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Abrams, Marc David

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EARLY PLANT SUCCESSION ON CLEARCUT AND BURNED JACK PINE SITES IN NORTHERN LOWER MICHIGAN

By

Marc David Abrams

A DISSERTATION

Submitted to
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in partial fulfillment of the requirements
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DOCTOR OF PHILOSOPHY

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ABSTRACT

EARLY PLANT SUCCESSION ON CLEARCUT AND BURNED JACK PINE SITES IN NORTHERN LOWER MICHIGAN

By

Marc David Abrams

Early plant succession was characterized on unburned clearcuts and burned sites in northern lower Michigan. Burning resulted in the establishment of numerous species not found on unburned areas. The longevity of most of these species was short, resulting in a large drop in species richness between one and two years after fire. Unburned clearcut sites were rapidly converted to *Carex* meadows with very low species diversity. Burned sites showed multiple successional patterns which included domination by shrub and early successional hardwoods, conversion to *Carex* meadows, and the establishment of jack pine. The domination of *Carex pensylvanica* on these sites indicates that it is an opportunistic species capable of monopolizing resources liberated following disturbances and suppressing or excluding other species.

Permanent plots were established on a 3-year-old jack pine clearcut prior to burning from which vegetational changes over three growing seasons were recorded and fire intensity was evaluated. Burned

blocks, compared to unburned blocks, showed greater cover of grass and tree and shrub species, lower cover of *Carex*, and a greater number of perennial herb species. Fire intensity on the burned blocks varied. Higher fire intensity resulted in lower species diversity, lower total plant cover, increased survivability of blueberry compared to *Carex*, and lower frequency of establishment of certain grass species.

Fertilization experiments on mature and clearcut jack pine sites showed that biomass of understory vegetation increased after fertilization, and that *C. pensylvanica* consistently showed an above average response.

Experiments conducted with surface soil samples from different aged jack pine sites indicated that the dominance of *Geranium bicknellii* restricted to 1-year-old burns was due to the heat-stimulated germination of buried seed.

Comparisons made by the index of similarity (S) showed that succession on each site is highly unique. Therefore, the individualistic nature of each site, rather than age following disturbance, becomes the dominant aspect in understanding the successional relationships in these communities.

I dedicate this work to my parents, who provided constant encouragement and love throughout my graduate studies, and all other friends and relatives who kept me going when the going got tough.

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I express deep appreciation to Dr. Donald I. Dickmann, who was responsible for much of my personal and professional growth during my graduate studies.

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I thank all my friends for their support over the last five years; however, Eric Menges deserves special mention for the guidance and energy he provided to my work, starting with our undergraduate days at S.U.N.Y. Binghamton.

I want to thank the North Central Forest Experiment Station of the U. S. Forest Service for their financial support of this research, and the Michigan Department of Natural Resources for administrative and field assistance they provided. Ron Wilson, Gerald Grieves, Albert Simard, and Richard Blank from these organizations deserve special mention.

Finally, I thank my parents for sharing all the joys and hardships I encountered in completing my Ph.D.

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CHAPTER I

INTRODUCTION

Jack pine (*Pinus banksiana* Lamb.) is a dominant forest type in the Lake States and has been the focus of many silvicultural and ecological studies. Jack pine is of interest to foresters because of its rapid juvenile growth, desirable wood properties for pulp and paper, its ability to grow on harsh sites, and because it provides the summer nesting habitat for the endangered Kirtland's warbler (*Dendroica kirtlandii*). Jack pine is a serotinous species that has been maintained in the Lake States by periodic fire (Heinselman 1973). In fact, the present area of jack pine in the Lake States is somewhat inflated due to its proliferation after the wildfires which followed early pine logging (Benzie 1977).

Jack pine is known as a "fire species", and traditionally clearcutting and burning have been used for its regeneration. However, virtually every known method of cutting, site preparation, and artificial regeneration has been tried in managing this species (Eyre and LeBarron 1944). It is now apparent that no one method will produce satisfactory results on a consistent basis.

In northern lower Michigan, large areas of jack pine are cut and burned each year. On these areas, initial failure of jack pine regeneration following treatment is more the rule than the exception. Therefore, there is much interest in the ecology and silviculture of this species. After a review of the literature, I realized that most studies of prescribed burning focused on slash reduction, seedbed preparation, and responses of seedlings to various environmental factors (Eyre and LeBarron 1944, Beaufait 1962). Limited detailed work, however, has been conducted on plant succession on jack pine sites following logging and/or burning in the Lake States (Ahlgren 1960, Vogl 1970, Krefting and Ahlgren 1974). In Michigan, studies of this type are, to my knowledge, nonexistent.

