were selected.

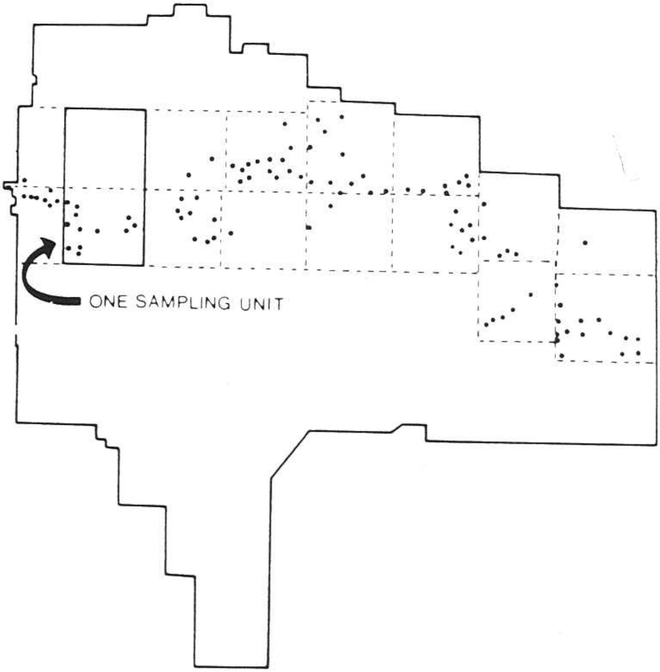
METHODS

FIELD

The typical upland vegetation of the park was sampled for overstory vegetation and environmental variables in 100 forest stands within a transect which was two townships wide extending across the approximate 72 km width of the park (Figure 6-2). Nine tree species were identified as typical upland forest dominants from a survey of Forest Resource Inventory (FRI) Maps (Ontario Ministry of Natural Resources, 1978). This survey consisted of a 15% systematic sample of the forest stands designated on the FRI map for each of the 16 townships included in the transect. The relative abundance of each upland forest dominant within a township was determined by summing the number of stands dominated by the species and converting that into a relative value (see Appendix II for results of the survey). This value was then used as a guide for stand selection within each sampling unit. For example, approximately 45% of the Fitzgerald-White sampling unit is dominated by poplar. Therefore, 45% of the stands sampled in these two townships were poplar or six out of 13 stands.

Selection of stands in the field was based on the following criteria: stands were (1) dominated by one of nine typical upland tree species, (2) restricted to upland sites on which surface runoff waters

FIGURE 6-1 - SAMPLING UNITS AND STAND LOCATIONS WITHIN ALGONQUIN PARK



never accumulate, (3) at least 6 ha in size, and (4) not recently disturbed by natural or human agency. Mature stands were selected in order to avoid as much as possible the sampling of early successional stands. To the extent possible, stands representing the variety of surficial geological deposits associated with each stand type were included in the sample set through the use of surficial geological maps (Ontario Ministry of Natural Resources, 1983). The location, cover type, substrate type, and size of each stand is provided in Appendix III.

The overstory was defined as all trees 2cm dbh and greater. During the 1983 and 1984 field seasons, the overstory was sampled by recording tree diameter at breast height (dbh) within three randomly placed 10m X 30m quadrats per stand. Once a stand was selected based on the four criteria, the quadrats were selected by subjectively identifying a representative portion of the stand, locating the center of that portion, and randomly selecting a compass bearing that served as the first side of a quadrat. Dbh measurements were converted to basal area values per ha for each species within each stand for analysis. Appendix IV provides the summarized basal area for overstory species within each stand. Nomenclature follows Fernald (1950).

Soil profile descriptions and homogenized soil samples from the 0 to 10cm portion of the mineral soil for lab analysis were obtained from each of the three excavated soil pits (1m depth) within each stand (see Appendix V). For the soil profiles, the following was measured: thickness of the LFH, Ae, Ah, A, and B horizons and the depth to the C horizon and depth to mottling. Latitude, longitude, and elevation for each stand were determined from topographic maps (see Appendix VI). Evidence of disturbance was noted at each site.

LABORATORY

Fire

The index to fire incidence was used to quantify fire. The index was obtained by calculating a weighted average of fire incidence probability for the stand using the fire incidence probability of each constituent species (see Table 5-1). The weighting of the species probability was based 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 $.103\times10^{-3}$/40ha/50yrs. The index to fire incidence was then used as one of the 24 independent variables in the canonical correlation analysis (see Appendix VI for the index to fire incidence values for each stand). The derivation of the index is described in greater detail in Chapter 5.

Since the derivation of the fire index showed that fires historically have occurred in all upland dominance-types in Algonquin Park, it was assumed that all upland stands in Algonquin have been affected to some extent by fire. This assumption is supported by

Soils

Three soil samples from each plot within a stand were combined into a composite stand soil sample. From these samples, the following Zparameters were analyzed for: % sand, % silt, % clay, % organic matter, total nitrogen, calcium, magnesium, potassium, phosphorus, and pH (see Appendices IX and X). Analysis of the latter five parameters was provided by Agri-Food Laboratories, Guelph, Ontario. Soil particle size distribution was determined using the hydrometer method (Day, 1965), percent organic matter was determined using the loss on ignition method (Ball, 1964), and the Kjeldahl method (Bremner, 1965) was used to analyze for total nitrogen. The soil moisture stress index was calculated by rescaling precipitation and the sum of %silt and %clay (inverse of %sand) from 0 to 100. The rescaled values for precipitation and soil texture were then summed, divided by two and subtracted from 100.

NUMERICAL

Detrended correspondence analysis (DCA) (Hill and Gauch, 1980) was used to ordinate overstory vegetation samples based on the basal area of each species within each stand using the computer program DECORANA (Hill, 1979) (see Appendix XI for stand scores on axes 1 and 2). In order to examine relationships between overstory vegetation composition and environmental variables, canonical correlation analysis (CCA)

TABLE 6-1 - OVERSTORY SPECIES LIST

Abies balsamea (L.) Mill. (balsam fir)
Acer pennsylvanicum L. (striped maple)
Acer rubrum L. (red maple)
Acer saccharum Marsh. (sugar maple)
Acer spicatum Lam. (mountain maple)
Alnus rugosa (Du Roi) Spreng. (speckled alder)
Betula lutea Michx. f. (yellow birch)
Betula papyrifera Marsh. (white birch)
Fagus grandifolia Ehrh. (American beech)
Fraxinus nigra Marsh. (black ash)
Ostrya virginiana (Mill.) K. Koch (hop hornbeam)
Picea glauca (Moench) Voss (white spruce)
Picea mariana (Mill.) B.S.P. (black spruce)
Pinus banksiana Lamb. (jack pine)
Pinus resinosa Ait. (red pine)
Pinus strobus L. (white pine)
Populus grandidentata Michx. (large-toothed aspen)
Populus tremuloides Michx. (trembling aspen)
Prunus serotina Ehrh. (black cherry)
Quercus rubra L. (red oak)
Thuja occidentalis L. (white cedar)
Tilia americana L. (basswood)
Tsuga canadensis (L.) Carr. (eastern hemlock)

Sugar maple type

In this dominance-type sugar maple constituted 71.5% of the overstory basal area, common associates included yellow birch (11.4%), hemlock (4.2%), and American beech (3.7%). Fifteen rare associates were found within this community and contributed 9.2% of the overstory basal area.

Intolerant Hardwood Forest

White birch type

For this dominance-type white birch constituted 43.4% of the overstory basal area, common associates included balsam fir (32.2%), sugar maple (9.0%), jack pine (4.7%), and red maple (3.3%), and nine rare associates occupied 7.5% of the overstory basal area.

Red oak type

Within this dominance-type red oak constituted 64% of the overstory basal area. The common associates included white pine (19.3%), large-toothed aspen (4.9%), and red maple (3.6%). Ten rare associates constituted 8.2% of the overstory basal area.

Poplar type

For this dominance-type poplar constituted 61.3% of the overstory basal area. This dominance-type also had the greatest number of common associates which was seven. They included white pine (10.2%), trembling aspen (6.5%), red pine (5.2%), sugar maple (3.8%), red maple (3.8%), white birch (3.2%), and white spruce (2.7%). The 13 rare associates occupied 3.1% of the overstory basal area.

Pine Forest

White pine type

In this dominance-type white pine constituted 61.5% of the overstory basal area. Six common associates included large-toothed aspen (7.3%), red pine (5.1%), trembling aspen (4.5%), white spruce (3.4%), red oak (2.7%), and white birch (2.7%). The 13 rare associates constituted only 6.4% of the overstory basal area.

Red pine type

For this dominance-type red pine constituted 63.8% of the overstory basal area. Common associates included white pine (16.5%), large-toothed aspen (8.0%), trembling aspen (4.6%), and jack pine (3.5%). The six rare associates made up only 2.7% of the overstory basal area.

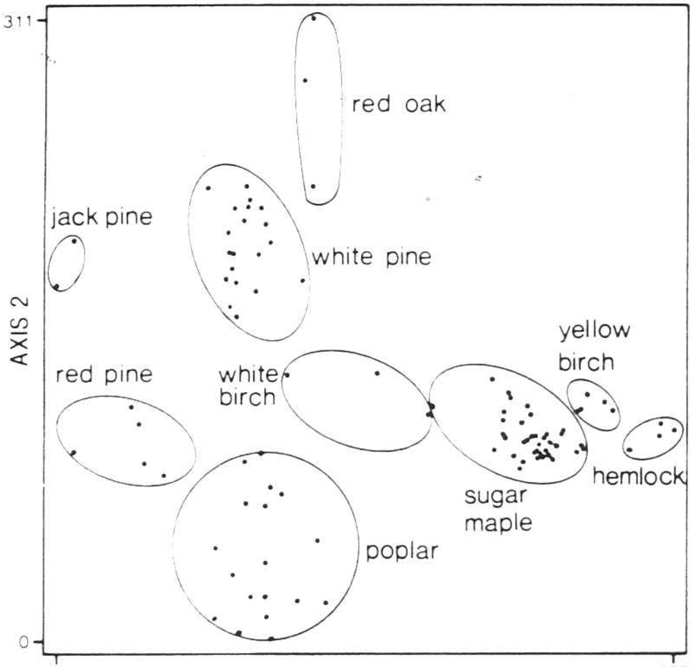
Jack pine type

For this dominance-type jack pine contributed 70.5% of the overstory basal area. The three common associates included trembling aspen (14.5%), red pine (9.0%), and white pine (4.6%). The two rare associates constituted only 1.4% of the overstory basal area.

STAND ORDINATION

Eigenvalues resulting from DCA for axes 1 through 4 were .870, .459, .211, and .173. Figure 6-2 shows each stand plotted with respect to their scores on DCA axis 1 and 2 and the dominance-type designations. Since the first DCA axis explains the greatest amount of variation in the species composition data, approximately 87%, the spatial arrangement of stands along the first axis is of greatest importance. It can be seen that along this axis, the pine dominance-types occupy the low end of the gradient, the tolerant hardwood dominance-types occupy the high end of the gradient and the intolerant hardwood dominance-types occupy an intermediate position. The greater the distance between two stands the more dissimilar is their species composition.

FIGURE 6-2 - SCATTERGRAM OF STANDS PLOTTED WITH RESPECT TO OVERSTORY DCA AXES 1 AND 2



INDIRECT GRADIENT ANALYSIS

Stand means and ranges for the selected environmental variables were summarized by dominance-type and are presented in Table 6-4. Dominance-types are arranged according to average stand position on the first DCA axis. Stand values used to obtain this summary of environmental variables were utilized in CCA along with stand scores from DCA which were used to represent overstory composition. The results of CCA facilitated the identification of important composition-environment relationships. Table 6-5 provides interset correlations between the first four DCA axes and the first four canonical variates.

Using Miller's (1975) F-ratio approximation it was possible to identify significant interset correlations. Results of this test indicated that the only significant interset correlation existed between DCA axis 1 and canonical variate 1 (.9069; $p < .001$). It is the relationship between these two linear models, therefore, that provides the greatest explanation for the joint variance within the biological and environmental data sets.

Each individual environmental variable was then assessed with regard to its contribution to the structure of the first canonical variate. This was done by examining factor loadings which are simply correlations of the individual factor values with the values obtained from projecting the real factor values onto the canonical variate. The greater the absolute value of the loading, the greater its contribution

TABLE 6-4 - STAND MEANS AND RANGES FOR ENVIRONMENTAL DATA BY DOMINANCE-TYPE

ENVIRONMENT	DOMINANCE TYPE								
	yellow birch	sugar maple	hemlock	white birch	poplar	white pine	red oak	red pine	jack pine
Soils									
sand (%)	55.0 43.5-64.1	53.1 39.3-77.7	51.3 31.7-63.4	59.4 50.0-71.7	61.3 38.0-78.4	61.8 47.0-65.8	50.6 40.8-58.5	77.7 70.8-84.0	85.5 84.5-86.5
silt (%)	38.5 29.3-49.9	41.4 18.6-55.6	40.1 28.6-53.9	35.5 23.6-45.0	32.0 17.8-50.9	31.9 10.3-45.8	41.7 38.7-49.0	16.9 11.0-24.2	9.9 9.4-10.4
clay (%)	6.5 4.4-8.0	5.5 3.5-8.8	8.9 3.8-14.4	5.1 4.7-5.7	6.7 2.6-12.1	6.3 2.6-8.8	7.7 6.0-10.2	5.4 5.0-5.7	4.8 4.1-5.1
organic (%)	7.9 6.5-11.7	6.5 2.0-22.0	7.1 1.9-12.8	6.2 1.2-9.2	4.7 3.2-7.3	5.1 2.5-10.4	7.2 5.2-9.5	3.3 3.0-4.0	2.8 2.3-3.3
total N (%)	.24 .15-.40	.27 .11-.67	.16 .13-.20	.15 .06-.24	.11 .06-.27	.11 .03-.23	.12 .09-.17	.07 .06-.08	.06 .05-.06
P (ppm)	10 4-22	14 5-53	8 6-12	25 17-40	28 7-61	23 7-62	11 4-16	13 6-22	16 9-24
K (ppm)	35 25-44	45 32-72	33 24-45	55 44-61	49 27-80	47 22-75	40 35-48	31 28-40	18 16-20
Ca (ppm)	256 81-680	272 62-1200	173 57-347	545 226-1130	259 64-650	247 63-550	132 122-150	175 86-300	175 150-200
Mg (ppm)	47 25-82	40 20-72	29 24-38	47 33-62	38 15-72	43 20-105	26 17-39	28 20-37	[illegible]
pH	4.8 4.4-5.3	4.8 4.0-5.4	4.6 4.2-4.9	5.2 4.9-5.7	5.0 4.1-5.4	4.8 4.4-5.2	4.7 4.4-5.1	4.8 4.5-5.4	4.8 4.6-4.9
C/N ratio	34.7 29.3-43.3	33.6 10.0-58.4	41.9 14.6-60.0	42.2 35.0-53.0	46.7 14.4-63.3	47.3 34.4-63.3	59.1 55.9-63.6	46.3 37.5-57.1	50.5 46.0-56.0
LFH (cm)	5.17 3.81-6.35	4.84 1.96-7.20	6.63 5.70-9.36	4.51 2.96-5.50	4.24 2.94-6.72	4.69 2.22-6.35	4.62 3.49-5.72	4.74 3.81-5.72	5.29 5.29
Ah (cm)	2.34 .85-3.81	2.49 .85-5.50	1.65 1.48-2.54	2.75 1.91-3.60	1.71 .64-3.81	1.88 .64-2.98	1.43 .85-2.17	1.99 1.36-3.18	1.59 1.36-2.12
Ae (cm)	5.44 4.45-7.20	5.18 1.91-9.74	7.78 5.51-9.94	3.64 3.17-4.23	4.53 1.27-7.94	4.44 1.91-7.62	3.85 2.81-5.32	3.64 2.86-6.19	2.23 1.91-2.58
A (cm)	7.48 5.93-9.42	7.81 3.81-13.34	9.63 6.98-11.86	6.60 6.04-6.98	6.17 3.71-9.94	6.30 3.91-9.95	5.48 3.65-7.48	5.63 4.45-7.25	3.81 3.60-4.02
B (cm)	43.75 37.90-49.96	44.59 33.34-64.35	38.74 34.93-43.82	32.99 23.64-37.88	43.55 32.71-58.45	42.66 30.51-63.71	40.23 33.13-50.49	46.88 34.29-68.26	51.56 36.63-68.47
Depth to C (cm)	51.90 48.14-58.42	53.12 44.87-72.39	48.90 44.03-53.34	43.74 40.64-45.72	50.86 41.49-68.27	51.19 42.33-73.66	44.81 39.37-50.30	52.07 40.64-73.24	57.08 43.87-70.28
Depth to R (cm)	51.90 48.14-58.42	53.46 43.18-73.29	48.90 45.72-50.80	45.30 40.64-49.53	52.59 43.18-63.50	52.67 45.09-76.20	52.21 48.68-57.15	54.77 40.64-74.02	58.77 43.87-73.66
Climate									
temperature (degrees C)	18.64 18.5-18.8	18.66 18.5-19.1	18.68 18.6-18.8	18.77 18.6-18.9	18.82 18.7-19.0	18.95 18.6-19.3	19.00 18.9-19.1	19.04 18.8-19.3	19.10 18.9-19.3
precipitation (mm)	870 843-907	861 725-907	849 841-858	835 827-848	813 738-863	798 735-859	765 738-813	784 734-828	782 742-821
light (%)	14.7 10.0-20.0	13.8 5.0-21.7	10.0 5.0-13.3	17.2 13.3-18.3	20.8 6.7-31.7	26.2 18.7-38.3	19.4 13.3-23.3	28.2 24.3-38.3	42.2 41.0-43.3
Disturbance									
fire index x10	.147 .142-.149	.090 .072-.116	.107 .102-.111	.209 .180-.228	.131 .116-.159	.153 .128-.170	.140 .135-.143	.201 .178-.225	.213 .207-.219
Physiography									
elevation (m)	408 320-457	425 259-493	393 320-427	366 320-396	312 213-427	289 198-213	302 264-336	233 183-290	214 168-259
latitude	45.50 45.41-46.00	45.51 45.43-46.04	45.54 45.49-46.01	45.57 45.50-46.03	45.57 45.50-46.01	45.57 45.52-46.03	45.54 45.52-45.57	45.57 45.54-46.00	45.58 45.55-46.00
longitude	78.44 78.30-78.59	78.40 77.60-79.03	78.35 78.20-78.40	78.24 78.08-78.36	78.12 77.47-78.43	78.01 77.47-78.41	77.50 77.46-77.57	77.56 77.45-78.16	77.50 77.45-78.08

TABLE 6-5 - INTERSET CORRELATIONS BETWEEN OVERSTORY DCA AXES AND CANONICAL VARIATES

	V1	V2	V3	V4
AX1	.9069*	.0136	.0314	.0017
AX2	-.2601	.1029	.5232	.2390
AX3	.2188	.0284	-.4713	.3116
AX4	.3497	-.5868	.1109	.1111

* P<.001 using Miller's (1975) F-ratio approximation; the remainder are not statistically significant

TABLE 6-6 - ENVIRONMENTAL FACTOR LOADINGS ON THE FIRST CANONICAL VARIATE FOR THE OVERSTORY PREDICTOR SET

Environmental Factor	Loading
elevation	.8397
fire	-.8351
longitude	.7470
temperature	-.7373
total nitrogen	.6948
precipitation	.6880
organic matter	.5904
sand	-.5803
latitude	-.5338
A horizon	.5330
carbon-nitrogen ratio	-.5102
Ae horizon	.4116
pH	-.4080

composition indirectly through affecting other more dynamic and physiologically influential environmental variables (Bormann et al., 1970; Siccama, 1974; Rheinhardt and Ware, 1984). Normally it is temperature which is most affected by elevation (Zobel, et al., 1976; Yarie, 1983). Other variables such as longitude and latitude also lack direct ecological meaning in that they are a means of measuring for geographic location. Due to the difficulty of dealing with a complex multitude of both direct and indirect environmental variables, it has been pointed out that it is most useful to focus on the primary ecological features of moisture supply, nutrient supply, and local climate (Hills, 1952; Loucks, 1962). Those factors most closely related to these primary ecological features were called "effective factors" by Waring and Major (1964). The significant effective factors identified in the current study included fire, climate measured by temperature and precipitation, and soil factors including total nitrogen, organic matter, % sand, and pH. Table 6-7 shows mean values of the significant effective factors for each of the three forest types.

