spruce, Poplar, Birch	100	Minnesota	Heinselman (1973)
Pine-Hardwoods	120-240	Michigan	Whitney (1986)
Northern Hardwoods	1200	Michigan	Whitney (1986)

SUPPRESSION

Forest Type	Fire Rotation (yrs)	Location	Reference
Pine	530	Maine	Fahey and Reiners (1981)
Pine	660	New Hampshire	Fahey and Reiners (1981)
Red Spruce-Hemlock-Pine	476	New Brunswick	Wein and Moore (1977)
Red Spruce-Hemlock-Pine	2000	Nova Scotia	Wein and Moore (1978)
Birch-Aspen	100	Maine	Fahey and Reiners (1981)
Birch-Aspen	510	New Hampshire	Fahey and Reiners (1981)
Sugar Maple-Yellow Birch-Fir	625	New Brunswick	Wein and Moore (1977)
Sugar Maple-Yellow Birch-Fir	3000	Nova Scotia	Wein and Moore (1978)
Northern Hardwoods	770	New Hampshire	Fahey and Reiners (1981)
Northern Hardwoods	910	Maine	Fahey and Reiners (1981)
Sugar Maple-Ash	>10,000	New Brunswick	Wein and Moore (1977)

the study area once the fire incidence probabilities and relative abundances are known for the overstory species within the stands of interest. This is done by simply calculating a weighted average of fire incidence probability for the stand using the fire incidence probability of each constituent species, basing the weight of the species probability on its relative abundance. For example, the index to fire incidence for a stand in Algonquin which is composed of 60% sugar maple, 30% yellow birch, and 10% hemlock would be $[(.60)(.068\times10^{-3})+(.30)(.172\times10^{-3})+(.10)(.106\times10^{-3})]$ which is equal to $.103\times10^{-3}$. This value can then be used in ecological analyses to represent naturally caused fire within that particular stand relative to other stands sampled in the study area for which the index is calculated.

CHAPTER 6 - OVERSTORY, ENVIRONMENT AND DISTURBANCE

INTRODUCTION

Modern forest ecological studies within the Great Lakes-St. Lawrence (GLSL) Forest Region have identified soil moisture as the primary determinant of forest composition over the landscape (Brown and Curtis, 1952; Fraser, 1954; Maycock and Curtis, 1960; Flaccus and Ohmann; 1964; Lopoukhine, 1974). These studies do not, however, incorporate natural disturbance as an important influence despite the obvious environmental changes and biological destruction which can result from it (Canham and Marks, 1985). Overlooking the role of disturbance in explaining community patterns often results in the misinterpretation of ecological data (Sousa, 1984; Pickett and White, 1985). For example, by incorporating the influence of fire and exotic species, Harmon et al. (1983) have revised Whittaker's (1956) original forest vegetation model of the Great Smoky Mountains.

Studies focussing on fire within the GLSL Forest Region have presented substantial evidence to show that fire plays an important role in developing and maintaining pine forests (Maissurow, 1935; Cary, 1936; Maissurow, 1941; Spurr, 1954; Heinselman, 1973; Swain, 1973; Cwynar, 1977; Cwynar, 1978) and aspen forests (Heinselman, 1973; Swain, 1973).

The prominent role of both soil moisture and fire as influences upon the composition of GLSL forests was addressed by Hills (1959) and

Anderson (1969) through their work in the Algonquin Park region of Ontario. Later a fire incidence gradient across the width of the park was identified by Terasmae and Weeks (1979).

Algonquin Park is located within Nichol's (1935) and Braun's (1950) Hemlock-White Pine Northern Hardwood Region of eastern North America. It can be further classified into the Great Lakes-St. Lawrence Division (Braun, 1950) or Forest Region (Rowe, 1972). The region is characterized by eastern white pine and red pine, hemlock and yellow birch. Associated with these species are more typically northern species such as jack pine, white spruce, aspen and white birch as well as some which are more characteristic of southern forests such as sugar maple, red oak, beech, and basswood. All of these are common species throughout the Algonquin landscape.

An hypothesis to explore the influences of soil moisture and fire along with other selected environmental variables upon forest composition within the GLSL Forest Region has not yet been examined. The purpose of this study is to examine this hypothesis using multivariate techniques that allow for the ranking of independent (environmental) variables with regard to the amount of variance they explain within a set of dependent variables (vegetation axes). These techniques are applied to the geographical distribution of plants rather than to the dynamics of plants over time. Although there are many factors that may affect vegetation composition some play a greater mediating role than others (Greig-Smith, 1979; Noy-Meir and van der Maarel, 1987). It was with this in mind that environmental variables