The objective of my research was to characterize early plant succession following clearcutting and/or burning on jack pine sites in northern lower Michigan. Field data were collected in Roscommon, Oscoda, Crawford, and Ogemaw counties during the summers of 1979, 1980, and 1981 from unburned clearcut sites and burned sites comprising a successional series from 0 to 6 years. Community data were also collected from intermediate-age and mature jack pine stands which were considered representative of the predisturbance condition of many of the sites. In addition a three-year investigation was undertaken, using permanent plots, of vegetational changes on burned and unburned blocks in a jack pine clearcut. When certain trends became apparent during early succession (e.g. large increases in *Carex* dominance and the first-year dominance of *Geranium bicknellii* Britt. on burned sites), I became interested in the mechanisms involved. Therefore, studies of the response of understory vegetation to fertilization in a mature jack pine stand and an adjacent clearcut, and the role of heat in the germination of buried seed from jack pine stands along a successional series were initiated.

CHAPTER II

DESCRIPTION OF STUDY AREA AND SITES

General Description of Study Area

Surface Formations, Soil, and Climate

The research sites were located in Roscommon, Crawford, Oscoda, and Ogemaw counties in the northeast lower peninsula of Michigan (Fig. 2.1). The elevation of these counties generally lies between 275 and 365 m above sea level. The topography of this area is a direct result of the Wisconsin glaciation; the final glaciation took place from 14800 B.P. to 9500 B.P., leaving vast areas of till and outwash plains with little variation in surface relief (Veatch *et al*. 1924).

Michigan shows high edaphic diversity, with over 350 soil series mapped (Sommers 1977). However, the four county area used in this study is dominated by Rubicon, Kalkaska, and Grayling series of the Haplorthod and Udipsamment great groups. In particular, the Grayling sand series predominates, and all sites included for study were located on this soil series. However, intergrading of associated soil series, such as the Graycalm, with the Grayling series on the study sites was possible; the extent of this intergrading

