FIRE, SUCCESSION AND COMMUNITY STRUCTURE IN A RED AND WHITE PINE STAND

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ABSTRACT

Two consecutive annual, low intensity experimental fires were conducted in a 90-year-old red and white pine stand. Damage to the overstory and consumption of the organic layer were minimal, the balsam fir understory was eliminated and shrubs and herbaceous species were considerably reduced. However changes one year after the fires, relative to the prefire condition three years earlier, amounted largely to changes in species density and biomass rather than changes in species composition. Thus changes were largely quantitative rather than qualitative, indicating no radical alteration of the ecosystem but merely creation of an environment more conducive to pine regeneration.

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INTRODUCTION

The purpose of this study was twofold; (i) to assess the feasibility of using fire in the red and white pine cover type to manipulate forest succession towards maintenance of pine; and (ii) to assess the impact of the fire on the vegetative components of the ecosystem in terms of abundance, diversity, succession and structure.

Considerable research has gone into the ecological effects of fire but the literature suffers from two limitations; (i) little indication is given of the intensity or frequency of the fires discussed so that considerable conflict exists between the results of different studies; and (ii) the great majority have been concerned with sites where a major portion of the vegetation has been removed either by prefire logging or by the fire itself. In contrast, the present study is concerned with effects associated with a relatively undisturbed overstory.

Both red and white pine are essentially subclimax or fire climax species (Maissurow 1935, Candy 1939, Horton and Bedell 1960) with regeneration and perpetuation being largely dependent on a seed supply coupled with disturbance, preferably fire. The essential consequence of fire in nature is to influence forest succession by creating conditions to which certain species have become adapted. It is natural, therefore, to suppose that fire might offer a useful silvicultural technique for the establishment and survival of natural pine regeneration.

In a series of experimental fires beneath red and white pine, Van Wagner (1963) found seedling counts after one year to be positively correlated with the severity of the fire, exposure of mineral soil and reduction of shrub weights per acre. Lightly burned plots, however, still contained appreciably more conifer seedlings than unburned plots after one year.

Achievement of a limited silvicultural objective, however, is no longer an adequate criterion for assessment of a practice. This must be done in terms of such parameters as changes in community structure and total site productivity, since, in an era of increasing human pressure and decreasing natural resources, questions relating to efficiency of energy production and aesthetic values take on increasing significance.

STAND AND SITE DESCRIPTION

The stand was located on the Petawawa Forest Experiment Station, Chalk River, Ontario (46°00'N and 77°26'W) which is situated in the L4C or Middle Ottawa Section of the Great Lakes-St. Lawrence Forest Region (Rowe 1959). The climate is continental with a mean annual temperature of 4.2°C and a mean annual preciptitation of 78.8 cm of which 55.0 cm falls as rain. The site aspect was westerly with a substrate composed of a thin drift veneer of glacial till over bedrock composed of Precambrian granitic gneisses.

The stand itself was approximately 90 years of age and probably originated from an extensive fire which occurred in 1878 (Smithers 1954). Composition of the stand, based on all trees exceeding five metres in height, may be found in Table 1 where it can be seen that the pines constituted 84 percent of the total basal area which amounted to 39 m^2h^{-1}. The diameter range of all trees fell between 6 cm and 52 cm with 77 percent of the pines falling between 16 and 36 cm.

METHOD AND MATERIALS

Due to the heterogeneity of the area and the practical limitations associated with fire it was decided that any attempt at replication was impractical. A single area was therefore chosen on which to carry out an intensive study.

An area of 0.41 hectares was marked out in the pine stand and surrounded with a bulldozed fire line. It was subdivided into four quadrants

Table 1. Stand description based on number of trees and basal area per hectare for all trees exceeding 5 meters in height.

Species	No. of Trees per Hectare	Basal Area m^2ha^{-1}	Basal Area Percent
Pinus resinosa	350	22.91	59.0
Pinus strobus	180	9.66	24.9
Picea glauca	140	2.64	6.8
Abies balsamea	70	0.40	1.0
Betula papyrifera	50	1.44	3.7
Quercus rubra	25	1.11	2.8
Populus tremuloides	10	0.41	1.0
Acer rubrum	15	0.22	0.5
	840	38.79	

within each of which was distributed, with the aid of a coordinate system, 25 random 1 m^2 and 0.1 m^2 nested permanent plots. Shrubs and saplings were tallied on the 1 m^2 plots and herbs on 0.1 m^2 plots except for bracken fern (Pteridium aquilinum (L.) Kuhn) and sarsaparilla (Aralia nudicaulis L.), which, because of their size, were tallied on the 1 m^2 plots. Density or number of stems was based on rooted stems and thus does not necessarily correlate with whole plants. Relative values are based on the percentage contribution of a single species relative to the contribution of all species combined.

Vegetation was tallied in the latter part of August in 1969, 1970, 1971, and 1972. (Fires were conducted on June 15 in 1970 and 1971). In order to convert density data to biomass, average individual weights per species were obtained by random destructive sampling at the time of the last collection in August 1972. Samples for application to the prefire condition were collected from the unburned portion of the stand. Average individual weights of the herbaceous species were based on 50 to 300 individuals, while those of tree and shrub species were based on 30 individuals per height class for the 0.3, 0.6 and 1.0 meter height classes and 10 individuals per height class for the 2.0, 3.0, 4.0 and 5.0 meter height c lasses.

Vegetation was divided into two strata for analysis, an upper stratum exceeding 5 meters in height and containing tree species only and a lower stratum under 5 meters in height composed of tree, shrub and herbaceous species.

Three of the 100 plots remained unburned and four more were lost over the course of the investigation so that all results are based on a total of 93 plots.