Fire

Fire, measured by the index to fire incidence, attained its maximum mean value in the jack pine dominance-type ($.213 \times 10^{-3}$) and its minimum mean value in the sugar maple dominance-type ($.090 \times 10^{-3}$). Figure 6-3 shows the relative values of fire overlayed on a scatterplot of the first two axes of the DCA stand scores. Considering mean values

TABLE 6-7 - MEAN STAND VALUES FOR OVERSTORY EFFECTIVE FACTORS BY FOREST TYPE

EFFECTIVE FACTOR	FOREST TYPES Tolerant Hardwoods	 Intolerant Hardwoods	 Pines
Fire	$.097 \times 10^{-3}$	$.141 \times 10^{-3}$	$.167 \times 10^{-3}$
Temperature (C)	18.66	18.84	18.98
Total Nitrogen (%)	.26	.12	.10
Precipitation (mm)	861	798	787
Organic Matter (%)	8.3	5.2	4.6
Sand (%)	53.1	59.8	66.7
pH	4.6	5.0	4.8
No. of Stands	49	25	26

FIGURE 6-3 - SCATTERGRAMS OF THE RELATIVE MAGNITUDES OF IMPORTANT ENVIRONMENTAL FACTORS ON THE OVERSTORY STAND ORDINATION BY DCA (circle size is proportional to the magnitude of the variable)

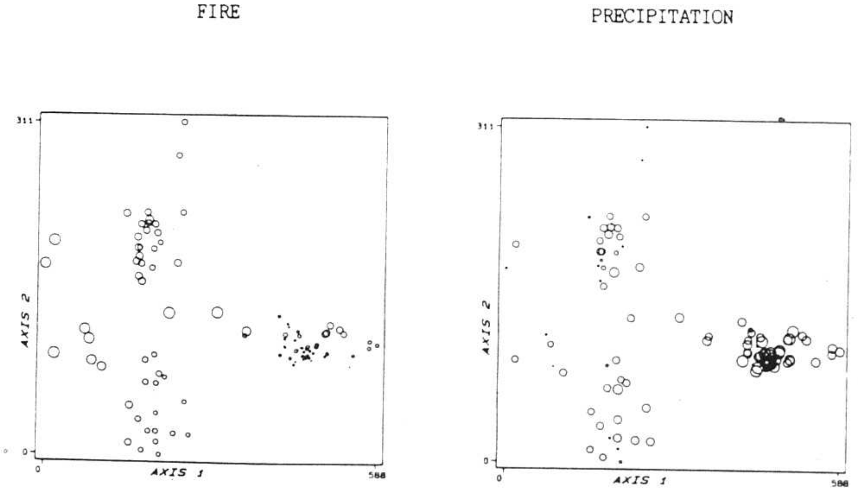
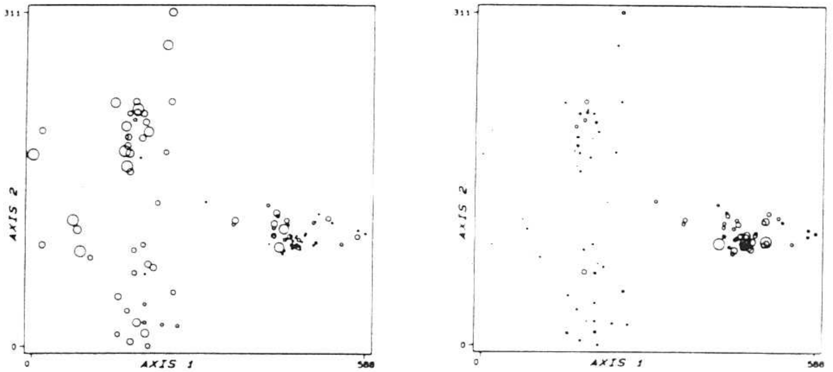
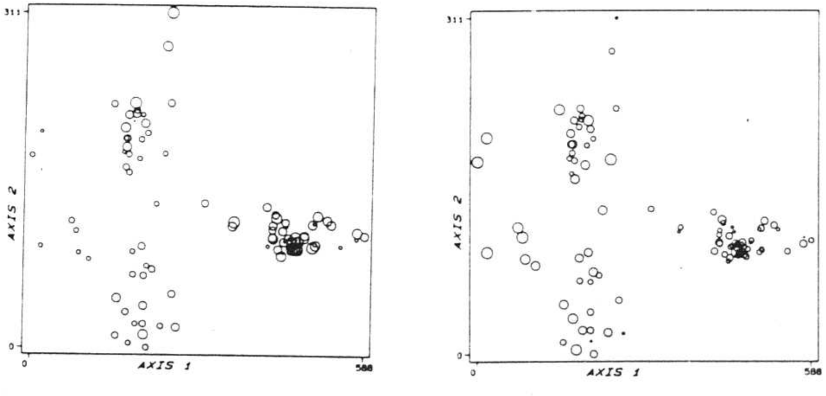


FIGURE 6-3 (CON'T)



TEMPERATURE

TOTAL NITROGEN



ORGANIC MATTER

SAND

for the three general forest types, the pines have the highest mean index to fire incidence (.167 X 10^{-3}), the tolerant hardwoods have the lowest (.097 X 10^{-3}), and intolerant hardwoods are intermediate (.141 X 10^{-3}). Almost one-half of the white and jack pine plots had charcoal in the upper part of the soil profile. Charcoal was found in approximately one-third of the poplar, white birch and red oak plots and in only a very few plots within the tolerant hardwood forest.

Climate

Among the nine dominance types, mean stand temperature (mean daily for July) ranged from 18.64 degrees C for the yellow birch dominance-type to 19.10 degrees C for the jack pine dominance-type. On average, mean stand temperature for the tolerant hardwoods (18.66 degrees C) was lower than that for the intolerant hardwoods (18.84 degrees C) which was lower than that for the pine forest type (18.98 degrees C). Figure 6-3 shows temperature for all stands plotted against DCA axes 1 and 2.

Mean stand precipitation ranged from a low of 765mm for the red oak dominance-type to a high of 870mm for the yellow birch dominance-type. The pine forest type averaged 787mm, the intolerant hardwood forest type averaged 798mm, and the tolerant hardwood forest type averaged 861mm (see Table 6-7).

Soils

The effective soil factors of the predictor set, from highest to lowest ranking on the first canonical variate, included total nitrogen, organic matter, sand, (see Figure 6-3) and pH. Of these four factors, total nitrogen is most highly correlated with upland forest overstory composition in Algonquin Park. Stand means varied from a low of .06% for the jack pine dominance-type to a high of .27% for the sugar maple dominance-type. The stand mean for the tolerant hardwood forest type (.26%) was over twice that for the intolerant hardwood forest type (.12%) and pine forest type (.10%).

Organic matter content of the mineral soil varied from 2.8% in the jack pine dominance-type to 8.5% in the sugar maple dominance-type. The amount of organic matter in the tolerant hardwood forest type (8.3%) was close to double the amount in the pine forest type (4.6%). The intolerant hardwoods had slightly more organic matter (5.2%) than the pines.

The percentage of sand in the top 10cm of the mineral soil varied substantially from 50.5% in the red oak dominance-type to 85.5% in the jack pine dominance-type. On average, the pine forest type had a greater percentage of sand (66.7) than the intolerant hardwoods (59.8) and the tolerant hardwoods (53.1).

The pH of the mineral soil was highest in the white birch dominance-type (5.2) and lowest in the tolerant hardwood dominance-types (all at 4.6). It showed little variation between forest types and

TABLE 6-8 - OVERSTORY PREDICTOR SET CORRELATION MATRIX

	EV	FR	LG	TP	TN	PP	OM	SD	LT	A	CN	A2	PH
EV	1 0000												
FR	- 6538	1 0000											
LG	- 8651	5414	1 0000										
TP	- 8730	5583	8954	1 0000									
TN	6288	- 5515	- 6082	- 6065	1 0000								
PP	8144	- 4805	- 9335	- 8905	6065	1 0000							
OM	5913	4847	- 5335	- 5264	8278	5091	1 0000						
SD	- 4917	5092	3467	3289	- 3460	- 2543*	- 4096	1 0000					
LT	- 5571	3985	4986	5059	- 5326	- 3973	- 5255	3052	1 0000				
A	2807	- 3299	- 3190	- 2826	2810	2661	NS	- 2163*	- 2431*	1 0000			
CN	3962	3538	4420	4316	- 5273	- 4736	NS	NS	NS	2518*	1 0000		
AE	NS	- 2739	NS	NS	NS	NS	NS	NS	NS	8595	NS	1 0000	
PH	3954	3438	4611	3604	- 4309	- 4695	3909	NS	- 4110	- 2851	NS	NS	1 0000

EV-elevation, FR-fire, LG-longitude, TP-temperature, TN-total nitrogen, PP-precipitation, OM organic matter
SD-sand, LT-latitude, A-A horizon thickness, CN-carbon-nitrogen ratio, AE Ae horizon thickness, PH pH

* p< 05, NS-not significant, all others p< 01

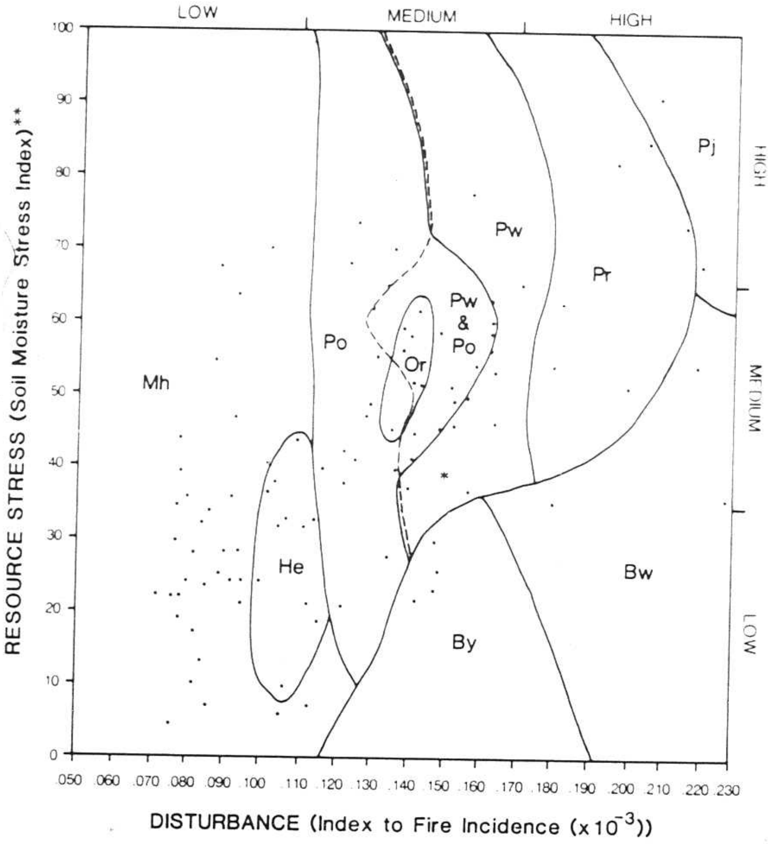
continuous gradients should produce unique vegetation types within any given landscape. Figure 6-4 provides a fit of this model to the fire and soil moisture stress data for the nine upland forest dominance-types in Algonquin Park.

The figure shows that jack pine and red pine occupy the "high to medium stress-high disturbance" portion of the matrix. At the opposite extreme, sugar maple and hemlock occupy the "low to medium stress-low disturbance" portion of the matrix. The other dominance-types occupy intermediate portions of the matrix. The greatest amount of dominance-type overlap occurs at the combination of medium disturbance and medium soil moisture stress. Red oak, white pine, and poplar all overlap in this area.

The forest types occupy the following portions of the matrix: tolerant hardwoods in the "low to medium stress-low to medium disturbance" area; intolerant hardwoods in the "low to medium stress-medium to high disturbance" area; and the pines in the "medium to high stress-medium to high disturbance" area.

The higher correlation between fire and forest composition versus soil moisture and forest composition can be observed in the figure. This is shown by the greatest amount of variation among samples in all dominance-types being along the direction of the resource stress axis.

FIGURE 6-4 - FOREST OVERSTORY COMPOSITION MATRIX WITH RESPECT TO RESOURCE STRESS AND DISTURBANCE



KEY: Bw-white birch, By-yellow birch, He-hemlock, Mh-sugar maple, Or-red oak, Pj-jack pine, Po-poplar, Pr-red pine, Pw-white pine

* yellow birch stand outside of the yellow birch matrix space

DISCUSSION

INFLUENCE OF FIRE

Results of the canonical correlation indicate that elevation is most highly correlated with variation in overstory composition. This relationship, however, has been manifested indirectly as variations in available moisture through the combination of precipitation and soil texture. Because fire ranked higher on the first environmental variate.. than these latter two variables, however, it is possible that naturally-caused fire may play a greater ecological role than soil moisture in affecting overstory forest composition within a large portion of Algonquin Park. As well as being highly correlated with overstory composition, fire is the only factor that is correlated with all other significant environmental variables. For the GLSL forests of Michigan, Whitney (1986) also found that "most of the forests can be placed along a fire frequency continuum". It should be noted, however, that all variables other than fire are derived independently of vegetation, whereas the fire incidence index is derived from mapped vegetation data.

Fire is particularly important in perpetuating the pine communities within Algonquin Park (Cwynar, 1977; 1978). Its ecological importance in eastern North America has been well documented for jack pine (Heinselman, 1973; Ahlgren, 1974; Cayford and McRae, 1983), red pine (Van Wagner, 1971; Burgess and Methven, 1977), and white pine

DISCUSSION

INFLUENCE OF FIRE

Results of the canonical correlation indicate that elevation is most highly correlated with variation in overstory composition. This relationship, however, has been manifested indirectly as variations in available moisture through the combination of precipitation and soil texture. Because fire ranked higher on the first environmental variate.. than these latter two variables, however, it is possible that naturally-caused fire may play a greater ecological role than soil moisture in affecting overstory forest composition within a large portion of Algonquin Park. As well as being highly correlated with overstory composition, fire is the only factor that is correlated with all other significant environmental variables. For the GLSL forests of Michigan, Whitney (1986) also found that "most of the forests can be placed along a fire frequency continuum". It should be noted, however, that all variables other than fire are derived independently of vegetation, whereas the fire incidence index is derived from mapped vegetation data.

Fire is particularly important in perpetuating the pine communities within Algonquin Park (Cwynar, 1977; 1978). Its ecological importance in eastern North America has been well documented for jack pine (Heinselman, 1973; Ahlgren, 1974; Cayford and McRae, 1983), red pine (Van Wagner, 1971; Burgess and Methven, 1977), and white pine communities (Maissurow, 1935; Maissurow, 1941; Frissell, 1973; Fahey and Reiners, 1981).

The intolerant hardwoods such as trembling and large-tooth aspen are less fire prone than conifers such as jack pine (Carleton and Maycock, 1978). However, Heeney et al. (1975) state that most of the present poplar stands in Ontario originated as a result of fire. This is probably because of the pioneer nature of poplar rather than its flammability.

Although fire also occurs in the tolerant hardwood forest, it is generally agreed that fire in this forest type has had a relatively minor ecological influence upon overall forest vegetation composition (Bormann and Likens, 1979a; Fahey and Reiners, 1981). Rather than fire, the creation of canopy gaps by windthrow and tree senescence are the major forms of disturbance within eastern North American tolerant hardwood forest types (Bormann and Likens, 1979b; Hibbs, 1982; Runkle, 1982).