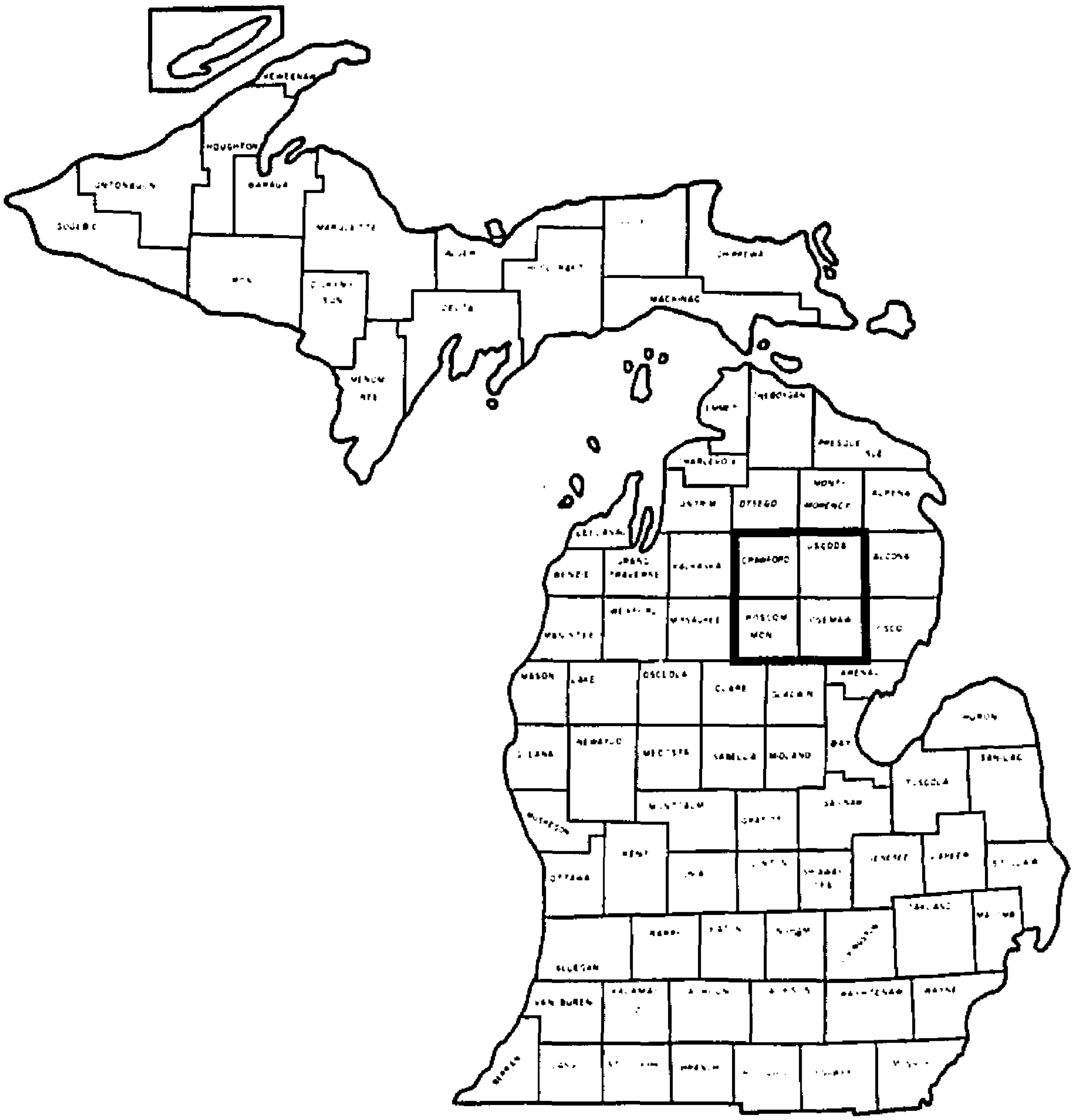

Fig. 2.1. Map of Michigan

is unknown because no formal soil analyses were conducted.

The Grayling sand series (a mixed, frigid, Typic Udipsamment) is characterized by its loose consistence, incoherent structure, sandy or single-grained texture throughout, and perviousness and nonretentiveness to moisture. Average moisture content during the growing season is very low to a depth of 1 m or more and fertility is correspondingly low. Reaction varies from medium to strongly acid to a depth of 1 m or more (Veatch et al. 1924, Appendix D).

The climate of the four county area is characterized by cold winters, short mild summers, a large number of cloudy days, low evaporation, and moderately high humidity (Veatch et al. 1924). The mean annual temperature is generally 6° to 7°C, with mean monthly temperatures ranging from -8° to 19°C. Precipitation is fairly well distributed throughout the year, with mean annual rainfall and snowfall of 77 and 180 cm, respectively. The length of the growing season is 100 to 120 days, with the last probable frost in the spring at the end of May, and the first probable frost in the fall in mid September (U.S.D.A. 1971).

In 1924, Veatch and associates wrote the following account of the forest communities in Roscommon county (nearly identical accounts were written for Oscoda, Ogemaw, and Crawford counties).

The whole land area at the time of occupation by white men was a dense forest except for a small acreage of bog or marsh and possibly some open land in the drier sand plains. The lumber industry started about 1870 and at the present time the original forest has been cut, except in a few small scattered areas and wood lots and in a few places in swamps. Several types of forest or tree associations were represented: (1) The hardwood forests in which hard maple or sugar maple (*Acer saccharum*) and beech were the dominant species and elm, ash, basswood, yellow birch, and hemlock were subordinate species; (2) the mixed hardwood and coniferous forest, in which common hardwoods were intimately associated with white pine, hemlock, and some Norway pine (red pine); (3) the pine forests in which white pine, Norway pine, or Norway and jack pine predominanted; and (4) the swamp forests in which the dominant species were arbor vitae, black spruce, white spruce (*Picea canadensis*), balsam fir (*Abies balsamea*), and tamarack. Much of the forest land is at present either desolate stump land covered with a dense growth of brush, briers, and grass or grown up to scrubby aspen, oaks, and red maple, with very little natural second growth of the original dominant species. The forest remains intact in some parts of the swamps, but this land also has been partly logged and desolated by fires. Some of the dry sandy plains land is characterized by a scattered growth of jack pine, low blueberries (mainly species of Vaccinium), the sweet fern (*Comptonia asplenifolia*), and bracken, together with various grasses, the most common of which are bluegrass (*Poa compressa*), wild oat grass or buffalo grass (*Danthonia* sp.), and beard grass (*Andropogon scoparius*). In the more open swamps or bogs there is a dense cover of heath shrubs, such as blueberries, Cassandra, and Labrador tea (*Ledum groenlandicum*), with some scattered black spruce and tamarack. In places the open marsh is covered with

> various sedges and bluejoint (*Calamagrostis canadensis*). It is estimated that about 10 per cent of the cut-over forest land has been cleared for farming purposes.

At present, the status of the forest communities of the four counties area is not that dismal. This in no way implies, however, a return to the original dense hardwood and coniferous forests. Today these counties are a patchwork of small woodlots, somewhat more extensive second- and third-growth hardwood and coniferous forests, farmland, bracken-grasslands, and swamp forests. Jack pine represents an extensive forest type in these counties, covering approximately 20% of the commercial forest land area. The present distribution of jack pine, a typical post-fire pioneer species, mainly reflects its proliferation following early pine logging and subsequent wildfires (Benzie 1977). Other important forest types and associations in these counties are oak-hickory, northern white cedar, maple-beech-basswood, and aspen.