The total study area was burned twice, in June 1970 and 1971, and on both occasions an attempt was made to burn the area with a headfire. Lines of fire were lit perpendicular to the wind direction and across the windward side and the centre of the area. Soon after ignition, however, winds became somewhat light and variable necessitating the use of several lines of fire. Because of this problem, it was not possible to characterise the fires as either headfires or backfires. Approximately 97% of the area was covered by fire and only 3 plots out of 100 remained unburned.

Fuel consumption was based on litter and duff (L and F+H layers) depths and weights obtained from 40 random locations before and after the fires by the use of a 0.1 m^2 template. Fuel moisture contents were based on 10 litter and 20 duff samples taken immediately before the fires. All fuel material was ovendried in a forced draught oven at 100°C for 24 hours to obtain dry weights. Rate of fire spread was estimated by timing the arrival of fire at a line of stakes spaces 10 metres apart.

All crown scorched pines were individually tagged and percentage crown scorch recorded for future application to growth effects. Overstory mortality was checked for all trees during the three years after the first fire.

RESULTS AND DISCUSSION

The Fires

Both fires were gentle on the average consuming only 3655kg ha^{-1} and 4425kg ha^{-1} of litter and leaving the duff untouched, the difference between prefire and postfire depths and weights of the latter being less than the standard error. The total reduction in depth of the organic layer was approximately 30 percent while the reduction in weight amounted to only 17 percent of the total. In addition to the litter, all vegetation less than 30 cm in height was consumed as well as the foliage of all balsam fir saplings. The total fuel consumption for the two fires was 5891 kg ha^{-1} and 4650 kg ha^{-1} with living vegetation contributing 21 percent and 5 percent of the totals respectively.

Both fires occurred under the same fire weather index (FWI) of 14 and the calculated intensities were virtually identical being 18.2 and 18.7 kcal $sec^{-1}m^{-1}$. The higher fuel consumption of the first fire was balanced by the faster rate of spread of the second fire, a result of a lower relative humidity, drier litter and greater windspeed. The calculated intensities, however, reflect only the average fire conditions and in fact the first fire resulted in some overstory damage due to localized but fairly widespread peaks of intensity. These were due to a clumped distribution of balsam fir saplings which resulted in live branches close to the ground and a foliage bulk density great enough to carry fire upwards. Wherever these concentrations of fire occurred, therefore, flame heights were raised from less than 30 cm to over 3 metres with a much increased energy output rate per unit ground area and scorching of overstory crowns. The increase in intensity was not so much a product of the increased fuel loading, which amounted to only 0.04 gm cm^{-2}, but to the rate of combustion of this fuel, which, due to its arrangement or bulk density, burned much more rapidly than an equivalent quantity of ground fuel.

Vegetation - Upper Stratum (>5m)

The first fire (1970) resulted in appreciable damage to the trees on the site. A total of 24 percent of the trees were killed but this represented only 8 percent of the basal area of which 6 percent was contributed by species other than the pines. The cause of injury and mortality was largely a function of species characteristics, particularly bark thickness. Damage to mature pines for example was largely a question of the degree of crown scorch due to localized peaks of fire intensity, which resulted in a 2 percent basal area mortality, while damage to spruce and fir was largely a consequence of cambial girdling, which resulted in a 66 percent basal area mortality. White birch displayed considerable resistance to this low intensity fire since the only tree killed was as a result of the ignition of a large nest in the major crotch of the crown. Other birches were scorched to a height of 10 meters, due to the flammability of the outer bark, with no visible effects on subsequent growth.

The second fire (1971) resulted in no further mortality in this upper stratum.

Vegetation - Lower Stratum (<5m)

The response of this stratum over the four-year period is analysed in terms of cumulative number of species, presence and absence, density (number of stems per unit area), relative density (the number of stems of a species relative to the total number of stems as a percent), percent frequency (the number of plots in which a species occurs as a percent of the total number of plots), biomass (weight in grams), relative biomass (weight of a species relative to the total weight of all species as a percent) and individual plant weight.

The number of species declined rapidly based on counts two and one-half months after each fire. From 35 species in 1969, the total dropped to 23 species in 1970 and 16 species in 1971. However, after one undisturbed year in 1972 the number of species rose to 29. It is clear from a comparison of the 1969 and 1972 species-area curves (Fig. 1) that, though the numbers of species are rapidly approaching initial values, the distribution or frequency of the species differs considerably. In 1969, 88 percent of the final total from 93 quadrats was achieved within 28 quadrats whereas in 1972 it required 63 quadrats to achieve the same percentage.

Presence and absence of species present in the lower vegetation stratum over the four-year period is given in Table 2. Two tree species, white spruce (*Picea glauca* (Moench) Voss) and red oak (*Quercus rubra* L.), and two herbaceous species, yellow clintonia (*Clintonia borealis* Ait.) and trailing-arbutus (*Epigaea repens* L.), were eliminated by the two fires, while woolly panic-grass (*Panicum lanuginosum* Ell.), ground-pine (*Lycopodium obscurum* L.) and Bicknell Geranium (*Geranium bicknellii* Britt.) became new members of the post-fire plot community. Of these only Geranium can be