The relationship between fire and overstory composition in Algonquin can be explained in terms of foliage flammability, tree and stand structure, reproductive strategies, anatomical features (Mutch, 1970; Kimmins, 1987), and natural firebreaks (Heinselman, 1973).

The greater flammability of pine needles than deciduous leaves results from a higher concentration of oils, waxes, and resins in the needles (Van Wagner, 1977) and from the lower needle moisture content (Van Wagner, 1967). The dead pine biomass on the forest floor is also very flammable (Van Wagner, 1972; Williamson and Black, 1981) because of communities (Maissurow, 1935; Maissurow, 1941; Frissell, 1973; Fahey and Reiners, 1981).

The intolerant hardwoods such as trembling and large-tooth aspen are less fire prone than conifers such as jack pine (Carleton and Maycock, 1978). However, Heeney et al. (1975) state that most of the present poplar stands in Ontario originated as a result of fire. This is probably because of the pioneer nature of poplar rather than its flammability.

Although fire also occurs in the tolerant hardwood forest, it is generally agreed that fire in this forest type has had a relatively minor ecological influence upon overall forest vegetation composition (Bormann and Likens, 1979a; Fahey and Reiners, 1981). Rather than fire, the creation of canopy gaps by windthrow and tree senescence are the major forms of disturbance within eastern North American tolerant hardwood forest types (Bormann and Likens, 1979b; Hibbs, 1982; Runkle, 1982).

The relationship between fire and overstory composition in Algonquin can be explained in terms of foliage flammability, tree and stand structure, reproductive strategies, anatomical features (Mutch, 1970; Kimmins, 1987), and natural firebreaks (Heinselman, 1973).

The greater flammability of pine needles than deciduous leaves results from a higher concentration of oils, waxes, and resins in the needles (Van Wagner, 1977) and from the lower needle moisture content (Van Wagner, 1967). The dead pine biomass on the forest floor is also very flammable (Van Wagner, 1972; Williamson and Black, 1981) because of the more open canopy structure of pine stands which allows for greater desiccation of the litter (Barden and Woods, 1974) and because of the dryer soil conditions (Kourtz, 1967; Vogl, 1970; Rowe and Scotter, 1973) associated with these stands. The low frequency of fire within Algonquin's tolerant hardwood forest is due mainly to the high moisture content of sugar maple foliage (Van Wagner, 1967). Because their moisture content is lower than that of sugar maple, poplar leaves tend to be more flammable than sugar maple but less than the drier foliage of the pines (Van Wagner, 1967). Poplar foliage flammability is also related to its high chemical extract content (Philpot, 1969).

Due to a well aerated needle litter which keeps it dry and a crown structure reaching close to the ground which acts as a fuel ladder, pine stands are more susceptible to crown fire than the tolerant and intolerant hardwoods (Van Wagner, 1971; Barden and Woods, 1974). Despite their high aromatic content, poplar stands do not normally support crown fires because of relatively low amounts of combustible fuel in and the high moisture content of the duff layer (Horton and Hopkins, 1965). These stands do, however, become extremely flammable when the stand turns decadent (Vogl, 1969). This is often due to the increased presence of balsam fir and other conifers as poplar stands age. It is the bark rather than the foliage of the white birch that is most flammable (Fowells, 1965).

Life history strategies affect the response of plant species to fire. The serotinous character of jack pine cones is the result of a reproductive strategy that renders jack pine dependent upon crown fires for seed release (Cameron, 1953; Beaufait, 1960). The reproductive strategies of red and white pine relate more to establishment and early growth than the release of their seeds which normally die in crown fire (Van Wagner, 1971; Rowe and Scotter, 1973; Burgess and Methven, 1977). They reproduce best when surface fires leave a mineral seedbed or thin litter layer, eliminate understory competition (Methven, 1973), and do not scorch the crowns (Van Wagner, 1971; Ahlgren, 1976). Jack pine is not impeded as much by understory competition (Methven, 1973). In the absence of fire, white pine regeneration has been found to be more successful than that for red and jack pine (Van Wagner, 1963).

One reproductive strategy of the intolerant hardwoods is that of sprouting and root suckering. Many workers have observed the sprouting and rapid growth of oaks (Brown, 1960; Heinselman, 1973; Forman and Boerner, 1981) and white birch (Heinselman, 1973) following fire. Root suckering of trembling and largetooth aspen, which is their primary mode of regeneration (Farmer, 1962), has been linked to an increase in soil temperature which can be caused by fire (Maini and Horton, 1966; Bartos and Mueggler, 1981). The ability to sprout, however, does not enable red oak to outcompete the pines (Cline and Spurr, 1942; Williamson and Black, 1981) mainly because of its thinner bark which makes it less resistant to fire than the pines. Following fire the oaks become highly susceptible to decay (Fowells, 1965). White birch is quite susceptible to intense fire due to its thin bark (Fowells, 1965). Severe fire can also eliminate aspen (Horton and Hopkins, 1965) which is better adapted to fires of low intensity (Lutz, 1956). In addition, white birch and the poplars are light seeded fast growing species which gives them a reproductive advantage on local open sites.

The thick bark of the pines enables them to resist fires that do not affect the living crown (Hare, 1965; Van Wagner, 1971). The bark of red pine is thought to be thicker and more resistant to fire than that of white pine (Van Wagner, 1971). White pine is also more susceptible than red pine to root injury by fire (McConkey and Gedney, 1951) which can facilitate root rot (Frissell, 1973). When roots are not injured by fire, large white pine can tolerate light to moderate surface fires about every 20 to 30 years (Wright and Bailey, 1982). When fire occurs in the tolerant hardwoods, the shallow roots of the hemlock can be damaged leading to mortality (Hough and Forbes, 1943; Cline and Spurr, 1942). This may account for its predominance on fire protected sites (Milne, 1985). The thin bark of young sugar maple and mature yellow birch renders them highly susceptible to fire (Fowells, 1965).

It is likely that fire on the pine-dominated east side has also been facilitated by fewer natural firebreaks because of the subdued relief, fewer lakes and streams, and fewer moist slopes. Conversely, the rugged topography, many lakes and streams, and moist slopes which are characteristic of Algonquin's west side have probably reduced the spread and influence of fire.

From the results of this study it is not possible to determine whether the variation in vegetation composition is controlled by fire or whether the variation in fire is controlled by vegetation. It is likely that each affects the other depending on species and environmental conditions.

INFLUENCE OF CLIMATE AND SOIL

In addition to fire, the results indicate that soil moisture is highly correlated with overstory composition of upland forests in Algonquin. For this study, soil moisture was assessed through the synthetic combination of both precipitation and and soil texture.

The majority of precipitation received in Algonquin Park comes from air masses that follow the Alberta cyclone track (Hills, 1959). As these dry western air masses move easterly over Lake Superior, northern Lake Michigan, and Georgian Bay, they absorb large quantities of moisture (Brown et al., 1980). They rise gradually as they move from the eastern shore of Georgian Bay (177 m elevation) towards Algonquin Park (580m elevation). Approximately 30km from the western park boundary elevation begins to increase rapidly causing orographically induced precipitation in the western highlands. As the air mass descends towards the eastern lowlands, it warms and becomes more stable resulting in the formation of a rain shadow. Even highlands such as Algonquin's, which rise to only 580m may thus become distinctly wetter than surrounding lowlands due to orographic precipitation (Trewartha, 1968).

To assess the moisture actually available to the growing plant, atmospheric moisture must be considered in combination with the ability of the soil to retain moisture. Moisture retention is directly related to soil texture (Brady, 1974) which, in Algonquin, is related to elevation through the effects of the most recent glacial activity approximately 10,000 years ago. During the Wisconsin glacial retreat, glacial meltwaters drained from ancient Lake Algonquin in a southeasterly direction through an expansive portion of the eastern lowlands area of the park called the Fossmill Outlet (Chapman, 1954). As a result, these meltwaters deposited large amounts of sorted and unsorted sands in the eastern lowland area. Due to their higher elevation, the western uplands were not subject to this major meltwater activity. Here instead, the advancing ice left compacted basal till, and retreating ice left loosely dumped ground moraine, both of which were lower in sand content and higher in silt than the majority of east side deposits.

Greater moisture availability in the uplands due to higher rainfall combined with greater soil moisture retention has facilitated the dominance of sugar maple, yellow birch, and hemlock which are more competitive on moist sites than white, red, and jack pine which in turn are more competitive on the drier sites (Alway and McMiller, 1933; Fraser, 1954; Hills, 1959; Horton and Brown, 1960; Maycock and Curtis, 1960; Lopoukhine, 1974). Among other things, superior root penetrating ability (Brown and Lacate, 1959), deep tap roots (Spurr and Barnes, 1980), and sinker roots (Fowells, 1968) contribute to the ability of the pine species to outcompete the other overstory dominants under low moisture conditions. Dominance of the tolerant hardwood species on sites with greater moisture is apparently enhanced by their greater photosynthetic efficiency (Logan and Krotkov, 1969; Logan, 1970) and their ability to maintain lower rates of respiration per unit leaf area (Grime, 1965; Loach, 1967) under shaded conditions.

The intolerant hardwood species are most competitive on those sites which are intermediate in moisture content (Scholz, 1937; Stoeckeler, 1948; Spurr, 1956; Stoeckeler, 1959, Carleton and Maycock, 1978). This is most likely because of their lower shade tolerance than the tolerant hardwoods and their greater need for moisture than the pine species.

As well as influencing vegetation, the factors of total nitrogen, organic matter, and pH of the mineral soil have all been to some degree affected by the growth and development of vegetation and by fire. Greater amounts of total nitrogen and organic matter in the upper mineral soil of the tolerant hardwood communities compared to intolerant and pine communities have commonly been found (Alway and McMiller, 1933; Pastor et al., 1982; Pregitzer and Barnes, 1984; Spies and Barnes, 1985). This may be due to the higher production of litter in deciduous forests compared to coniferous forests (Bray and Gorham, 1964), the faster rate of deciduous litter decomposition (Millar, 1974), and to the higher nitrogen content in deciduous leaves (Williams and Gray, 1974). The latter observation was confirmed in the present study by obtaining generally lower carbon-nitrogen ratios for the tolerant hardwood communities compared to the pine communities.

The pines seem to compensate for low nitrogen availability by retranslocating nitrogen within the tree (Miller et al., 1979; Spurr and Barnes, 1980). In addition, nitrogen mineralization has been associated with the white pine rhizosphere (Fisher and Stone, 1969). Fire can also reduce the amount of total nitrogen in the mineral soil and increase soil pH (Ahlgren and Ahlgren, 1960; Boerner, 1982; MacLean et al., 1983).

Although pH was included as one of the effective factors within the predictor set, it was not considered a major determinant of composition because of the minor differences observed among forest types and because of the extensive range overlap between community types.

There are also other factors which may affect the composition of overstory vegetation in Algonquin Park. Those of greatest significance include disturbances such as grazing by insects and mammals, disease, wind storms, logging and possibly acid precipitation. Assessment of these disturbances, however, was beyond the scope of this study.

COMMUNITY DYNAMICS

As in all forests, the composition of forests in Algonquin Park has changed with successional development. Thus the species composition of the stands sampled may, in part, reflect a range in successional stages as well as a range in environmental conditions. Evidence of historical forest composition in Algonquin Park obtained by Terasmae and Weeks (1979) provide for a general comparison of present to past forest composition in the Park. Their palynological data from a site on the west side of Algonquin (Terasmae and Weeks, 1979), which is dominated by the tolerant hardwood forest, indicate that 8,000 to 10,000 years ago there was more pine forest and less tolerant hardwood forest in this area. Similar data obtained by Cwynar (1978) for Algonquin's east side indicate that the percentage of pine increased steadily there between 770 and 1200 A.D.

Work on the present forests in Algonquin by Hills (1959) and Martin (1959) indicate that white and red pine stands establish as early to mid-successional community dominants within the tolerant hardwood forest of Algonquin mainly on dry, shallow exposed ridges and upland flats. These dry soil conditions are similar to those in eastern Algonquin where pines are more common. Hills (1959) and Martin (1959) also observed that poplar and white birch usually dominate the first successional communities on all site types within the upland tolerant hardwood forest of Algonquin.

This regional climax view of forest communities, however, must be tempered by the now accepted fact that "xeric, mesic, and hydric environments will support different equally valid climax communities" (Marks and Harcomb, 1981; pg. 299; see also Finegan, 1984; Tilman, 1985). From the data obtained in this study it was not possible to determine the successional nature of sampled stands. It is likely, however, that some of the birch, poplar and white pine stands sampled, particularly those within the tolerant hardwood forest, were early as opposed to later successional stands.

CONCLUSION

Approximately 60% of the upland forest landscape in Algonquin Park is dominated by sugar maple, white pine, and large-toothed aspen, in order of decreasing dominance. The remainder is dominated by yellow birch, hemlock, red pine, white birch, trembling aspen, red oak, and jack pine. Variation within the overstory composition of these upland forest dominance-types is best related to a fire incidence-soil moisture complex gradient.

The high fire-high moisture stress end of the complex gradient supports mainly pine forest communities dominated by jack, red, and white pine. Whitney (1986) suggests that for a similar substrate in Upper Michigan "the coarse textured outwash soils favored the pines, which in turn initiated a fire regime that perpetuated the more flammable pine species". The tolerant hardwood forest species dominate the low fire-low moisture stress end of the complex gradient due to their superior adaptation to moist sites and their low flammability. Occurring at an intermediate position along the gradient are the intolerant hardwood forest communities which are dominated by poplar, white birch and red oak.

Because of its higher ranking on the first canonical variate, its greater dynamic association with other environmental factors, and because of the human tendency to modify it, naturally-caused fire is considered of greater ecological concern than soil moisture for long-term forest management in Algonquin Park. In Algonquin, humans have interfered with naturally-caused fire mainly in two ways. Slash left by timber harvesting which began in the 1830's, probably increased the destructiveness of natural fires (Smith, 1968; Cwynar, 1977) and since 1921, fire suppression has dramatically decreased the role of naturally-caused fire in forest development (Brown, 1980).

In addition to affecting forest development, suppression of forest fire also results in the accumulation of live and dead forest fuels which in turn increases the hazard of fire (Dodge, 1972; Parsons and DeBenedetti, 1979). Both increased fire intensity due to slash and a decreased fire rotation due to fire suppression can result in a modification of forest composition (Chandler et al., 1983; Kimmins, 1987). In eastern North America, fire suppression has modified pine community composition in the Pine Barrens of New Jersey (Boerner, 1981; Forman and Boerner, 1981), in central New York (Milne, 1985), in northern New England (Fahey and Reiners, 1981), and in Minnesota (Spurr, 1954). Fire suppression may ultimately lead to a reduction in biological diversity (Heinselman, 1973; Taylor, 1973; Kessell, 1979), pest outbreaks (Heinselman, 1971), and even species extinctions under specialized circumstances (Oberle, 1969; Forman and Boerner, 1981). Due to the suppression of naturally-caused fire in Algonquin Park since 1921, it is likely that human-caused changes in vegetation composition within Algonquin's pine and intolerant hardwood communities has and will continue to occur.

CHAPTER 7 - UNDERSTORY AND ENVIRONMENT

INTRODUCTION

The forest understory is important for a number of reasons. It plays a significant role in animal food chains, it is subject to major modification by grazing herbivores, it contributes significantly to the circulation of nutrients within the forest, and through arboreal reproduction it influences overstory composition (Siccama et al., 1970; Spurr and Barnes, 1980; Maguire and Forman, 1983). In addition, understory species can be used as indicators of site quality for forest management purposes (Rowe, 1956; Coffman and Willis, 1977; Carleton et al., 1985).

A variety of environmental factors have been identified as key influences upon understory composition within the mixed temperate forest of North America. These include light (Bratton, 1976; Davison and Forman, 1982; Menges, 1986), soil moisture (Maycock and Curtis, 1960; Siccama, 1974; Hicks, 1980; Pregitzer and Barnes, 1984), and nutrients (Graves and Monk, 1982; Rheinhardt and Ware, 1984; Graves and Monk, 1985). These studies have not, however, included the potential influence of disturbance upon understory vegetation composition. Disturbance may result in subtle to severe changes in environmental conditions as well as biological destruction (Canham and Marks, 1985). Misinterpretation of ecological data may result when the role of disturbance is overlooked in explaining community patterns (Sousa, 1984; Pickett and White, 1985).

To date, the analysis of plant population responses to the complete environmental complex has been lacking due to the difficulty of relating populations to one another along two- or three-dimensional continua in a rigorous manner (Rowe, 1983). The purpose of this study was to determine the effect of an entire range of environmental variables, including fire, on the composition of understory forest vegetation through rigorous quantitative description. Field data were collected in Algonquin Park which is centrally located within the Great Lakes-St. Lawrence (GLSL) Forest Region.

METHODS

FIELD

Understory vegetation and environmental factors were sampled in 100 upland forest stands within a transect which was two townships wide extending across the approximate 72 km width of Algonquin Park (Figure 6-2). The understory included saplings (sa), seedlings (se), shrubs, and vascular herbaceous plants. Cryptogams were not included in the survey. Saplings were sampled by recording the percent cover and species for all tree species less than 2cm dbh and greater than .5m in height within 15 systematically placed 2.5m x 2.5m quadrats per stand. Five sapling quadrats were placed along the length of the three 10x30m tree quadrats per stand - three within the tree quadrat and one placed on the outside of each end of the quadrat. Within the entire transect 1500 sapling quadrats were sampled. The remainder of the understory was sampled by recording percent cover and species type within 21 systematically placed 1m x 1m quadrats per stand. Seven of these quadrats were placed along the length of the three 10x30m tree quadrats per stand - three within the tree plot, and one placed at each end and at each side of the tree quadrat. In total, 2100 of the quadrats were sampled. Sampling occurred during summer months, thus certain spring ephemerals such as <u>Claytonia</u> <u>caroliniana</u> and <u>Erythronium</u> <u>americanum</u> were not encountered. Appendix XII provides summarized cover values for understory species within each stand. Nomenclature follows Fernald (1950).