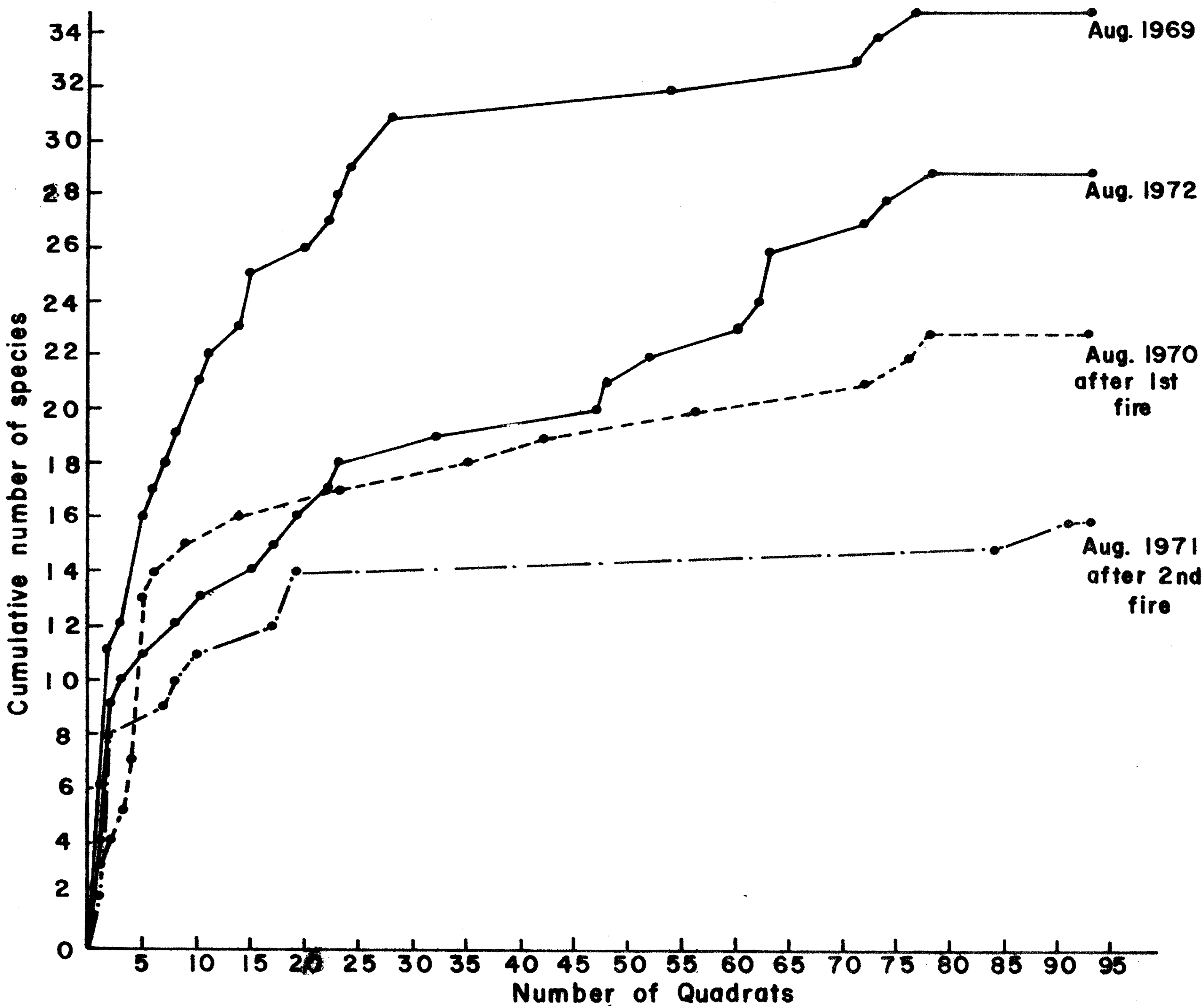

Figure 1. Species-area curves for August 1969, 1970, 1971 and 1972. Fires in June 1970 and 1971.

Table 2. Presence and absence of species in vegetation (<5m).
Fires in June 1970 and 1971.

1969 - 1972

\+ = presence; - = absence

Trees < 5m	Prefire	Postfire		
	1969	1970	1971	1972
Abies balsamea (L) Mill	+	-	-	+
Acer rubrum L.	+	+	+	+
Betula papyrifera Marsh.	-	+	-	-
Pinus strobus L.	+	-	+	+
Pinus resinosa Ait.	+	-	-	+
Picea glauca (Moench) Voss	+	-	-	-
Populus tremuloides Michx.	+	-	-	+
Prunus pennsylvanica L.f.	-	+	-	-
Quercus rubra L.	+	+	-	-
Shrubs				
Amelanchier sp.	+	+	-	+
Corylus cornuta Marsh.	+	+	+	+
Diervilla lonicera Mill.	+	+	+	+
Lonicera canadensis Bartr.	+	+	+	+
Rubus ideaus var. strigosus (Michx.) Maxim	+	+	-	+
Vaccinium sp.	+	+	+	+
Viburnum cassinoides L.	+	+		+
Herbs				
Aster macrophyllus L.	+	+	+	+
Aralia nudicaulis L.	+	+	+	+
Clintonia borealis Ait.	+	-	-	-
Cornus canadensis L.	+	+	+	+
Epigaea repens L.	+	-	-	-
Gaultheria procumbens L.	+	+	+	+
Geranium bicknellii Britt.	-	-	-	+
Kalmia angustifolia L.	+	-	+	+
Linnaea borealis L.	+	+	-	+
Lycopodium obscurum L.	-	-	-	+
Maianthemum canadense Desf.	+	+	+	+
Pteridium aquilinum (L.) Kuhn	+	+	-	+
Trientalis borealis Raf.	+	+	-	+
Viola sp.	+	+	-	+
Waldsteinia fragarioides (Michx.) Tratt.	+	+	+	+

considered as a true post-fire invader. The other two, though originally absent from the plots, were present in the stand. None of the above species however was particularly important in terms of numbers or weight contribution.

Within the ten-week period following the first fire six shrub species, one tree species and one herbaceous species increased their actual stem number as against the previous year at the same time. The shrubs were blueberry (Vaccinium sp.) serviceberry, beaked hazel (Corylus cornuta Marsh.) bush-honeysuckle (Diervilla lonicera Mill.), witherod viburnum (Viburnum cassinoides L.) and Canada honeysuckle (Lonicera canadensis Bartr.), the tree species red maple (Acer rubrum L.) and the herbaceous species big-leaf aster (Aster macrophyllus L.). All of the above species suffered a decrease in stem numbers after the second fire except bush honeysuckle which displayed another increase. Red maple was the only other species to maintain a stem number above the prefire level (Table 3).

After one undisturbed growing season following two successive annual fires blueberry, serviceberry, beaked hazel and big-leaf aster had decreased in numbers as compared to the prefire condition, while red maple, bush-honeysuckle, witherod viburnun and Canada honeysuckle increased in numbers. These increases in stem numbers were not reflected in a wider distribution since percent frequencies were reduced or remained relatively unchanged except for Canada honeysuckle which increased from 1 to 5 percent. The remaining species all declined in numbers after the first fire, but Canada maianthemum (Maianthemum canadense Desf.) maintained its dominance throughout the study period (Table 4).

Table 3. Changes in density (no. of stems) per hectare of lower stratum vegetation (< 5m) over a four year period. Data collected in August of each year, fires in June 1970 and 1971.

Species	Density			
	Prefire	Postfire		
	1969	1970	1971	1972
Maianthemum canadense Desf.	6731	2387	1032	5666
Gaultheria procumbens L.	2258	881	462	966
Cornus canadensis L.	1602	247	129	301
Linnaea borealis L.	1969	10	-	10
Waldsteinia fragarioides (Michx.) Tratt.	1236	645	161	161
Vaccinium sp.	1118	1419	354	709
Pteridium aquilinum (L.) Kuhn	232	127	153	249
Aralia nudicaulis L.	225	172	21	110
Aster macrophyllus L.	225	430	161	215
Abies balsamea (L.) Mill.	194	-	-	8
Acer rubrum L.	173	285	197	209
Viola sp.	150	10	-	32
Trientalis borealis Raf.	107	10	-	10
Epigaea repens L.	96	-	-	-
Amelanchier sp.	78	90	-	38
Kalmia angustifolia L.	64	-	64	107
Pinus strobus L.	58	-	1	6
Clintonia borealis Ait.	43	-	-	-
Corylus cornuta Marsh.	41	52	33	35
Diervilla lonicera Mill.	15	17	34	64
Picea glauca (Moench) Voss	15	-	-	-
Viburnum cassinoides L.	8	17	-	20
Quercus rubra L.	6	1	-	-
Rubus idaeus var. strigosus (Michx.) Maxim	3	4	-	1
Lonicera canadensis Bartr.	2	13	6	8
Populus tremuloides Michx.	2	-	-	3
Pinus resinosa Ait.	1	-	-	2
Prunus pennsylvanica L.f.	-	45	-	-
Betula papyrifera Marsh	-	10	-	-
Lycopodium obscurum L.	-	-	-	10
Geranium bicknellii Britt.	-	-	-	10

Table 4. Changes in relative density (no. of stems of a species relative to the total stems of all species x 100) of lower stratum vegetation (< 5m) over a four year period. Data collected in August of each year, fires in June of 1970 and 1971.

Species	Relative Density Prefire 1969	Postfire 1970	1971	1972
Maianthemum canadense Desf.	41.42	34.73	36.74	63.31
Gaultheria procumbens L.	13.89	12.82	16.44	10.79
Cornus canadensis L.	9.86	3.59	4.59	3.36
Linnaea borealis L.	9.65	0.14	-	0.11
Waldsteinia fragarioides (Michx.) Tratt.	7.60	9.38	5.73	1.80
Vaccinium sp.	6.88	20.64	12.60	7.92
Pteriduim aquilinum (L.) Kuhn	1.43	1.85	5.45	2.78
Aralia nudicaulis L.	1.38	2.50	0.75	1.23
Aster macrophyllus L.	1.38	6.26	5.73	2.40
Abies balsamea (L.) Mill	1.19	-	-	0.09
Acer rubrum L.	1.06	4.15	7.01	2.34
Viola sp.	0.92	0.14	-	0.36
Trientalis borealis Raf.	0.66	0.14	-	0.11
Epigaea repens L.	0.59	-	-	-
Amelanchier sp.	0.48	1.31	-	0.42
Kalmia angustifolia L.	0.39	-	2.28	1.20
Pinus strobus L.	0.36	-	0.04	0.07
Clintonia borealis Ait.	0.26	-	-	-
Corylus cornuta Marsh.	0.25	0.76	1.17	0.39
Diervilla lonicera Mill.	0.09	0.25	1.21	0.72
Picea glauca (Moench) Voss	0.09	-	-	-
Viburnum cassinoides L.	0.05	0.25	-	0.22
Quercus rubra L.	0.04	0.01	-	-
Rubus idaeus var. strigosus (Michx.) Maxim	0.02	0.06	-	0.01
Lonicera canadensis Bartr.	0.01	0.19	0.21	0.09
Populus tremuloides Michx.	0.01	-	-	0.03
Pinus resinosa Ait.	0.01	-	-	0.02
Prunus pennsylvanica L. f.	-	0.65	-	-
Betula papyrifera Marsh.	-	0.14	-	-
Lycopodium obscurum L.	-	-	-	0.11
Geranium bicknellii Britt.	-	-	-	0.11

In terms of distribution only five species had percent frequencies in excess of 50 percent before the fires, namely Canadian maianthemum, sarsaparilla (Aralia nudicaulis L.), bracken fern (Pteridium aquilinum (L.) Kuhn.), red maple and balsam fir. Of these species only one bracken fern increased its percent frequency, from 56 percent in 1969 to 70 percent in 1972 (Table 5).