The environmental variables included in this study can be grouped as follows: microclimate, macroclimate, soils, physiography, and disturbance. The influence of microclimate was assessed through the use of indices that were composed of stand basal area values for each of the nine dominant overstory species. These species included yellow birch, sugar maple, hemlock, white birch, poplar, red oak, white pine, red pine, and jack pine. The use of overstory species basal area was based on the assumption that the overstory canopy will have major effects on microclimatic conditions at the forest floor. The amount of light reaching the forest floor was also evaluated by visually estimating the amount of unoccupied space in the forest canopy. Macroclimate, soils, physiography and fire variables were sampled and measured as described

RESULTS

DESCRIPTION OF UNDERSTORY COMPOSITION

In total, 130 vascular plant species were found growing in the understory of upland forests in Algonquin Park (see Table 7-1). These included 25 tree species, 22 shrub species, and 84 herbaceous species. The five most abundant understory species were Acer saccharum (se) (15.2%), Aralia nudicaulis (7.7%), Acer saccharum (sa) (7.0%), Corylus cornuta (6.7%), and Pteridium aquilinum (6.2%). There were 32 species that had 0.5% or greater relative abundance in the entire study area (see Table 7-2). The abundances for the more important understory species by overstory dominance-type are shown in Table 7-3. This included species with an average of at least 5.0% cover per stand or 80% relative stand frequency. Those species that met both criteria were considered the understory dominants and were classified into overstory dominance-types and forest types which included tolerant hardwoods, intolerant hardwoods, and pines (see Chapter 6 for explanation of these dominance- and forest types.

Tolerant Hardwood Forest

Yellow birch type

The three dominant understory species within this overstory

TABLE 7-1 - UNDERSTORY SPECIES LIST

Abies balsamea
Acer pennsylvanicum
Acer rubrum
Acer saccharum
Acer spicatum
Actaea pachypoda
Actaea rubra
Alnus rugosa
Amelanchier sanguinea
Apocynum androsaemifolium
Aralia nudicaulis
Arctostaphylos uva-ursi
Arisaema triphyllum
Aster macrophyllus
Aster umbellatus
Athyrium Felix-femina
Betula lutea
Betula papyrifera
Botrychium virginianum
Brachyelytrum erectum
Carex arctata
Carex communis
Carex deweyana
Carex intumescens
Carex leptonervia
Carex spp.
Chimaphila umbellata
Cinna latifolia
Circaea alpina
Clintonia borealis
Comptonia peregrina
Coptis groenlandica
Cornus canadensis
Cornus rugosa
Corylus cornuta
Cypripedium candidum
Diervilla lonicera
Dirca palustris
Dryopteris spinulosa
Epigaea repens
Equisetum scirpoides
Fagus grandifolia
Fragaria vesca
Fragaria virginiana
Fraxinus americana
Fraxinus nigra
Galium trifolium
Gaultheria hispidula
Gaultheria procumbens
Goodyera repens
Gramineae spp.
Gymnocarpium dryopteris
Habenaria orbiculata
Hepatica americana
Impatiens capensis
Kalmia angustifolia
Linnaea borealis
Lonicera canadensis
Lycopodium annotinum
Lycopodium clavatum
Lycopodium complanatum
Lycopodium lucidulum
Lycopodium obscurum
Medeola virginiana
Melampyrum lineare
Maianthemum canadense
Milium effusum
Mitchella repens
Monotropa uniflora
Onoclea sensibilis
Ostrya virginiana
Oxalis montana
Pedicularis canadensis
Picea glauca
Picea mariana
Pinus banksiana
Pinus resinosa
Pinus strobus
Polygala pauciflora
Polygonatum biflorum
Polygonum cilinode
Polypodium virginianum
Populus grandidentata
Populus tremuloides
Prunus pumila
Prunus serotina
Pteridium aquilinum
Pyrola elliptica
Pyrola rotundifolia
Pyrola secunda
Pyrola virens
Quercus rubra
Ribes glandulosum
Ribes lacustre
Rubus canadensis
Rubus pubescens
Rubus strigosus
Rubus spp.
Sambucus canadensis

TABLE 7-1 (CON'T)

Sanicula marilandica
Solidago canadensis
Solidago squarrosa
Smilacina racemosa
Streptopus amplexifolius
Taxus canadensis
Thelypteris noveboracensis
Thelypteris phegopteris
Thuja occidentalis
Tiarella cordifolia
Tilia americana
Trientalis borealis
Trillium cernuum
Trillium erectum
Trillium grandiflorum
Trillium undulatum
Tsuga canadensis
Vaccinium angustifolium
Vaccinium myrtilloides
Viburnum acerifolium
Viburnum alnifolium
Viburnum cassinoides
Viola adunca
Viola cucullata
Viola incognita
Viola pubescens
Viola renifolia
Viola selkerkii
Viola septentrionalis
Viola spp.
Waldsteinia fragariodes

TABLE 7-2 - TOTAL COVER (%) OF THE UNDERSTORY SPECIES FOUND WITHIN THE STUDY AREA (>0.5% relative abundance)

SPECIES	TOTAL COVER (%)
Acer saccharum (se)	15.2
Aralia nudicaulis	7.7
Acer saccharum (sa)	7.0
Corylus cornuta	6.7
Pteridium aquilinum	6.2
Maianthemum canadense	3.9
Acer rubrum (sa)	3.8
Dryopteris spinulosa	3.3
Acer rubrum (se)	3.3
Aster macrophyllus	2.6
Abies balsamea (sa)	2.5
Acer pennsylvanicum (sa)	2.0
Lycopodium obscurum	1.9
Viburnum alnifolium	1.8
Acer pennsylvanicum (se)	1.7
Abies balsamea (se)	1.7
Vaccinium angustifolium	1.6
Trientalis borealis	1.5
Gramineae spp.	1.2
Gaultheria procumbens	1.2
Fagus grandifolia (sa)	1.1
Cornus canadensis	1.1
Lonicera canadensis	1.0
Clintonia borealis	.9
Ostrya virginiana (sa)	.7
Pinus strobus (sa)	.7
Carex spp.	.7
Lycopodium lucidulum	.7
Acer spicatum (se)	.6
Amelanchier sanguinea	.6
Streptopus amplexifolius	.6
Tiarella cordifolia	.5

TABLE 7-3 - DOMINANT UNDERSTORY SPECIES BY OVERSTORY DOMINANCE-TYPE
(includes species with at least 80% relative stand frequency
(first value) or at least 5% cover (second value) - asterisks
indicate those species that satisfy both conditions)

	Dominance-Type																	
Understory Species	Yellow Birch		Sugar Maple		Hemlock		White Birch		Poplar		White Pine		Red Oak		Red Pine		Jack Pine	
Oxalis montana	100	4.8																
Betula lutea (sa)	80	0.4			100	1.1												
Lycopodium lucidulum	100	1.5																
Dryopteris spinulosa	*100	7.6	*95	7.3	100	4.5												
Acer saccharum (sa)	100	4.0	100	3.4			100	0.9										
Thelypteris phegopteris	80	4.3																
Acer saccharum (se)	*100	19.1	*100	37.1	100	2.1												
Tsuga canadensis (sa)					100	3.6												
Acer pennsylvanicum (se)	80	2.4	85	2.7	*100	5.7												
Viola spp.	80	1.7					100	1.4										
Streptopus amplexifolius	100	2.0			100	1.0												
Acer pennsylvanicum (sa)	80	1.0	80	0.7	100	0.3	100	0.5										
Lycopodium obscurum	100	4.1	88	3.0														
Acer spicatum (se)	*100	5.2																
Trientalis borealis	100	1.4	93	2.2	100	2.1	*100	5.7	95	3.0	95	1.5			80	0.8		
Lonicera canadensis	80	0.5					100	1.6										
Aralia nudicaulis	100	4.1			*100	5.1	*100	11.3	*95	15.3	*100	13.9	*100	8.8	*80	12.2		
Corylus cornuta									*100	11.7	*100	16.5			*80	10.9		
Maianthemum canadense	100	1.9			100	4.7	100	3.5	*100	7.0	100	3.2	100	4.1	*100	13.4	*100	8.1
Acer rubrum (se)							*100	5.9	*100	7.2	95	4.6	*100	6.9	100	1.6		
Abies balsamea (sa)					100	0.6	100	0.7							80	0.9		
Abies balsamea (se)							*100	6.3			90	2.9						
Acer rubrum (sa)	80	0.2					100	0.4	100	2.2	95	1.5	100	1.4				
Clintonia borealis	80	0.4																
Carex spp.	80	0.6											100	3.0	100	2.8		
Gramineae spp.	80	0.3					100	1.2	100	1.5	100	1.9	*100	6.3	100	3.0	100	4.9
Cornus canadensis							100	2.3										
Aster macrophyllus									*100	6.2	*95	5.7	100	4.9	100	3.5		
Quercus rubra (se)													100	4.3				
Gaultheria procumbens									95	2.1	95	2.5	100	3.0	100	2.0	*100	7.1
Quercus rubra (sa)													100	2.4				
Pteridium aquilinum									*95	13.0	*95	11.3	*100	6.6	*100	17.0	*100	35.2
Linnaea borealis											84	1.3			100	2.7		
Populus tremuloides (sa)															80	1.0		
Pinus strobus (sa)															80	0.6		
Vaccinium angustifolium									84	2.3	90	2.5	100	4.4	80	3.6	*100	23.4
Pinus strobus (se)															80	1.7		
Amelanchier sanguinea													100	3.2	100	1.6	100	1.8
Melampyrum lineare															100	0.8		
Kalmia angustifolia																	100	3.6
Comptonia perigrina																	100	3.2
Pinus resinosa (sa)																	100	1.0

TABLE 7-3 - DOMINANT UNDERSTORY SPECIES BY OVERSTORY DOMINANCE-TYPE
(includes species with at least 80% relative stand frequency
(first value) or at least 5% cover (second value) - asterisks
indicate those species that satisfy both conditions)

Dominance-Type

Understory Species	Yellow Birch		Sugar Maple		Hemlock		White Birch		Poplar		White Pine		Red Oak		Red Pine		Jack Pine	
Oxalis montana	100	4.8																
Betula lutea (sa)	80	0.4			100	1.1												
Lycopodium lucidulum	100	1.5																
Dryopteris spinulosa	*100	7.6	*95	7.3	100	4.5												
Acer saccharum (sa)	100	4.0	100	3.4			100	0.9										
Thelypteris phegopteris	80	4.3																
Acer saccharum (se)	*100	19.1	*100	37.1	100	2.1												
Tsuga canadensis (sa)					100	3.6												
Acer pennsylvanicum (se)	80	2.4	85	2.7	*100	5.7												
Viola spp.	80	1.7					100	1.4										
Streptopus amplexifolius	100	2.0			100	1.0												
Acer pennsylvanicum (sa)	80	1.0	80	0.7	100	0.3	100	0.5										
Lycopodium obscurum	100	4.1	88	3.0														
Acer spicatum (se)	*100	5.2																
Trientalis borealis	100	1.4	93	2.2	100	2.1	*100	5.7	95	3.0	95	1.5			80	0.8		
Lonicera canadensis	80	0.5					100	1.6										
Aralia nudicaulis	100	4.1			*100	5.1	*100	11.3	*95	15.3	*100	13.9	*100	8.8	*80	12.2		
Corylus cornuta									*100	11.7	*100	16.5			*80	10.9		
Maianthemum canadense	100	1.9			100	4.7	100	3.5	*100	7.0	100	3.2	100	4.1	*100	13.4	*100	8.1
Acer rubrum (se)							*100	5.9	*100	7.2	95	4.6	*100	6.9	100	1.6		
Abies balsamea (sa)					100	0.6	100	0.7							80	0.9		
Abies balsamea (se)							*100	6.3			90	2.9						
Acer rubrum (sa)	80	0.2					100	0.4	100	2.2	95	1.5	100	1.4				
Clintonia borealis	80	0.4																
Carex spp.	80	0.6											100	3.0	100	2.8		
Gramineae spp.	80	0.3					100	1.2	100	1.5	100	1.9	*100	6.3	100	3.0	100	4.9
Cornus canadensis							100	2.3										
Aster macrophyllus									*100	6.2	*95	5.7	100	4.9	100	3.5		
Quercus rubra (se)													100	4.3				
Gaultheria procumbens									95	2.1	95	2.5	100	3.0	100	2.0	*100	7.1
Quercus rubra (sa)													100	2.4				
Pteridium aquilinum									*95	13.0	*95	11.3	*100	6.6	*100	17.0	*100	35.2
Linnaea borealis											84	1.3			100	2.7		
Populus tremuloides (sa)															80	1.0		
Pinus strobus (sa)															80	0.6		
Vaccinium angustifolium									84	2.3	90	2.5	100	4.4	80	3.6	*100	23.4
Pinus strobus (se)															80	1.7		
Amelanchier sanguinea													100	3.2	100	1.6	100	1.8
Melampyrum lineare															100	0.8		
Kalmia angustifolia																	100	3.6
Comptonia perigrina																	100	3.2
Pinus resinosa (sa)																	100	1.0

dominance-type included *Acer saccharum* (se), *Dryopteris spinulosa*, and *Acer spicatum* (se). Other less abundant dominant understory species that characterized this overstory dominance-type in order of decreasing abundance included *Oxalis montana*, *Thelypteris phegopteris*, *Lycopodium obscurum*, *Aralia nudicaulis*, *Acer saccharum* (sa), *Acer pennsylvanicum* (se), *Streptopus amplexifolius*, *Maianthemum canadense*, *Viola* spp., *Trientalis borealis*, *Lycopodium lucidulum*, *Acer pennsylvanicum* (sa), *Carex* spp., *Lonicera canadensis*, *Clintonia borealis*, *Betula lutea* (sa), *Gramineae* spp., and *Acer rubrum* (sa). Approximately 80.5% of the forest floor was covered by vascular understory growth.

Sugar maple type

The two dominant understory species within this overstory dominance-type included *Acer saccharum* (se) and *Dryopteris spinulosa*. Other less abundant dominant understory species that characterized this overstory dominance-type in order of decreasing abundance included *Acer saccharum* (sa), *Lycopodium obscurum*, *Acer pennsylvanicum* (se), *Trientalis borealis*, and *Acer pennsylvanicum* (sa). Approximately 76.1% of the forest floor was covered by vascular understory growth.

Hemlock type

The two dominant understory species for this overstory dominance-type included *Acer pennsylvanicum* (se) and *Aralia nudicaulis*.

Other less abundant dominant understory species that characterized this overstory dominance-type in order of decreasing abundance included Maianthemum canadense, Dryopteris spinulosa, Tsuga canadensis (sa), Acer saccharum (se), Trientalis borealis, Betula lutea (sa), Streptopus amplexifolius, Abies balsamea (sa), and Acer pennsylvanicum (sa). Approximately 46.0% of the forest floor was covered by vascular understory growth.

Intolerant Hardwood Forest

White birch type

The four dominant understory species in this overstory dominance-type included Aralia nudicaulis, Abies balsamea (se), Acer rubrum (se), and Trientalis borealis. Other less abundant dominant understory species that characterized this overstory dominance-type in order of decreasing abundance included Maianthemum canadense, Cornus canadensis, Lonicera canadensis, Viola spp., Gramineae spp., Acer saccharum (sa), Abies balsamea (sa), Acer pennsylvanicum (sa) and Acer rubrum (sa). Approximately 90.5% of the forest floor was covered by vascular understory growth.

Poplar type

The six understory dominants for this dominance-type included

Aralia nudicaulis, *Pteridium aquilinum*, *Corylus cornuta*, *Acer rubrum* (se), *Mianthemum canadense*, and *Aster macrophyllus*. Other less abundant dominant understory species that characterized this overstory dominance-type in order of decreasing abundance include *Trientalis borealis*, *Vaccinium angustifolium*, *Acer rubrum* (sa), *Gaultheria procumbens*, and *Gramineae* spp. Approximately 90.5% of the forest floor was covered by vascular understory growth.

Red oak type

The four dominant understory species in this dominance-type included *Aralia nudicaulis*, *Acer rubrum* (se), *Pteridium aquilinum*, and *Gramineae* spp. Other less abundant dominant understory species that characterized this overstory dominance-type in order of decreasing abundance include *Aster macrophyllus*, *Vaccinium angustifolium*, *Quercus rubra* (se), *Maianthemum canadense*, *Amelanchier sanguinea*, *Carex* spp., *Gaultheria procumbens*, *Quercus rubra* (sa), and *Acer rubrum* (sa). A total of 62.9% of the forest floor was covered by vascular understory growth.

Pine Forest

White pine type

The four understory dominants within this dominance-type included

Corylus cornuta, *Aralia nudicaulis*, *Pteridium aquilinum*, and *Aster macrophyllus*. Other less abundant dominant understory species that characterized this overstory dominance-type in order of decreasing abundance include *Acer rubrum* (se), *Maianthemum canadense*, *Abies balsamea* (se), *Gaultheria procumbens*, *Vaccinium angustifolium*, *Gramineae* spp., *Trientalis borealis*, *Acer rubrum* (sa), and *Linnaea borealis*. Approximately 83.8% of the understory was covered by vascular plants.

Red pine type

The three understory dominants for this dominance-type included *Pteridium aquilinum*, *Maianthemum canadense*, and *Aralia nudicaulis*. Other less abundant dominant understory species that characterized this overstory dominance-type in order of decreasing abundance include *Vaccinium angustifolium*, *Aster macrophyllus*, *Gramineae* spp., *Linnaea borealis*, *Carex* spp., *Gaultheria procumbens*, *Pinus strobus*, *Acer rubrum* (se), *Amelanchier sanguinea*, *Populus tremuloides* (sa), Abies balsamea (sa), *Melampyrum lineare*, *Trientalis borealis*, and *Pinus strobus* (sa). A total of 77.7% of the understory was covered by vascular plants.