A graphical group summary (Figure 2) of herbs, shrubs and saplings indicates the somewhat different responses of these three groups of vegetation to fire. Herbs were immediately reduced to one third of their original population by the first fire, further reduced by the second, but recovered strongly after one undisturbed growing season, trebling their population to a value over one half the original. Shrubs, on the other hand, demonstrated a much different response, increasing their density by one third after the first fire, but being considerably reduced to less than one third the original population after two fires. Recovery was slower than that for herbs, resulting in a doubling of the population to a value approximately 70 percent of the original. Saplings and seedlings suffered only a one third reduction in population after one fire but this was a result of the increase in population of red maple, a species with strong sprouting ability. The sapling and seedling population was further reduced after the second fire with a slow recovery to approximately one half the original population. If red maple were not included in the calculations the sapling response would have appeared to be accentuated. After one fire the total population was reduced to one fifth the original value, after two fires it was virtually eliminated and after an undisturbed growing season recovery was slow, rising to only 6 percent of the original

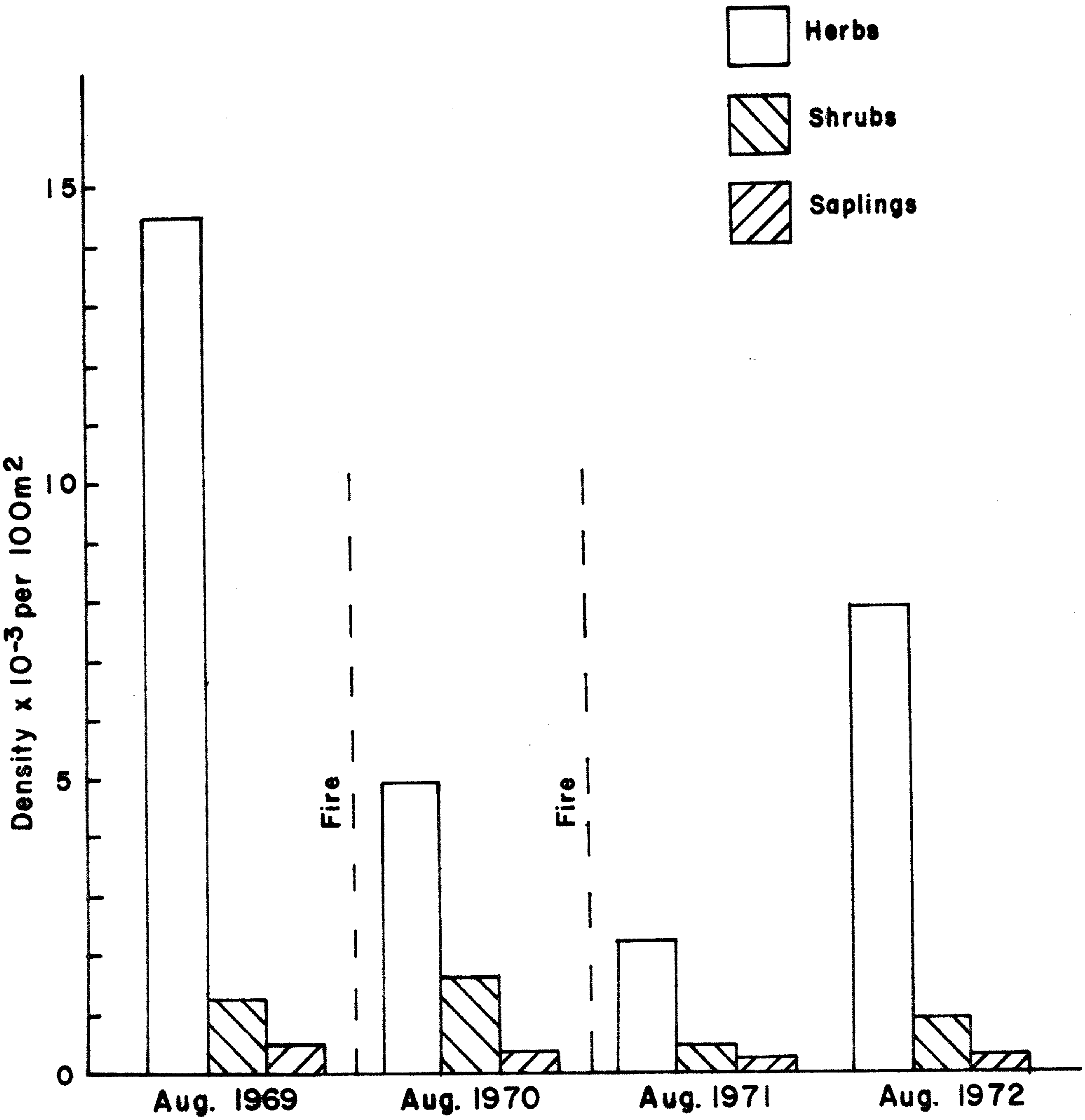

Figure 2. Change in density of herbs, shrubs and saplings over time. Fires in June 1970 and 1971.

Table 5. Changes in percent frequency of lower stratum vegetation (<5m) over a four year period. Data collected in August of each year, fires in June 1970 and 1971.

Species	Percent Frequency Prefire 1969	Postfire 1970	1971	1972
Maianthemum canadense Desf.	85	67	34	80
Abies balsamea (L.) Mill.	68	-	-	2
Acer rubrum L.	60	54	41	45
Pteridium aquilinum (L.) Kuhn	56	46	55	70
Aralia nudicaulis L.	56	52	13	46
Gaultheria procumbens L.	40	33	26	37
Cornus canadensis L.	39	18	9	15
Pinus strobus L.	36	-	1	5
Vaccinium sp.	31	39	20	32
Waldsteinia fragarioides (Michx.) Tratt	29	15	9	9
Amelanchier sp.	23	20	-	13
Aster macrophyllus L.	15	18	10	12
Linnaea borealis L.	14	1	-	1
Corylus cornuta Marsh.	12	12	11	11
Picea glauca (Moench) Voss	10	-	-	-
Diervilla lonicera Mill.	8	7	5	7
Trientalis borealis Raf.	6	1	-	1
Quercus rubra L.	6	1	-	-
Kalmia angustifolia L.	3	-	1	2
Viola sp.	2	1	-	2
Epigaea repens L.	2	-	-	-
Clintonia borealis Ait.	2	-	-	-
Viburnum cassinoides L.	2	1	-	2
Populus tremuloides Michx.	2	-	-	2
Rubus idaeus var. strigosus (Michx.) Maxim	1	1	-	1
Lonicera canadensis Bartr.	1	5	2	3
Pinus resinosa Ait.	1	-	-	2
Prunus pennsylvanica L.f.	-	5	-	-
Betula papyrifera Marsh.	-	1	-	-
Lycopodium obscurum L.	-	-	-	1
Geranium bicknellii Britt.	-	-	-	1

prefire population. These differences are a function of regeneration tactics, those species with sprouting and suckering ability or perennating buds beneath the surface having a distinct initial competitive advantage over those species with regeneration and survival dependent upon seed.

Although density is a valuable measure, providing an index of individual response, it is limited in making comparisons between individuals or species with a considerable size differential, because in this case contribution to present community structure is more a function of mass than numbers. Biomass or dry weight of plant material per unit area was therefore estimated for the prefire condition in 1969 and the postfire condition in 1972.

The prefire contribution of balsam fir in 1969 overshadowed that of all the other species with a weight of 2017 kg ha^{-1} amounting to 66 percent of the total. The next most important species in terms of biomass was red maple with a relative contribution of only 6.5 percent followed by bracken fern with approximately 5 percent (Table 6). By August 1972, after the two consecutive annual fires in 1970 and 1971, the situation had changed radically as a result of the 99.8 percent reduction in balsam fir. The dominant postfire species was bracken fern with a relative weight of 36 percent, followed by blueberry with 9 percent and Canada maianthemum with 8 percent.

The reduction in biomass of most of the shrubs was largely a consequence of an altered size distribution, rather than a reduction in numbers.

Table 6. Comparison between 1969 and 1972 of lower stratum vegetation (<5m) based on weight in kg ha^{-1} and a relative weight contribution in excess of 0.05. Fires in June 1970 and 1971.

Species	Wt kg ha^{-1}		% Relative Wt.	
	1969	1972	1969	1972
Abies balsamea (L.) Mill	2016.6	4.8	65.85	2.18
Acer rubrum L.	199.4	15.5	6.51	7.04
Pteridium aquilinum (L.) Kuhn	150.2	78.5	4.90	35.68
Vaccinium sp.	116.3	20.5	3.80	9.32
Amelanchier sp.	114.6	8.4	3.74	3.82
Gaultheria procumbens L.	101.6	8.6	3.32	3.91
Picea glauca (Moench) Voss	89.3	-	2.92	-
Maianthemum canadense Desf.	47.1	17.0	1.54	7.73
Aralia nudicaulis L.	42.6	9.3	1.39	4.23
Corylus cornuta Marsh.	41.0	7.0	1.34	3.18
Cornus canadensis L.	35.2	3.9	1.15	1.77
Aster macrophyllus L.	17.1	16.7	0.56	7.59
Pinus strobus L.	14.4	0.5	0.47	0.23
Linnaea borealis L.	14.1	-	0.46	-
Populus tremuloides Michx	13.8	14.3	0.45	6.50
Waldsteinia fragarioides (Michx.)Tratt	13.6	1.4	0.44	0.64
Viburnum cassinoides L.	13.2	3.1	0.43	1.41
Epigaea repens L.	5.3	-	0.17	-
Kalmia angustifolia L.	4.3	4.3	0.14	1.95
Rubus idaeus var. strigosus (Michx.) Maxim	3.4	-	0.11	-
Diervilla lonicera Mill.	2.9	4.9	0.09	2.23
Clintonia borealis Ait.	1.7	-	0.06	-
Viola sp.	-	0.4	-	0.18
Lonicera canadensis Bartr.	-	0.2	-	0.09
Pinus resinosa Ait.	-	0.2	-	0.09
Others	4.9	0.5	0.16	0.23
Total	3062.4	220.0	100.00	100.00

In order to ascertain the major influence on the herbaceous biomass reduction individual weights of species present in both 1969 and 1972 were obtained (Table 7).

An analysis of these individual weights indicated that for bracken fern and sheep laurel biomass reduction was purely a function of the reduction in weight per individual, for barren-strawberry it was a reduction in numbers while for sarsaparilla, blueberry, wintergreen, bunchberry (Cornus canadensis L.) and Canada maianthemum both numbers and weight per individual were responsible. Big-leaf aster occupied a unique position in that number of individuals, weight per individual and therefore total biomass was the same in 1969 (prefire) and 1972. In other words this species appeared to remain relatively unaffected by two successive annual fires followed by one undisturbed growing season.

Although the postfire community of lower stratum vegetation had fewer species, fewer individuals and a lower biomass, that biomass was much more evenly distributed among the existing species. In other words the lower total biomass was accompanied by a convergence of relative abundances.

This change in species richness or variety and relative abundances can be expressed much more succintly by a numerical index derived from information theory. The information content of any system is proportional to the logarithm of the number of possible states the system can assume. If the system consists of a number of individuals of several different types, the information content can be considered as a measure of uncertainty about the system or the probability of predicting the type of the next individual.