Jack pine type

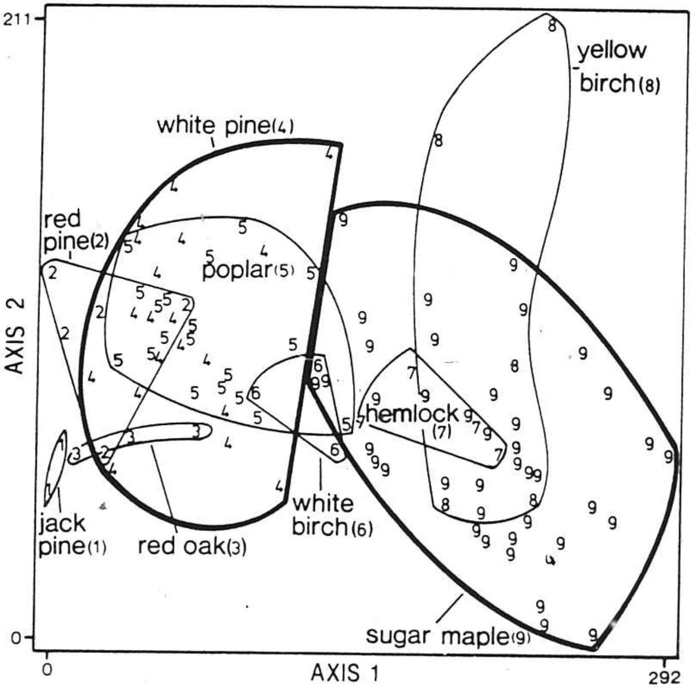
The four understory dominants for this dominance-type included *Pteridium aquilinum*, *Vaccinium angustifolium*, *Maianthemum canadense* and *Gaultheria procumbens*. Other less abundant dominant understory species that characterized this overstory dominance-type in order of decreasing abundance include Gramineae spp., Kalmia angustifolia, Comptonia perigrina, Amelanchier sanguinea, and Pinus resinosa (sa). A total of 94.0% of the understory was covered by vascular plants.

STAND ORDINATION

Eigenvalues resulting from DCA for axes 1 through 4 were .378, .154, .110, and .087. The relatively large difference between the first and second axis of the DCA compared to the much smaller difference between the remaining successive axes indicates that the first DCA axis contains a large portion of the variation in the vegetation composition data. Figure 7-1 shows each stand plotted with respect to both its DCA axes (1 and 2) scores and the dominance-type designations. The most obvious pattern in this figure is the separation of the tolerant hardwood understory at the high end of axis one from the intolerant hardwood and pine understories at the lower extreme of this same axis. This is with the exception of one poplar and one white birch stand, both of which fall within the understory ordination space of the tolerant hardwood forest.

From Figure 7-1 it can also be seen that 92 of the 100 stands fall within one of two dominance-type ordination spaces. Except for two yellow birch stands, the understory composition of the hemlock and yellow birch dominance-types forms a subset of the sugar maple understory ordination space. To a lesser extent, the same situation

FIGURE 7-1 - SCATTERGRAM OF STANDS PLOTTED WITH RESPECT TO DCA AXES 1 AND 2 FOR THE UNDERSTORY



occurs with the other two forest types. The understory composition of the poplar, red pine, red oak, and white birch dominance-types generally falls within the understory ordination space of the white pine dominance-type.

A notable exception is the understory composition of the jack pine dominance-type which occupies the only non-overlapping region of the ordination space compared with other dominance-types. The understory dominants which are unique to this dominance-type include Vaccinium angustifolium and Gaultheria procumbens. It should be noted, however, that the degree of understory composition similarity between dominance-types is affected by the number of stands sampled. In this case only two jack pine stands were sampled.

SPECIES ORDINATION

In addition to providing a stand ordination, DCA provides a species ordination. Table 7-4 provides three sets of 20 species: one at either end of the first ordination axis and one representing the mid-portion of the axis. Those species at the high end are characteristic of the tolerant hardwood forest, those at the low end are characteristic of the pine forest and those in the intermediate portion are characteristic of the intolerant hardwoods. Some of these species such as Trientalis borealis, Aralia nudicaulis, Mianthemum canadense, and Acer rubrum (se) are among the most common understory species in the study area. Not only do they occur within the intolerant hardwood forest but also within

TABLE 7-4 - UNDERSTORY SPECIES CHARACTERISTIC OF THE EXTREME ENDS AND INTERMEDIATE PORTION OF THE FIRST DCA AXIS OF THE STAND ORDINATION

(species also listed in Table 7-3 appear in dark print - numbers represent position along first axis of the DCA species ordination)

HIGH END (dominated by tolerant hardwoods)

1 ***Milium effusum***
2 *Thelypteris noveaboracensis*
3 *Viola cucullata*
4 *Viola septentrionalis*
5 *Impatiens capensis*
6 ***Brachyelytrum erectum***
7 *Viola selkerkii*
8 ***Carex arctata***
9 ***Trillium erectum***
10 *Trillium grandifolium*
11 ***Ribes glandulosum***
12 *Monotropa uniflora*
13 *Viola incognita*
14 *Prunus serotina* (sa)
15 *Betula lutea* (se)
16 ***Oxalis montana***
17 *Cinna latifolia*
18 *Viburnum alnifolium*
19 ***Betual lutea*** (sa)
20 *Gymnocarpium dryopteris*

LOW END (dominated by pines)

111 ***Pinus strobus*** **(sa)**
112 ***Vaccinium angustifolium***
113 *Viburnum cassinoides*
114 *Apocynum androsaemifolium*
115 ***Pinus strobus*** **(se)**
116 *Diervilla lonicera*
117 *Polypodium virginianum*
118 ***Amelanchier sanguinea***
119 ***Waldsteinia fragariodes***
120 ***Melampyrum lineare***
121 ***Chimaphila umbellata***
122 ***Epigaea repens***
123 ***Lycopodium complanatum***
124 ***Kalmia angustifolia***
125 ***Solidago squarrosa***
126 ***Taxus canadensis***
127 *Comptonia peregina*
128 ***Pinus banksiana*** (sa)
129 *Pinus resinosa* (sa)
130 *Cypripedium candidum*

INTERMEDIATE (dominated by intolerant hardwoods)

55 *Fagus grandifolia* (sa)
56 ***Medeola virginiana***
57 *Fagus grandifolia* (se)
58 *Carex deweyana* (se)
59 *Rubus pubescens*
60 *Botrychium virginianum*
61 ***Trientalis borealis***
62 *Polygonatum biflorum*
63 *Viola pubescens*
64 *Coptis groenlandica*
65 ***Habenaria orbiculata***
66 ***Lonicera canadensis***
67 ***Aralia nudicaulis***
68 ***Mitchella repens***
69 *Corylus cornuta*
70 ***Maianthemum canadense***
71 *Sanicula marilandica*
72 ***Acer rubrum*** **(se)**
73 ***Abies balsamea*** **(sa)**
74 *Aster umbellatus*

the tolerant hardwood and pine forests. Whereas Table 7-3 includes only common or dominant species, Table 7-4 includes those that are less common or rare as well as some that are more common.

INDIRECT GRADIENT ANALYSIS

Mean stand basal area for the nine overstory species that were used as indices to microclimate are presented for each of the nine dominance-types in Table 6-3. The rest of the environmental variables are summarized by dominance-type in Table 6-4. Stand values for the environmental variables were used in CCA along with stand scores from DCA which were used to represent understory composition.

Because of suspected collinearity between the nine microclimate indices (overstory species basal areas) and the 25 directly measured environmental factors, the final predictor set was identified in three steps. First, the interset correlations between the four environmental variates and the four DCA axes obtained from CCA were tested for significance using Miller's (1975) F-ratio approximation (see Table 7-5). Using Miller's (1975) F-ratio approximation, five significant interset correlations were identified. However, because the eigenvalues for axis 2 (.154), axis 3 (.110) and axis 4 (.087) were so low relative to the axis 1 eigenvalue (.378), only the relationship between DCA axis 1 and environmental variate 1 was considered important.

Second, the significance of the cumulative intraset correlation for each of the 34 environmental factors was tested to identify a

TABLE 7-5 - INTERSET CORRELATIONS BETWEEN ORDINATION AXES AND CANONICAL VARIATES FOR THE UNDERSTORY

	V1	V2	V3	V4
AX1	-.973**	.080	.022	-.013
AX2	.463	.507*	.516*	-.176
AX3	-.136	-.747*	.444	.061
AX4	-.020	-.211	.350	-.565*

** p<.001; Miller's (1975) F-ratio approximation
 * p<.01

TABLE 7-6 - ENVIRONMENTAL FACTOR LOADINGS ON THE FIRST CANONICAL VARIATE FOR THE UNDERSTORY PREDICTOR SET

Environmental Factor	Loading
elevation	.872
sugar maple	.871
longitude	-.815
precipitation	.793
temperature	-.784
fire	-.782
total nitrogen	.742
light	-.707
c/n ratio	-.650

preliminary predictor set, again using Miller's (1975) F-ratio approximation. This resulted in the selection of eleven variables.

Third, a CCA was performed using only the first DCA axis, which was identified from step one, and the preliminary predictor set of 11 variables which was identified from step two. Of these 11 environmental variables, calcium and magnesium were dropped because they did not contribute significantly to the interset correlation due to their low intraset correlations (.022 and .124).

Table 7-6 shows the environmental factors and their loadings for the final predictor set. Elevation had the highest loading on the first canonical variate and sugar maple canopy effect had the next highest loading. Excluding longitude, precipitation and temperature ranked next. Fire, total nitrogen, light and the carbon:nitrogen ratio followed.

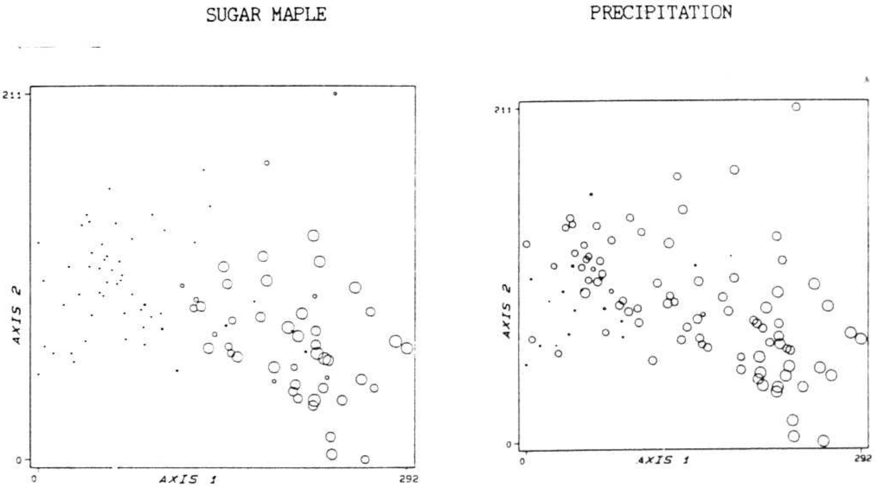
EFFECTIVE FACTORS

A discussion and description of effective factors can be found in Chapter 6. Table 7-7 shows the effective factors identified for this study. Those that are not included in the overstory predictor set are sugar maple canopy effects, % canopy opening (light) and carbon:nitrogen ratio. The sugar maple canopy effect varied from a mean high of 25.85 m^2/ha in the sugar maple dominance-type to a mean low of 0 m^2/ha in the red oak, red pine, and jack pine dominance-types. The mean sugar maple canopy effect was greatest for the tolerant hardwood

TABLE 7-7 - MEAN STAND VALUES FOR EFFECTIVE FACTORS BY FOREST TYPE FOR THE UNDERSTORY

EFFECTIVE FACTOR	FOREST TYPES		
	Tolerant Hardwoods	Intolerant Hardwoods	Pines
Sugar Maple (m^2/ha)	22.2	1.7	0.3
Precipitation (mm)	861	798	787
Temperature (degrees C)	18.66	18.84	18.98
Fire	$.097 \times 10^{-3}$	$.141 \times 10^{-3}$	$.167 \times 10^{-3}$
Total Nitrogen (%)	.26	.12	.10
Light (% canopy open)	13.6	20.2	28.0
C/N Ratio	34.4	47.7	47.3
No. of Stands	49	25	26

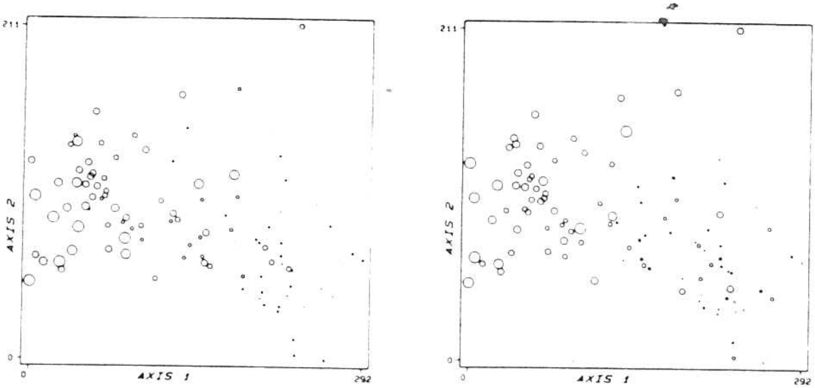
FIGURE 7-2 - SCATTERGRAMS OF THE RELATIVE MAGNITUDE OF IMPORTANT ENVIRONMENTAL FACTORS ON THE STAND ORDINATION BY DCA (circle size is proportional to the magnitude of the variable)



SUGAR MAPLE

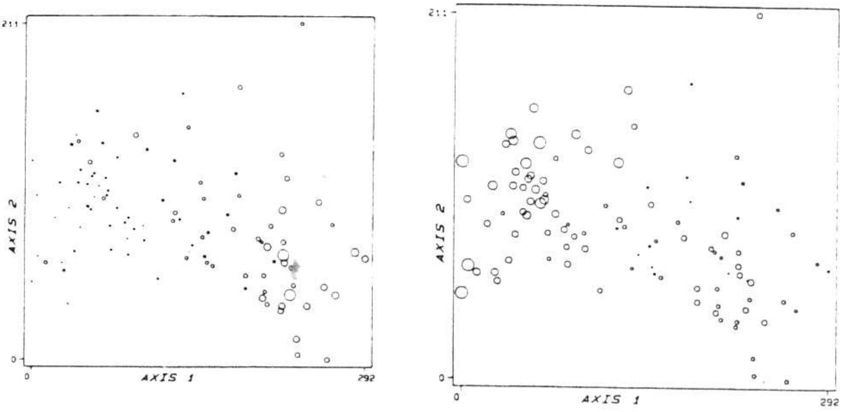
PRECIPITATION

FIGURE 7-2 (CON'T.)



TEMPERATURE

FIRE

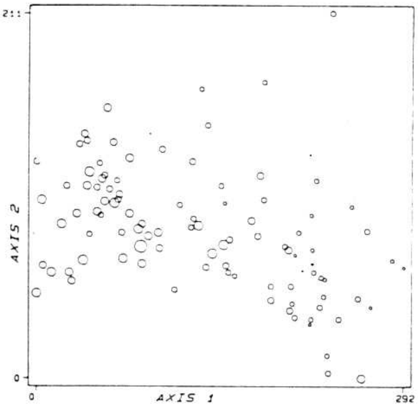


TOTAL NITROGEN

LIGHT

FIGURE 7-2 (CON'T.)

C/N RATIO



forest type (22.2m^2/ha), least for the pine forest type (0.3m^2/ha) and intermediate for the intolerant hardwood forest type (1.7m^2/ha).

Light (% canopy opening) varied from a mean of 42.2% for the jack pine dominance type to a mean of 10.0% for the hemlock dominance-type. Mean values for light also varied from a high of 28.0% for the pine forest type to a low of 13.6% for the tolerant hardwood forest type with an intermediate value of 20.2% for the intolerant forest type.

The carbon:nitrogen ratio varied from a mean of 59.1 for the red oak dominance-type to a mean of 33.6 for the sugar maple dominance-type. The intolerant hardwood forest had the highest carbon:nitrogen ratio (47.7), the tolerant hardwood forest had the lowest value (34.4) and the pine forest had an intermediate value (47.3). Figure 7-5 shows the magnitude of these effective factors plotted with respect to the first and second DCA axes.