Table 7. Average weights of individuals of herbaceous species contributing more than 0.05 percent to the total weight and present in both 1969 and 1972. Averages based on 50 to 300 individuals.

Fires - June 1970 and 1971. Weights in August 1972.

Species	Avg. Wt. per Individual gm.		Post fires as per cent of unburned
	Unburned	After two annual fires	
Pteriduim aquilinum (L.) Kuhn	6.47	3.15	48
Aralia nudicaulis L.	1.89	0.85	44
Vaccinium sp.	1.04	0.29	27
Aster macrophyllus	0.76	0.78	102
Kalmia angustifolia L.	0.67	0.40	59
Gaultheria procumbens L.	0.45	0.09	20
Cornus canadensis L.	0.22	0.13	59
Waldsteinia fragarioides (Michx.) Tratt.	0.10	0.09	90
Maianthemum canadense Desf.	0.07	0.03	42

the greater the uncertainty or the lower the probability, the greater the information content. In other words, a system where each individual is of a different type would be one with maximum information content, whereas one where all the individuals were of one type would have minimum content. It is immediately apparent that a measure of information content would form a measure of biotic diversity since it is a composite function of both the number of species (richness) and the distribution of individuals among species (relative abundance).

A useful measure of diversity or information content is provided by Shannon's formula (Shannon and Weaver 1963).

$$H = - \Sigma p_i \log p_i$$

where H is a diversity index measured in what may be most simply regarded as probability units, and p_i is the proportion or probability of occurrence of the i^{th} species.

If the individuals are not of equal size (i.e. the collection is a non-stratified one containing individuals of all sizes), the diversity index will be grossly distorted. It is therefore necessary to divide non-comparable species into comparable units and this is most simply done by substituting grams of biomass for numbers of individuals present. This has the added advantage that grams of biomass may be considered roughly analogous to units of energy and that diversity would therefore be expressed in probability units per unit of energy.

On this basis therefore $p_i = \frac{b_i}{B}$, where b_i is the biomass in grams dry weight of the i^{th} species and B is the total biomass.

The values for H in 1969 and 1972, using natural logarithms ($\log_e$) were 1.5 and 2.3 respectively, indicating an appreciable increase in diversity in spite of the reduction in the total number of species. This can be explained as being due to the overwhelming weight of balsam fir and its virtual elimination from the community, which resulted in a much more even distribution of biomass, increased uncertainty, a higher information content and therefore greater diversity.

The responses of herbs, shrubs and saplings is graphically illustrated in Figure 3, which demonstrates the unchanged relationship between the three groups of vegetation in terms of density, in contrast to the radical change in terms of biomass. In the latter case the major position of the saplings before the fires was unsurped by the herbs after the fires while the shrubs doubled their relative contribution.

Although the reduction in biomass or energy capital amounted to 93 percent of the lower stratum vegetation, this was not a significant proportion of the total biomass of the system. A rough calculation indicates that the biomass of the total vegetation on the site, including trees, amounted to at least 100×10^3 kg ha^{-1}. The reduction in biomass of the subordinate vegetation was 2842 kg ha^{-1} which amounted to less than 3 percent of the total only one year after two successive annual fires.

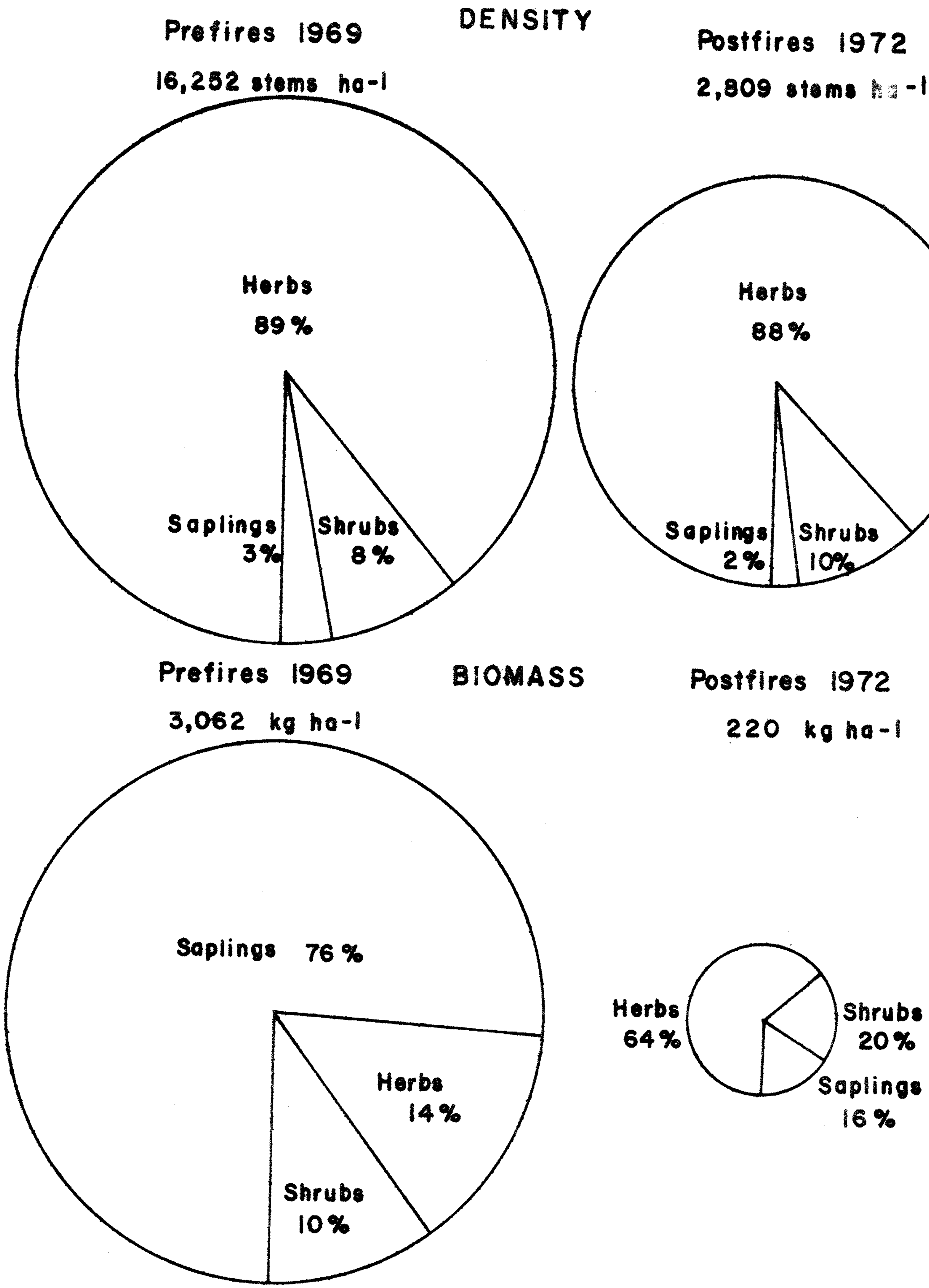

Figure 3. The effect of two annual fires on the distribution of density and biomass between three lower stratum components. Circle areas proportional to actual values. Fires in June 1970 and 1971.

CONCLUSIONS

Fire is a natural agent to which many species and associations have become adapted so that it cannot in any way be considered detrimental to the biosphere. However when considered as a force operating on or within man's environment it must be assessed by man-related criteria such as effects on site productivity, energy distribution, commercial value, recreational potential and aesthetic appeal.

The experimental fires were undoubtedly successful in that they demonstrated the practicality and safety of utilising fires in the pine cover type. Overstory damage was minimal, being confined largely to balsam fir and white spruce, the former a commercially undesirable species in this region and the latter not particularly suited to the site. The two species constituted less than 8 percent of the total basal area and were largely composed of non-commercial sized individuals. Furthermore, such fires, if incorporated into a silvicultural system would be associated with shelterwood cutting so that any damaged trees could be salvaged in a subsequent cut.

Fuel consumption of the forest floor was confined to the litter layer, leaving the duff or F and H layers virtually untouched, thereby causing minimal damage to an important conversion intermediate in the forest nutrient cycle.

Undoubtedly the major competitive component leading to suppression and mortality of pine regeneration was balsam fir, which was virtually eliminated with one fire. The secondary competition was provided by red maple plus the various shrubs. This group however, though radically reduced in biomass by one fire, was stimulated into prolific basal sprouting and increase in density indicating a strong potential for rapid reestablishment. The second fire resulted in a much reduced density and potential for reestablishment by red maple and the various shrubs, but these species were by no means eliminated, merely reduced and retarded.

A situation dominated by saplings (composed largely of balsam fir) and shrubs was converted to one dominated by herbaceous species, which offer much less competition to pine regeneration. The change, however, was largely quantitative rather than qualitative since it involved changes in relative abundance and individual weight rather than species composition.

Within a few days of each fire green shoots were making their appearance while within two weeks red maple, for example, was sprouting strongly. After one undisturbed growing season there was strong recovery of vegetation and the ground was once again carpeted with fresh litter and green vegetation, thereby obliterating most evidence of the fire. Furthermore, although the total number of species was reduced the diversity increased, thereby improving ease of access for commercial or recreational purposes and presenting more open forest vistas.

Although it is too early to assess the impact of the fires on pine regeneration the initial conditions for establishment appear to have been much improved with a reduced organic layer and reduced competition for available light, water and nutrients. However, if the overstory were left undisturbed the system would tend to revert to its original state. Some form of shelterwood cut would be necessary therefore to enable the pine regeneration to compete successfully with the more tolerant species while these were in a reduced condition as a result of the fires.

The net result of the fires, therefore, was to remove suppressed intermediate individuals and other coniferous species from the pine overstory, to remove the entire level occupied by the balsam fir understory and the larger shrubs and to leave a forest composed essentially of two sharply defined levels; an overstory composed purely of dominant and co-dominant individuals and a low-growing level composed primarily of herbaceous species plus much reduced shrubs and initial tree regeneration.

Prescribed fire therefore has demonstrated considerable potential for safe manipulation of forest structure to attain a desired end, without causing any radical or irreversible change to the forest system.

LITERATURE CITED

CANDY, P.H. 1939. Discussion on the reproduction and development of white pine. Forest. Chron. 15:90-92.

HORTON, K.W., and G.H. BEDELL. 1960. White and red pine: ecology silviculture and management. Can. Dep. N. Aff. and Nat. Res. Forest. Br. Bul. 124.

MAISSUROW, D.R. 1935. Fire as a necessary factor in the perpetuation of pine. J. Forest. 33:373-379.

ROWE, J.S. 1959. Forest regions of Canada. Can. Dep. N. Aff. Nat. Res. Forest. Br. Bul. 123.

SHANNON, C.E., and W.W. WEAVER. 1963. The mathematical theory of communication. University of Illinois Press, Urbana.

SMITHERS, L.A. 1954. Thinning in red and white pine stands at Petawawa Forest Experiment Station. Can. Dep. N. Aff. and Nat. Res. Silv. Res. Note No. 105.

VAN WAGNER, C.E. 1963. Prescribed burning experiments - red and white pine. Can. Dep. Forest. Publ. No. 1020.