FACTOR INTERACTIONS

Because the factors of an environmental complex do not vary alone (McIntosh 1970), it is necessary to consider factor interactions when describing a model of environmental influence upon understory composition. The relationships between environmental factors in the predictor set are presented in Table 7-8 in the form of Pearson product-moment correlations. The highest correlation between effective factors is between temperature and precipitation (-.888). High correlations also exist between fire and sugar maple canopy (-.790),

TABLE 7-8 - PREDICTOR SET CORRELATION MATRIX
(all correlations are significant at the p<.01 level)

	EV	MH	LG	PP	TP	FR	TN	LT	CN
EV	1.000								
MH	.667	1.000							
LG	-.875	-.566	1.000						
PP	.814	.533	-.934	1.000					
TP	-.870	-.539	.893	-.888	1.000				
FR	-.654	-.790	.541	-.481	.557	1.000			
TN	.619	.650	-.600	.592	-.580	-.507	1.000		
LT	-.515	-.565	.435	-.351	.358	.621	-.322	1.000	
CN	-.423	-.563	.476	-.524	.513	.426	-.540	.292	1.000

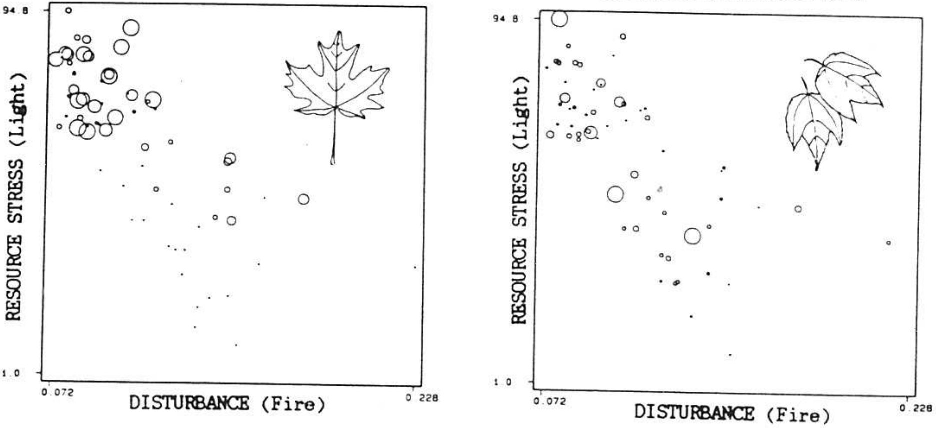
EV-elevation, MH-sugar maple, LG-longitude, PP-precipitation, TP-temperature, FR-fire, TN-total nitrogen, LT-latitude, CN-carbon-nitrogen ratio total nitrogen and sugar maple canopy (.650), and fire and % canopy opening (.621).

DIRECT GRADIENT ANALYSIS

To examine plant growth strategies, species abundance can be viewed in relation to resource stress and disturbance (Grime, 1979). Results of the indirect gradient analysis show that light, represented by both the sugar maple canopy effect and percent canopy opening, is the most highly correlated plant growth resource with the first environmental variate. Disturbance in the form of fire is also highly correlated with the first environmental variate. Therefore, the abundance of the 15 most common understory species (those with both >80% stand frequency and >5% cover per stand) was plotted against fire (disturbance gradient) and light (resource stress gradient).

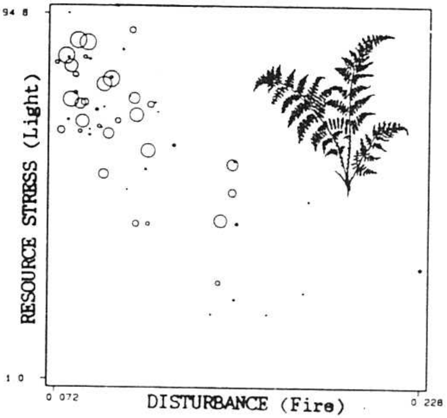
The dominant understory species from Table 7-3 that are associated mainly with the low fire-low light condition include Acer pennsylvanicum (se), Acer saccharum (se), and Dryopteris spinulosa (see Figure 7-2). Those dominants having a greater association with the high fire-low light stress include Aralia nudicaulis, Corlylus cornuta, Gaultheria procumbens, Gramineae spp., Maianthemum canadense, Pteridium aquilinum, and Vaccinium angustifolium (see Figure 7-3). And those dominant species having no particular association with a disturbance or resource stress condition include Abies balsamea (se), Acer rubrum (se), Acer spicatum (se), Aster macrophyllus, and Trientalis borealis (see Figure 7-4).

FIGURE 7-3 - RELATIVE ABUNDANCE OF SPECIES OCCUPYING THE LOW DISTURBANCE-HIGH RESOURCE STRESS CONDITION



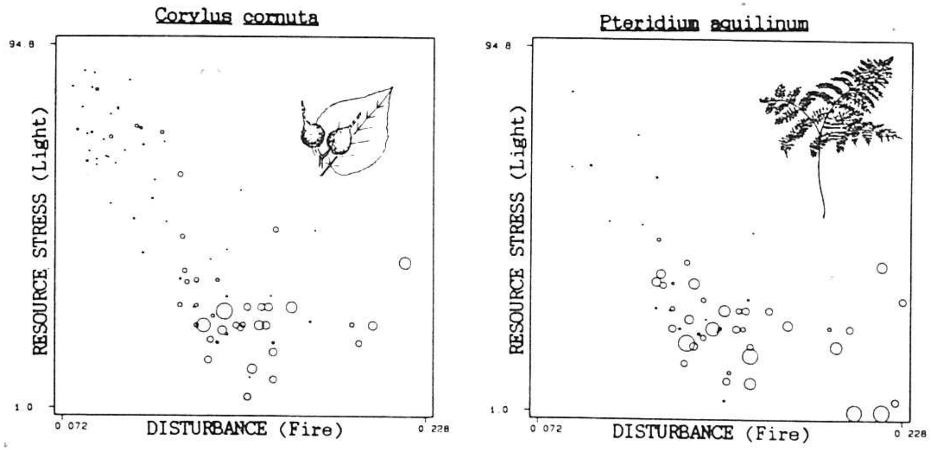
Acer saccharum (se)

Acer pennsylvanicum (se)



Dryopteris spinulosa

FIGURE 7-4 - RELATIVE ABUNDANCE OF SPECIES FAVORING THE HIGH DISTURBANCE-LOW RESOURCE STRESS CONDITION



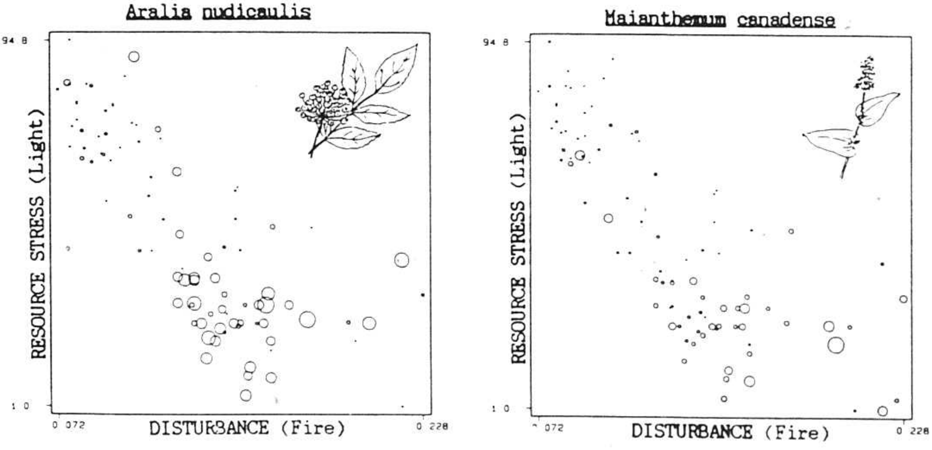
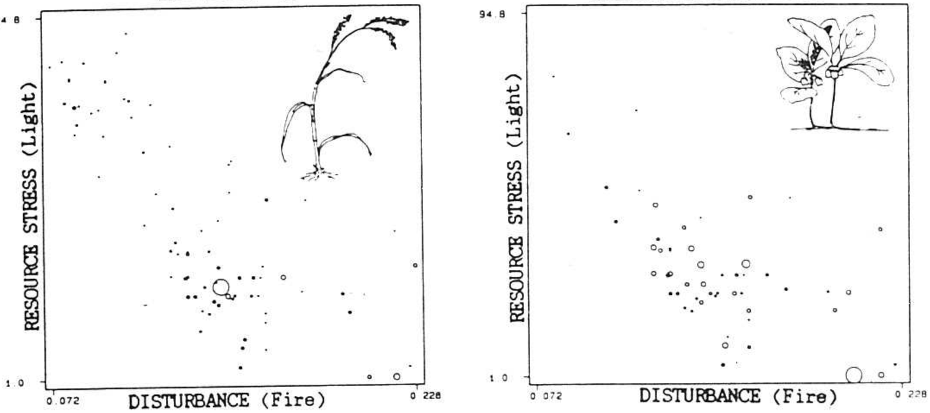


FIGURE 7-4 (CON'T)



Gramineae spp.

Gaultheria procumbens

Vaccinium angustifolium

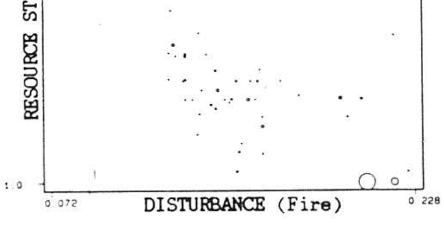


FIGURE 7-5 - RELATIVE ABUNDANCE OF SPECIES WITH NO STRONG ASSOCIATION FOR A PARTICULAR DISTURBANCE OR RESOURCE STRESS CONDITION

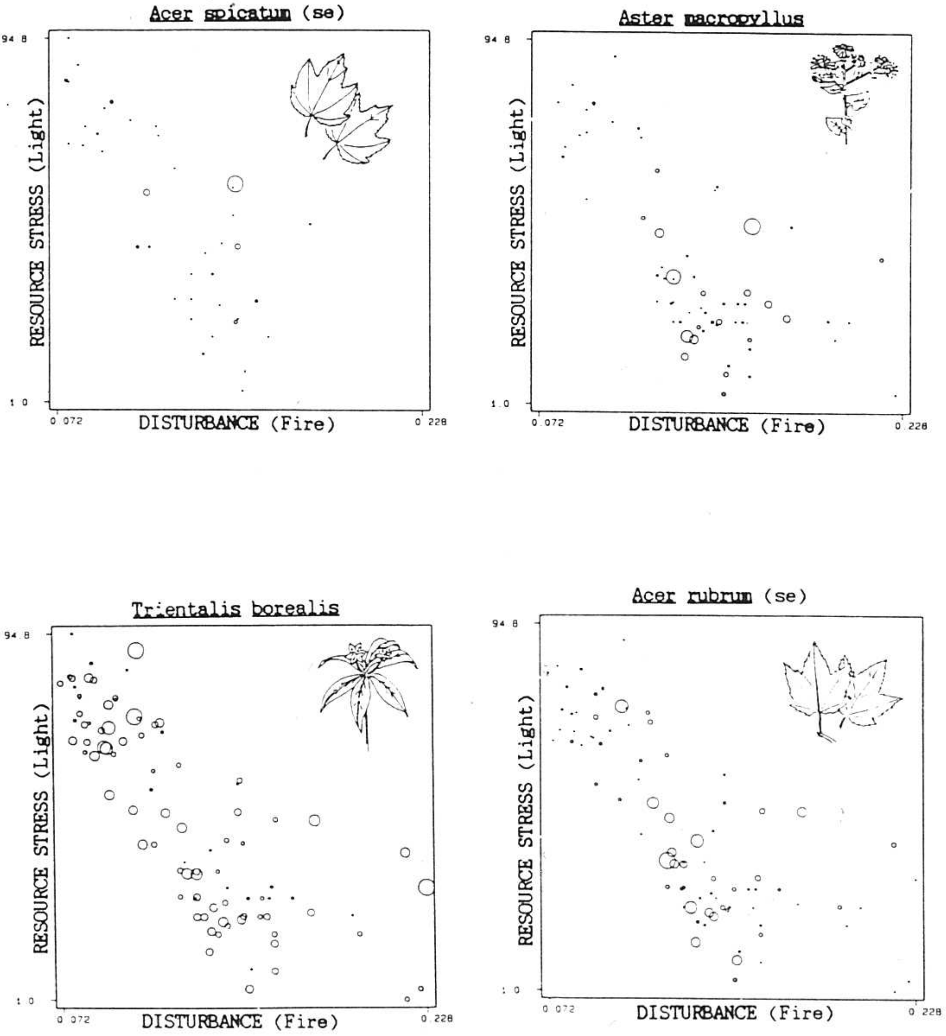
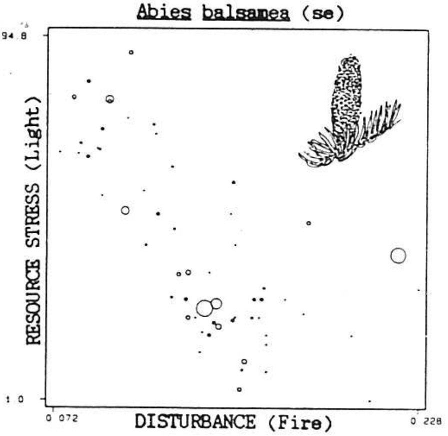


FIGURE 7-5 (CON'T)



Figures 7-2 through 7-4 show that the more abundant understory species are clearly associated with one of three major portions of the light-fire gradient. Taking this one step further, Table 7-9 classifies all the understory species into one of three growth strategy categories according to their relative abundance along the complex gradient. The stress tolerators/avoiders are most abundant at the high stress/low disturbance end of the gradient, the generalists are most abundant in the middle portion of the gradient (medium stress/medium disturbance), and the ruderals/endurers are most abundant at the low stress/high disturbance end of the gradient.

The stress tolerators/avoiders category includes 33 species dominated mainly by trees (*Acer saccharum*, *Acer pennsylvanicum*, *Fagus grandifolia*, *Ostrya virginiana*, *Prunus serotina*, and *Betula lutea*), ferns (*Dryopteris spinulosa*) and Lycopods (*Lycopodium obscurum* and *Lycopodium lucidulum*). The generalist category includes 47 species dominated mainly by trees (*Acer rubrum*, *Quercus rubra*, *Acer spicatum*, and *Populus tremuloides*), shrubs (*Viburnum alnifolium*, *Lonicera villosa*, and *Rubus pubescens*), and summer herbs (*Trientalis borealis*, *Streptopus amplexifolius*, *Tiarella cordifolia*, and *Medeola virginiana*). The ruderals/endurers category includes 45 species dominated mainly by shrubs (*Corylus cornuta*, *Vaccinium angustifolium*, *Lonicera canadensis*, and *Amelanchier sanguinea*) and summer herbs (*Aralia nudicaulis*, *Maianthemum canadense*, *Aster macrophyllus*, *Gaultheria procumbens*, *Cornus canadensis*, and *Clintonia borealis*).

TABLE 7-9 - UNDERSTORY SPECIES AND THEIR ABUNDANCES GROUPED BY GROWTH STRATEGIES AND STRESS/DISTURBANCE CATEGORIES (Values are presented as average % cover per stand; species are ordered within each growth strategy group according to decreasing total abundance in study area; see end of table for growth strategy and stress/disturbance grouping criteria)

GROWTH STRATEGY GROUP/SPECIES	ABUNDANCE WITHIN STAND STRESS/DISTURBANCE CATEGORIES		
	High Stress/ Low Disturbance Stands (38)	Medium Stress/ Medium Disturbance Stands (24)	Low Stress/ High Disturbance Stands (38)
Stress Tolerators/Avoiders			
Acer saccharum (se)	37.36	9.30	0.43
Acer saccharum (sa)	21.78	9.31	0.48
Dryopteris spinulosa	6.87	3.34	0.35
Acer pennsylvanicum (sa)	4.59	3.54	1.18
Lycopodium obscurum	2.77	2.27	1.03
Acer pennsylvanicum (se)	2.93	2.72	0.20
Fagus grandifolia (sa)	3.31	0.81	0.37
Ostrya virginiana (sa)	1.74	0.76	0.70
Lycopodium lucidulum	1.52	0.78	0.03
Ostrya viginiana (se)	0.80	0.48	0.23
Fagus grandifolia (se)	0.85	0.28	0.05
Prunus serotina (sa)	0.78	0.18	0.21
Betula lutea (sa)	0.63	0.46	0.00
Betula lutea (se)	0.43	0.32	0.03
Rubus strigosus	0.48	0.23	0.04
Galium triflorum	0.18	0.18	0.03
Prunus serotina (se)	0.31	0.04	0.04
Thelypteris noveboracensis	0.29	0.06	0.00
Lycopodium annotinum	0.22	0.12	0.01
Trillium erectum	0.26	0.01	0.00
Tilia americana (sa)	0.12	0.00	0.00
Ribes glandulosum	0.07	0.01	0.00
Cinna latifolia	0.04	0.02	0.01
Viola incognita	0.06	0.00	0.00
Trillium undulatum	0.04	0.02	0.00
Athyrium Felix-femina	0.04	0.01	0.00
Viola selkerkii	0.03	0.02	0.00
Brachyelytrum erectum	0.04	0.01	0.00
Viola pubescens	0.03	0.00	0.01
Trillium grandiflorum	0.04	0.00	0.00
Carex arctata	0.01	0.01	0.00
Impatiens capensis	0.01	0.01	0.00
Milium effusum	0.01	0.00	0.00

TABLE 7-9 (CON'T)

	High Stress/ Low Disturbance Stands (38)	Medium Stress/ Medium Disturbance Stands (24)	Low Stress/ High Disturbance Stands (38)
Generalists			
Acer rubrum (sa)	2.02	9.32	7.43
Acer rubrum (se)	1.94	5.88	3.77
Trientalis borealis	2.26	2.85	1.68
Viburnum alnifolium	2.95	3.55	0.00
Quercus rubra (sa)	0.72	0.81	1.38
Acer spicatum (se)	0.29	1.91	0.30
Streptopus amplexifolius	0.79	1.13	0.22
Tiarella cordifolia	0.35	1.75	0.03
Medeola virginiana	0.70	0.86	0.11
Viola spp.	0.51	0.89	0.21
Oxalis montana	0.18	1.10	0.00
Lonicera villosa	0.28	0.33	0.54
Thelypteris phegopteris	0.10	0.95	0.01
Rubus pubescens	0.14	0.67	0.15
Populus tremuloides (sa)	0.29	0.15	0.46
Kalmia angustifolia	0.22	0.25	0.41
Tsuga canadensis (sa)	0.06	0.68	0.00
Tsuga canadensis (se)	0.06	0.59	0.00
Mitchella repens	0.16	0.12	0.31
Pyrola rotundifolia	0.11	0.20	0.21
Smilacina racemosa	0.09	0.35	0.03
Coptis groenlandica	0.00	0.37	0.09
Lycopodium clavatum	0.00	0.28	0.08
Polygonatum biflorum	0.13	0.08	0.09
Polygala paucifiora	0.07	0.13	0.10
Betula papyrifera (sa)	0.03	0.13	0.10
Populus tremuloides (se)	0.05	0.09	0.08
Gymnocarpium dryopteris	0.06	0.14	0.01
Populus grandidentata (se)	0.08	0.05	0.05
Viola cucullata	0.07	0.10	0.01
Ribes lacustre	0.00	0.16	0.01
Rubus spp.	0.00	0.09	0.08
Polygonum cilinode	0.03	0.14	0.00
Fragaria virginiana	0.05	0.02	0.08
Betula papyrifera (se)	0.01	0.09	0.04
Viburnum cassinoides	0.02	0.06	0.02
Onoclea sensibilis	0.01	0.05	0.00
Alnus rugosa (sa)	0.00	0.06	0.00

TABLE 7-9 (CON'T)

	High Stress/ Low Disturbance Stands (38)	Medium Stress/ Medium Disturbance Stands (24)	Low Stress/ High Disturbance Stands (38)
Equisetum scirpoides	0.00	0.04	0.00
Sambucus canadensis	0.00	0.03	0.00
Goodyera repens	0.00	0.03	0.00
Sanicula marilandica	0.00	0.02	0.01
Circaea alpina	0.01	0.00	0.01
Pyrola elliptica	0.01	0.00	0.01
Habenaria orbiculata	0.00	0.01	0.01
Viola septentrionalis	0.01	0.01	0.00
Monotropa uniflora	0.00	0.01	0.00
Ruderals/Endurers			
Pteridium aquilinum	6.77	5.37	14.34
Aralia nudicaulis	2.95	9.33	13.11
Corylus cornuta	2.46	5.60	13.29
Maianthemum canadense	2.19	4.56	9.00
Abies balsamea (sa)	1.40	2.33	6.90
Aster macrophyllus	0.35	4.26	4.45
Vaccinium angustifolium	1.75	1.03	3.93
Abies balsamea (se)	0.90	2.22	2.48
Pinus strobus (sa)	1.33	0.96	2.84
Gaultheria procumbens	0.03	1.06	2.71
Gramineae spp.	0.31	0.81	2.58
Lonicera canadensis	0.64	1.36	1.49
Cornus canadensis	0.03	0.68	2.68
Clintonia borealis	0.29	1.27	1.60
Carex spp.	0.18	0.43	2.09
Amelanchier sanguinea	0.70	0.39	1.57
Linnaea borealis	0.46	0.05	1.17
Waldsteinia fragariodes	0.43	0.15	1.03
Picea glauca (sa)	0.17	0.40	0.88
Pinus strobus (se)	0.35	0.15	0.82
Quercus rubra (se)	0.13	0.34	0.66
Comptonia peregrina	0.17	0.04	0.42
Vaccinium myrtilloides	0.03	0.03	0.48
Cypripedium candidum	0.01	0.00	0.48
Populus gradidentata (sa)	0.07	0.04	0.37
Acer spicatum (sa)	0.00	0.17	0.25
Chimaphila umbellata	0.10	0.06	0.23
Viburnum acerifolium	0.01	0.12	0.26
Melampyrum lineare	0.09	0.03	0.21
Lycopodium complenatum	0.07	0.03	0.18
Picea glauca (se)	0.00	0.07	0.16
Apocynum androsaemifolium	0.06	0.02	0.15
Pinus banksiana (sa)	0.05	0.00	0.13
Prunus pumila	0.05	0.00	0.13
Cornus rugosa	0.01	0.07	0.09

TABLE 7-9 (CON'T)

	High Stress/ Low Disturbance Stands (38)	Medium Stress/ Medium Disturbance Stands (24)	Low Stress High Disturba Stands (38
Actaea pachypoda	0.04	0.00	0.09
Botrychium virginianum	0.02	0.03	0.08
Viola renifolia	0.01	0.05	0.06
Pinus resinosa (sa)	0.03	0.00	0.08
Epigaea repens	0.03	0.02	0.06
Hepatica americana	0.00	0.00	0.06
Aster umbellatus	0.00	0.01	0.04
Fragaria vesca	0.01	0.00	0.03
Solidago squarrosa	0.01	0.00	0.03
Carex deweyana	0.01	0.00	0.03

STRESS/DISTURBANCE CATEGORY CRITERIA: "High Stress/Low Disturbance" -light (stres range: 63.5-94.8, mean: 74.2, fire (disturbance) range: $.072 \times 10^{-3}$-$.115 \times 10^{-3}$, mean: $.090 \times 10^{-3}$ (38 stands); "Medium Stress/Medium Disturbance" - light range: 33.2-61.0, mean: 44.8, fire range: $.092 \times 10^{-3}$-$.219 \times 10^{-3}$, mean: $.133 \times 10^{-3}$ (24 stands); "Low Stress/High Disturbance" - light range: 0-29.8, mean: 19.8, fire range: $.122 \times 10^{-3}$-$.228 \times 10^{-3}$, mean: $.159 \times 10^{-3}$ (38 stands).

GROWTH STRATEGY GROUPING CRITERIA: "Stress Tolerators/Avoiders" - abundance in th High Stress/Low Disturbance category was higher than both the other two categorie and at least 2X greater than abundance in the Low Stress/High Disturbance categor "Ruderals/Endurers" - abundance in the Low Stress/High Disturbance category was higher than both the other two categories and at least 2X greater than the abunda in the High Stress/Low Disturbance category; "C-S-R Strategists" - abundance in t Medium Stress/Medium Disturbance category was higher than both the other two categories, or abundance in the High Stress/Low Disturbance category was higher t the other two categories but less than 2X the abundance in the Low Stress/High Disturbance category, or abundance in the Low Stress/High Disturbance category wa higher than the other two categories but less than 2X the abundance in the High Stress/Low Disturbance category.

Only species that occurred in two or more stands were included in this table

TABLE 7-9 (CON'T)

	High Stress/ Low Disturbance Stands (38)	Medium Stress/ Medium Disturbance Stands (24)	Low Stress/ High Disturbance Stands (38)
Actaea _pachypoda_	0.04	0.00	0.09
Botrychium _virginianum_	0.02	0.03	0.08
Viola _renifolia_	0.01	0.05	0.06
Pinus _resinosa_ (sa)	0.03	0.00	0.08
Epigaea _repens_	0.03	0.02	0.06
Hepatica _americana_	0.00	0.00	0.06
Aster _umbellatus_	0.00	0.01	0.04
Fragaria _vesca_	0.01	0.00	0.03
Solidago _squarrosa_	0.01	0.00	0.03
Carex _deweyana_	0.01	0.00	0.03

STRESS/DISTURBANCE CATEGORY CRITERIA: "High Stress/Low Disturbance" -light (stress) range: 63.5-94.8, mean: 74.2, fire (disturbance) range: $.072X10^{-3}$-$.115X10^{-3}$, mean: $.090X10^{-3}$ (38 stands); "Medium Stress/Medium Disturbance" - light range: 33.2-61.0, mean: 44.8, fire range: $.092X10^{-3}$-$.219X10^{-3}$, mean: $.133X10^{-3}$ (24 stands); "Low Stress/High Disturbance" - light range: 0-29.8, mean: 19.8, fire range: $.122X10^{-3}$-$.228X10^{-3}$, mean: $.159X10^{-3}$ (38 stands).

GROWTH STRATEGY GROUPING CRITERIA: "Stress Tolerators/Avoiders" - abundance in the High Stress/Low Disturbance category was higher than both the other two categories and at least 2X greater than abundance in the Low Stress/High Disturbance category; "Ruderals/Endurers" - abundance in the Low Stress/High Disturbance category was higher than both the other two categories and at least 2X greater than the abundance in the High Stress/Low Disturbance category; "C-S-R Strategists" - abundance in the Medium Stress/Medium Disturbance category was higher than both the other two categories, or abundance in the High Stress/Low Disturbance category was higher than the other two categories but less than 2X the abundance in the Low Stress/High Disturbance category, or abundance in the Low Stress/High Disturbance category was higher than the other two categories but less than 2X the abundance in the High Stress/Low Disturbance category.

Only species that occurred in two or more stands were included in this table

DISCUSSION

The success of plant populations is dependent upon their growth and reproductive adaptations to variations in resource stress and disturbance (Grime, 1979). Light, which supplies energy for photosynthesis, is one of the more critical resources required for plant growth (Kimmins, 1987; Woodward, 1987). Many species have adapted to varying light conditions through the processes of germination, establishment, growth and reproduction (Grime, 1965; Whigham, 1974; Clough et al., 1979; Ernst, 1979; Barkham, 1980; Morgan and Smith, 1981). For understory vegetation, the nature of the canopy and the creation of canopy gaps have the greatest effect on the condition of light that eventually reaches the forest floor (MacLean and Wein, 1977; Barbour et al., 1980; Spurr and Barnes, 1980; Collins et al., 1985).

Studies have shown that overstory composition and density are significantly related to forest understory composition (Outcalt and White, 1981; Woods and Whittaker, 1981; Carleton, 1984; Carleton et al., 1985; Moloney, 1986). Variation in understory light was considered the most important effective influence on understory composition within a New Jersey deciduous forest (Davison and Forman, 1982), a Wisconsin hardwood forest (Menges, 1986), and a southern Appalachian hardwood forest (Bratton, 1976).

The results of this study indicate that light, evaluated by the sugar maple canopy variable and percent canopy opening, is considered to have the greatest influence on variation in understory composition. The dominance of sugar maple in the canopy severely reduces the amount of light reaching the forest floor relative to the pine and intolerant hardwood dominance-types. In addition to affecting understory light, however, overstory sugar maple may also affect understory plants through processes such as allelochemistry and seed production. These additional influences could not be assessed for this study. Disturbance, in the form of fire, was also found to be highly correlated with understory species composition. Through destruction of the forest canopy fire may drastically affect the intensity of light reaching the forest floor. It may also result in the release of other resources such as water and soil nutrients which then become available for plant growth.

There are two main mechanisms by which this may occur (Canham and Marks, 1985). First, resource use is reduced immediately following the destruction of biomass. An obvious example is the increase in light intensity at the forest floor due to the creation of canopy gaps. Secondly, disturbance causing increased insolation at the soil surface may increase nutrient availability by increasing the rate at which soil organic matter is decomposed (Bormann and Likens, 1979b).

Generally, the larger and more intense the disturbance, the greater the resulting availability of resources for plant growth (Canham and Marks, 1985). As a result of the immediate stimulation in growth, this resource availability is transient in nature. Variations in resource availability are more characteristic of disturbed areas and result in greater morphological and physiological plasticity in the resident plant species (Bradshaw, 1965; Bazzaz, 1979) allowing them to accumulate resources quickly upon their availability (Marks, 1975; Vitousek, 1977). Thus, by affecting competition for resources the frequency, intensity, and spatial distribution of disturbance has played a major role in the evolutionary selection of plant regeneration strategies (Grime, 1979).

In general, the understories of the pine dominance-types in Algonquin Park tend to be characterized by greater amounts of light compared to the intolerant hardwood dominance-types. These in turn have greater light levels than the understories of the tolerant hardwood dominance-types. This light gradient corresponds to an associated variation in the presence of understory plant species.

Within the study area, the understories of the tolerant hardwood dominance-types are dominated mainly by trees, ferns and Lycopods. Typical dominant tree species such as <u>Acer saccharum</u> and <u>Acer pennsylvanicum</u> have developed adaptations to carry out efficient photosynthesis at low light levels (Woods and Whittaker, 1981). Ferns such as <u>Dryopteris spinulosa</u> and Lycopods such as <u>Lycopodium obscurum</u> and <u>Lycopodium lucidulum</u> are also shade tolerant. Because of their semi-evergreen nature, they are able to commence photosynthesis prior to canopy leaf-out and before most other species of the understory. In general, trees and ferns are also more competitive in a low light environment due to their greater height growth relative to other understory growth forms, enabling them to minimize the effect of shade from other plants (Horn, 1975; Givnish, 1982). Shade tolerant species have been classified as "shade plants" by Collins et al. (1985) and "stress tolerators" by Grime (1979).

With respect to disturbance, however, most understory species which are typical of the tolerant hardwood forest do not generally possess anatomical and reproductive adaptations that enable them to survive the effects of fire or to effectively exploit those environmental conditions created by such disturbance. Thus, these species have been called "avoiders" (of fire) by Rowe (1983).

Within the study area, the highest light intensities at the forest floor are found in the pine dominance-types which are dominated mainly by shrubs and summer herbs. Because these understory species are not well suited to shaded conditions, they may be classified as "sun plants" (Collins et al., 1985). They are, however, well adapted to the destructive as well as the environmental changes that result from fire. Thus, this group of species may also be called "endurers" (Rowe, 1983).

Sprouting of various species including *Corylus cornuta* (Van Wagner, 1963) and *Vaccinium* (Trevett, 1962; Smith and Sparling, 1966; Boerner, 1981) may occur as a result of increased soil temperature that results from fire. *Pteridium aquilinum* also shows rapid regrowth following fire (McMinn, 1951; Boener, 1981) due to the ability of its extensive underground rhizome system to survive fire (Martin, 1955). Other species that reappear rapidly following fire due to their adaptations to post-fire conditions, include *Maianthemum canadense* (Ahlgren, 1960; Sidhu, 1973), *Aralia nudicaulis* (Cayford et al., 1967; Ahlgren, 1974), and *Aster macrophyllus* (Methven, 1973). The increased growth of certain shrubs and herbs following fire may also be due to seed germination stimulated by heat and/or an increase in available nutrients due to organic matter combustion (Ahlgren and Ahlgren, 1960; Cushwa et al., 1968).

Some plants are able to exploit a wide variety of light conditions but seem to be best adapted to intermediate levels. These species are called "light flexible plants" by Collins et al. (1985) and "C-S-R strategists" by Grime (1979) who defines them as species that are "restricted by moderate intensities of both stress and disturbance". These generalist species are represented by all the major growth forms including trees, shrubs, and summer herbs. They tend to be most abundant at intermediate levels of light and fire incidence showing greatest abundances in the intolerant hardwood forests.

In addition to light, plant growth is also affected by water and nutrient supply (Chapin et al., 1987). The greater amounts of soil moisture on the Park's west side relative to the east side are typical due to the combined conditions of higher rainfall and a finer soil texture. This difference in soil moisture has probably also contributed to variation in forest understory species composition in Algonquin Park. Although the response of northern temperate understories to moisture has been little studied (Collins et al., 1985), a few studies have shown that species such as <u>Dryopteris</u> <u>spinulosa</u> and <u>Acer</u> <u>saccharum</u> are associated with mesic to moist conditions and species such as <u>Pteridium</u> <u>aquilinum</u> and <u>Vaccinium</u> <u>angustifolium</u> are associated with dry to dry-mesic conditions (Maycock and Curtis, 1960; Pregitzer and Barnes, 1984). Other studies have shown soil moisture to be generally important in determining understory composition (Siccama, 1974; Hicks, 1980).

A nutrient gradient, represented by a variation in soil nitrogen is also associated with variation in understory composition in Algonquin. Nutrient gradients are related to understory composition within the boreal forests of Ontario (Carleton and Maycock, 1980; Carleton et al., 1985) and southern Appalachian forests (Graves and Monk, 1982; Rheinhardt and Ware, 1984; Graves and Monk, 1985).

Through the products of decomposition, the carbon:nitrogen balance of the upper soil layer (which was measured in this study) is a direct reflection of the carbon:nitrogen balance in the vegetation (Alban et al., 1978). In addition to determining features of resource aquisition in plants, the plant carbon:nitrogen balance determines its susceptibility to herbivores and pathogens that in turn affect the trophic dynamics of the ecosystem (Chapin et al., 1987). Under resource limitations, some plants may accumulate carbon in order to support the synthesis of secondary metabolites (Bryant et al., 1983) such as lignin, tannin, and phenolics. This may deter herbivores and prolong the life of the plant (Chapin et al., 1987).

Finally, to understand fully the responses of understory species to resource gradients, the interaction of competition for light, water and nutrients must be addressed (Schulze and Chapin, 1987). The results obtained from this study do not allow for the identification of these interactions. However, a review of the variation in strategies used by plants to acquire and allocate resources with respect to above- and below-ground plant parts may help to shed light on these interactions

(Caldwell, 1987). Below-ground competition may be just as intense as above-ground competition and is of greater importance in low moisture/nutrient environments (Schulze and Chapin, 1987). Thus in the tolerant hardwood forest, where fire incidence is relatively low, light is most limiting, and water and nutrients are in good supply, understory species generally maximize the efficiency of their above-ground parts to capture light. The best example is the sugar maple which can attain height dominance in a few years because of its perennial woody nature and its ability to photosynthesize efficiently at low light levels. Few understory plants can outcompete it or survive in its shade.

In contrast, plant species in the pine forest must maximize the efficiency of and carbohydrate storage in their below-ground parts in order to survive and reproduce quickly after fire and to capture limited amounts of water and nutrients which are relatively less abundant than light. A good example is the perennial herb Clintonia borealis which has a rhizome system that may remain physiologically active for up to 15 years (Angevine and Handel, 1986) enduring the stress of fire and low levels of moisture and nutrients.

A focus on the role of above-and below-ground plant parts with respect to resource acquisition and allocation will contribute to a better understanding of the influence of primary producers on higher trophic levels and the movement of nutrients into the community. These studies would benefit from the use of controlled conditions in order to determine the interactive effects of competition for light, water, and nutrients.

In the long term, continued fire suppression in Algonquin Park will result in a shift in species composition towards the stress tolerators/avoiders (tolerant hardwood forest species) which are competitive on all but the driest sites at comparatively low levels of fire incidence. This shift in understory species composition is expected to translate eventually into changes in overstory composition in view of the importance of tree seedlings in the tolerant hardwood vegetation.

CHAPTER 8 - GENERAL DISCUSSION AND SYNTHESIS

The overstory analysis indicated that the fire regime was most strongly related to canopy composition within the Algonquin uplands. The understory analysis indicated that the light climate and the fire regime respectively were the most strongly related factors to compositional variation within the upland understory. However, the light climate in the understory is primarily determined by the density, structure, and composition of the overstory. Therefore, the disturbance regime emerges as the pre-eminent influence upon the composition of the upland forest complex as a whole.

At the high-disturbance end of this gradient, even-aged stands dominated by jack pine, red pine, white birch, and white pine prevail (see Figure 6-5). These tree species characteristically regenerate well following forest fire or are resistant to fire due to various silvical characteristics and adaptations (Fowells, 1965). They are also well adapted to moisture and nutrient stress which characterize their habitats. The understory of such stands is dominated by perennial herbs such as <u>Pteridium aquilinum</u>, <u>Aralia nudicaulis</u>, <u>Corylus cornuta</u>, <u>Maianthemum canadense</u>, <u>Gaultheria procumbens</u>, grasses, <u>Cornus canadensis</u>, <u>Clintonia borealis</u> and various sedges. These are geographically widespread taxa with the capacity to regenerate rapidly from persistent, below-ground parts especially following forest fire (Ahlgren, 1976).

In the mid-region of the fire-disturbance gradient, intolerant hardwoods dominated by poplar, red oak and to a lesser extent yellow birch predominate in the overstory (see Figure 6-5). These species possess some resprouting capability following all but severe forest fire, but are less tolerant of moisture and nutrient stress than those species at the high end of the disturbance gradient. The understory vegetation of such stands is characterized by a mixture of trees, shrubs and herbs including Acer rubrum, Trientalis borealis, Viburnum alnifolium, Acer spicatum, Streptopus amplexifolius, Tiarella cordifolia, and Mediola virginiana. These taxa are all capable of rapid regeneration after destruction of above-ground parts but may not be able to withstand the extreme thermal stress occasionally associated with forest fire. In addition, they are less tolerant of moisture and nutrient stress than those plants which typify the high end of the fire regime gradient. However, all species appear to be able to withstand moderate shade which may confer some competitive advantage over species which are more light-demanding.

The overstory of stands at the low end of the fire disturbance gradient are characterized by sugar maple and eastern hemlock. These species are extremely shade tolerant and can regenerate beneath an existing tree canopy. However, they are also intolerant of moisture stress and to a lesser extent nutrient stress (Fowells, 1965). Whereas sugar maple can actively resprout following canopy removal, eastern hemlock must establish by seed following disturbance. The understory of such stands is typified by woody vegetation, especially the saplings and seedlings of sugar maple stands. In addition, gap phase species such as <u>Acer pennsylvanicum</u>, <u>Fagus grandifolia</u>, and <u>Ostrya virginiana</u> frequently occur. The herbaceous understory in these stands is sparse and typified by extremely shade tolerant plants such as <u>Dryopteris spinulosa</u> and species of <u>Lycopodium</u>. Other taxa are more typical of spring flora, including <u>Trillium</u> and <u>Viola</u>.

With a decline in the fire incidence index the stands change from a primarily even-aged structure to an uneven-aged condition. This may be associated with differences in total stand age but is most likely to be related to the qualitative differences between disturbance by fire versus disturbance by windthrow and dominant tree death. In the tolerant hardwoods, sugar maple and other tree species form a "seedling bank" on the forest floor. In the event of gap formation from windthrow and tree death those seedlings which encounter increased irradiance enter a stage of increased or "release" growth and compete to fill the gap. In this way the tolerant hardwood canopy is rapidly filled to maximum capacity resulting in a reasonably uniform, deep shade beneath.

In contrast, postfire establishment in the pine stands is dependent on the availability and germination of viable seed. Maximum tree density may not be achieved by this method of regeneration. The result is likely to be an understocked stand in which gaps or a low canopy density prevails. In addition, the canopy characteristics of the pine and intolerant hardwood stands are such that relatively large amounts of diffuse radiation pass through. This is in contrast to the tolerant hardwoods with determinate growth patterns and highly efficient light interception characteristics in the canopy. An associated trend in the understory vegetation is the notable shift from a primarily herbaceous cover in the pine forest to one dominated by tree seedlings and saplings in the tolerant hardwood forest. It should be noted, however, that maple stands do have a significant herbaceous component, but this has been excluded from the main portion of the growing season and persists only as spring flora.

Clearly associated trends in canopy and understory characteristics emerge from this study and these have been related primarily to the incidence of fire. However, it is equally clear that the fire incidence index is also linked to the soil moisture regime (Figure 6-5) and to the available light in the understory (Figures 7-2 to 7-4). Thus the upland forest vegetation complex in Algonquin Park varies in relation to a complex primary gradient in which the type of disturbance, light and soil moisture all play a linked role. This single, complex gradient implies that plants adapted to one environmental feature must of necessity be adapted to other associated environmental constraints in order to survive. For example, _Vaccinium_ _angustifolium_ in the pine forest understory can regenerate following forest fire, but is also quite drought tolerant.

On a fundamental level, the models developed from this work provide a basic framework for making general predictions for overstory vegetation composition based on changes in soil moisture and fire; and for understory based on changes in light and fire. For the overstory model, a reduction in soil moisture drives upland overstory composition towards the pine communities and a reduction in fire incidence drives the overstory towards the tolerant hardwood composition. For the understory model, an increase in the amount of light reaching the forest floor drives the upland understory composition towards the pine understory types and a reduction in fire incidence results in a shift towards the tolerant hardwood understory vegetation.

Simple univariate effects of environmental variables on vegetation composition, however, do not account for the effects of numerous interactions among environmental variables. To account for these interactions, data on the spatial and temporal nature of environmental change in disturbed forest patches are required. Of particular importance are the effects of resource combinations and resource change on plant resource acquisition and allocation.

To understand the effects of resource combinations on vegetation composition using survey data such as that collected in this study, a multiple regression approach could be used. As the dependent variable, ordination axis scores would be predicted from a set of significant interacting environmental variables. The large amount of variance explained by the first ordination axis for overstory composition in this study suggests that criterion data set editing of a few sample outliers would suffice to obtain groups of stand scores, each of which would represent a homogeneous community type. Continuous ranges of stand scores on the primary ordination axis would then be used to represent a specific forest composition type.

On a more practical level, the results of this work provide the most detailed and comprehensive consideration of forest site influence upon upland forest composition in Algonquin Park. Assuming that timber harvesting and fire suppression have not significantly affected the composition of the stands sampled, the relationships established from this work can serve to refine long-term forest management objectives on sites defined by specific environmental conditions. If a reasonable regression model can be developed, forest management scenarios could be examined with a known degree of error and a continuous cycle of hypothesis generation, hypothesis testing, and hypothesis refinement could be initiated.

The results of this study, however, represent only a single snapshot in time of a very dynamic system. Thus the study findings can only be confirmed through a detailed analysis of forest ecosystem development over time. These ecosystem development studies should begin with the use of chronosequences, or spatially distinct stands chosen to represent various stages of ecosystem development within various community and site types. When plots are established within these stands they should be permanently marked within nature reserves or other protected areas so that they can be easily relocated and continuously remeasured.

Long-term studies of permanent plots that are selected to represent the variety of forest ecosystem types and successional stages will yield the knowledge necessary to understand and predict natural forest succession. Finally, by applying this approach to represent the variety of forest management practices that occur within a number of forest types in Algonquin Park it will be possible to develop a more reliable science of forest resource management.

CHAPTER 9 - SUMMARY

The development of the index to fire incidence allowed for examination of the relative influence of fire upon forest vegetation composition within upland forests in Algonquin Park. In the process of developing this index it was shown, using historical data, that forest types in Algonquin differ significantly in terms of fire incidence. For example, the data show that red pine and jack pine have a significantly higher fire incidence than poplar, hemlock, and sugar maple. As well, it was found that the tolerant hardwood forest as a unit has a significantly lower fire incidence than the intolerant hardwood and pine forest. The data for both species and forest types also form a smooth gradient from low to high fire incidence probability.

The importance of this fire gradient in relation to present forest composition in Algonquin Park was verified through multivariate studies which related both overstory and understory vegetation to environmental conditions. An environmental complex consisting of 13 factors was identified as having a significant influence upon the composition of the forest overstory. The variation in forest overstory composition is best explained by a fire-soil moisture gradient in which (1) the two influences are inversely related and (2) fire is most likely of greater importance in maintaining current overstory composition.

At the low fire-high moisture end of the gradient the landscape is dominated by species characteristic of the tolerant hardwood forest. At the high fire-low moisture end of the gradient the landscape is dominated by the pine forest and occurring at an intermediate position along the gradient are the intolerant hardwood communities. The relationship between fire and overstory composition in Algonquin is influenced by variations in foliage flammability, tree and stand structure, reproductive strategies, anatomical features, and natural firebreaks. Although they are affected to some degree by vegetation, the variation in total soil nitrogen, soil organic matter, and soil pH also plays a role in the distribution of overstory species.

Relative to the variation explained in overstory species composition by the ordination (87%), less of the variation in understory species composition was explained through ordination (38%). This is most likely because (1) there were over five times more species in the understory compared to the overstory which complicates ordination, and (2) the overstory was sampled more subjectively than the understory. An environmental complex consisting of nine factors was identified as having a significant influence upon the composition of the forest understory. Unlike the overstory composition of upland forests in Algonquin Park, the variation in understory composition is most highly correlated with light, and with fire as a secondary factor.

Given the methods and objectives of this study only broad understory-overstory associations could be addressed. The major feature of these associations in Algonquin is the unique quality of the understory composition within the tolerant hardwood forest type and the sugar maple dominance-type relative to the other forest and dominance-types. Also, biomass of the sugar maple canopy was found to be directly related to understory composition variation. This most likely is due to the effect of the sugar maple canopy on the amount of light reaching the forest floor.

Aside from human influence, the single most important factor influencing the future of Algonquin's upland forest composition is the occurrence of naturally-caused fire. It is particularly important in maintaining overstory composition within the pine communities and, to a lesser extent, the poplar communities. This, however, is not to discount the importance of fire within the understory of these communities. Those understory species which are known to be associated with the incidence of fire (e.g. Corylus cornuta, Vaccinium angustifolium, Pteridium aquilinum, Maianthemum canadense, and Aster macrophyllus) are most abundant in those overstory dominance types in Algonquin which are also most highly associated with fire, namely the pine and poplar dominance-types. Assumming that the effects of fire render a competitive advantage to these understory species, fire suppression in Algonquin Park may also significantly alter the composition of the understory within the pine and poplar forest ecosystems.

REFERENCES

Adams, F. D. and A. E. Barlow. 1910. Geology of the Haliburton and Bancroft Areas, Memoir #6. Canadian Department of Mines, Ottawa, Ontario.

Ahlgren, C. E. 1960. Some effects of fire on reproduction and growth of vegetation in Northeastern Minnesota. Ecology 41:431-445.

Ahlgren, C. E. 1974. Effects of fire on temperate forests: North Central United States. In: Fire and Ecosystems, Ed. by T.T. Kozlowski and C.E. Ahlgren, Academic Press, New York. pp. 195-223.

Ahlgren, C. E. 1976. Regeneration of red pine and white pine following wildfire and logging in northeastern Minnesota. J. For. 74:135-140.

Ahlgren, I. F. and C. E. Ahlgren. 1960. Ecological effects of forest fires. Bot. Rev. 26:483-533.

Alban, D. H., D. A. Perala, and B. E. Schlaegel. 1978. Biomass and nutrient distribution in aspen, pine, and spruce stands on the same soil type in Minnesota. Can. J. For. Res. 8:290-299.

Alway, F. J. and P. R. McMiller. 1933. Interrelationships of soil and forest cover on Star Island, Minnesota. Soil Sci. 36:281-295.

Allee, W. C., A. E. Emerson, O. Park, and K. P. Schmidt. 1949. Principles of Animal Ecology. W. B. Saunders Co., Philadelphia. 838 pp.

Anderberg, M. R. 1973. Cluster Analysis for Applications. Academic Press, New York.

Anderson, H. W. 1969. Ecology of Algonquin Park. Ont. Dept. Lands and Forests. Typewritten manuscript. 14 pp.

Angevine, M. W. and S. N. Handel. 1986. Invasion of forest floor space, clonal architecture, and population growth in the perennial herb Clintonia borealis. J. Ecol. 74:547-560.

Archives of Ontario. 1930-1979. Provincial Fire Reports - Record Group 1, Series J-1. Archives of Ontario, Ministry of Citizenship and Culture, Toronto, Ontario.

Atmospheric Environment Service. 1982. Canadian Climate Normals - Temperature and Precipitation for Ontario. Canadian Climate Centre, Environment Canada, Downsview, Ontario.

Bailey, A.W. and C.E. Poulton. 1968. Plant communities and environmental interrelationships in a portion of the Tillamook burn, Northwestern Oregon. Ecology 49:1-13.

Ball, D. F. 1964. Loss on ignition as an estimate of organic matter and organic carbon in non-calcareous soils. J. Soil. Sci. 15:84-92.

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1980. Terrestrial plant ecology. Benjamin/Cummings Publ. Co., Menlo Park, Calif.

Barden, L. S. and F. W. Woods. 1974. Characteristics of lightning fires in southern Appalachian forests. Proc. Tall Timbers Fire Ecology Conference 13:345-361.

Barkham, J. P. 1980. Population dynamics of the wild daffodil (Narcissus pseudonarcissus). I. Clonal growth, seed reproduction, mortality and the effects of density. J. Ecol. 69:607-633.

Bartos, D. L. and W. F. Mueggler. 1981. Early succession in aspen communities following fire in western Wyoming. J. Range Mngmt. 34:315-318.

Bazzaz, F. A. 1979. The physiological ecology of plant succession. Ann. Rev. Ecol. Syst. 10:351-371.

Beaufait, W. R. 1960. Some effects of high temperatures on the cones and seeds of jack pine. For. Sci. 6:194-199.

Billings, W.D. 1952. The environment complex in relation to plant growth and distribution. Quat. Rev. Biol. 27:251-265.

Boerner, R. E. J. 1981. Forest structure dynamics following wildfire and prescribed burning in the New Jersey Pine Barrens. Am. Midl. Nat. 105:321-333.

Boerner, R. E. J. 1982. Fire and nutrient cycling in temperate ecosystems. BioScience 32:187-92.

Boerner, R. E. J. 1984. Forest composition on the Lake Erie Islands. Am. Midl. Nat. 111:173-184.

Borchert,M.and M. Hibberd. 1984. Gradient analysis of a north slope motane forest in the western tranverse ranges of southern California. Madrona 31:129-139.

Bormann, F. H. and G. E. Likens. 1979a. Catastrophic disturbance and the steady-state in northern hardwood forests. Amer. Sci. 67:660-669.

Bormann, F. H. and G. E. Likens. 1979b. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York. 253 pp.

Bormann, F.H., G.E. Likens, T.G. Siccama, R.S. Pierce, and J.S. Eaton. 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. Ecol. Monogr. 44:255-277.

Bormann, F. H., T. G. Siccama, G. E. Likens and R. H. Whittaker. 1970. The Hubbard Brook Ecosystem Study: Composition and dynamics of the tree stratum. Ecol. Monogr. 40:373-388.

Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. Adv. Genet. 13:115-155.

Brady, N. C. 1974. The Nature and Properties of Soils. MacMillan Publishing Co., Inc., New York. 639.

Bratton, S. P. 1976. Resource division in an understory herb community: responses to temporal and microtopographic gradients. Am. Midl. Nat. 110:679-693.

Braun, E. L. 1950. Deciduous Forests of Eastern North America. Hafner Press, New York. (reprinted 1974). 596 pp.

Bray, J. R. and E. Gorham. 1964. Litter production in forests of the world. Adv. Ecol. Res. 2:101-157.

Bremner, J. M. 1965. Total nitrogen. In: Methods of Soil Analysis, Part 2. Ed. by C. A. Black. American Society of Agronomy, Madision, Wisc. pp. 1149-1178.

Brown, D. M., G. A. Mckay and L. J. Chapman. 1980. The climate of southern Ontario. Climatological Studies No. 5, Atm. Env. Serv., Environment Canada, Hull, Quebec, Canada.

Brown, J. H., Jr. 1960. The role of fire in altering the species composition of forests in Rhode Island. Ecology 41:310-316.

Brown, R.T. and J.T. Curtis. 1952. The upland conifer-hardwood forests of northern Wisconsisn. Ecol. Monogr. 22:217-234.

Brown, W. G. E. and O. S. Lacate. 1959. Rooting habits of white and red pine. Canada Dept. North Affairs and Nat. Res., Forestry Br., For. Res. Div. Mines Report.

Brown, W. J. 1980. Forest Management Plan - Algonquin Provincial Park. Algonquin Forestry Authority, Huntsville, Ontario. 84 pp.

Brunton, D. F. 1981. A managment model for Algonquin Region Nature Reserves: an analysis and classification of life science data and the development of management strategies. Ont. Min. Nat. Res., Parks and Recreation Branch, Queen's Park, Toronto, Ontario.

Brush, S. 1974. Should the history of science be x-rated? Science 183:1164-1172.

Bryant, J. P., F. S. Chapin III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357-368.

Burgess, D. M. and I. R. Methven. 1977. The historical interaction of fire, logging and pine: A case study at Chalk River, Ontario. Petawawa For. Exp. Stn. Inf. Rep. PS-X-66. 17 pp.

Caldwell, M. M. 1987. Plant architecture and resource competition. In: Potentials and Limitations of Ecosystem Analysis, Ed. by E. D. Schulze and H. Zwolfer. Springer-Velag, New York. pp. 164-179.

Cameron, H. 1953. Melting point of the bonding material in lodgepole and jack pine cones. Can. Dept. Resource and Development For. Br., For. Res. Div., Silv. Leaflet No. 86.

Canada Soil Survey Committee. 1978. The Canadian System of Soil Classification. Research Branch, Canada Dept. Agriculture, Ottawa. 164pp.