Description of Sites Included for Study

A total of 25 jack pine sites were used for detailed study: 8 unburned clearcuts, 10 summer-burned areas, two 35-year-old stands, and 4 mature (55-years or greater) stands (Table 2.1). The 10 burned areas included 3 prescribed burns through

TABLE 2.1

SUMMARY OF STUDY SITES

Site designation	County	Legal Description	Year of establishment	area (ha)
Unburned clearcuts				
1A	Crawford	T27N,R1W,sec 9,NE¼	1979	16
1B80-81	Crawford	T25N,R2W,sec 1,N½,NW¼	1980	16
2	Oscoda	T28N,R1E,sec 32,NE¼,SW¼	1978	24
3A	Crawford	T26N,R3W,sec 34,SE¼,SW¼	1978	16
3B79-80-81	Oscoda	T27N,R2E,sec 7,N½,SE¼	1977	16
4A79-80-81	Oscoda	T27N,R2E,sec 17,NE¼	1976	32
5A79-80-81	Roscommon	T27N,R2W,sec 17,SW¼,SE¼	1975	4
6	Roscommon	T22N,R2W,sec 25,NE¼,NW¼	1974	16
Burned clearcuts				
7C80-81	Crawford	T27N,R1W,sec 9,NE¼	1979	16
7D79-80-81	Oscoda	T27N,R2E,sec 7,NE¼,NW¼	1977	24
10A79-80-81	Crawford	T25N,R3W,sec 10,E½,NE¼	1975	26
10B79-80-81	Ogemaw	T24N,R2E,sec 5,S½,NW¼ and SW¼,NE¼	1975	23
Burned 35-year-old jack pine				
7A80-81	Ogemaw	T24N,R1E,sec 21,SE¼,SE¼	1979	19
7B79-80-81	Ogemaw	T24N,R1E,sec 28,SE¼,SE¼	1978	26
9A79-80-81	Ogemaw	T24N,R1E,sec 27,E½,SW¼	1976	31
Wildfires				
8A79-80-81	Ogemaw	T24N,R1E,sec 26,S½,SE¼+sec 25,S½,SW¼	1977	32
9B79-80-81	Crawford	T26N,R2W,sec 31,SE¼	1976	30
11	Roscommon	T22N,R2W,sec 26,NE¼,SE¼	1973	6
Jack Pine Stands				
12A	Ogemaw	T24N,R1E,sec 8,NE¼,SE¼	1946	16
12B	Ogemaw	T24N,R1E,sec 22,NW¼,SW¼	1946	24
13A	Roscommon	T24N,R2W,sec 17,NE¼,NW¼	prior to 1926	12
13B	Roscommon	T24N,R2W,sec 17,S½,SW¼,SE¼	prior to 1926	4
13C	Ogemaw	T24N,R1E,sec 19,E½,NE¼,NE¼	prior to 1926	8
13D	Crawford	T25N,R3W,sec 1,E½,SW¼,NW¼	prior to 1926	3

standing 35-year-old jack pine, 4 prescribed burns through clearcut jack pine, 2 wildfires through mature jack pine, and 1 wildfire through clearcut mature jack pine. Also included was one site used for a controlled burn from which early succession on burned and unburned clearcut blocks was monitored during three consecutive seasons. All unburned clearcuts were previously mature jack pine greater than 50 years old.

All sites used for study were located on the Grayling sand series, with as little variation in topography and other environmental factors as possible. The following discussion will outline the silvicultural management and natural disturbance history of each site. Unique physical features or aspects of the adjacent vegetation will also be included.

The study sites are presently being managed by the Michigan Department of Natural Resources (DNR), and were acquired in the 1930's or thereafter; no site history data are available before their acquisition. Therefore, stand origin information is not available for sites 50 years or older. However, no widescale plantings were conducted prior to 1930, and frequent wildfires were common in this region. Therefore, most forest managers agree that mature jack pine stands of this area of Michigan are of postfire origin; this will be assumed unless otherwise noted.

Stand age of burned standing timber was determined by boring at least 10 trees in an adjacent stand that appeared representative of the treated area before burning. Overstory basal area in mature and 35-year-old jack pine stands was measured using a 10-factor prism at 10 random locations. Zero-year clearcuts are defined as areas harvested the winter and spring before summer sampling; 1-year-old burns are defined as areas burned the summer before sampling; no areas were surveyed the same growing season they were burned.

Unburned clearcuts*

Site 1A. This area is north of a trail road and adjacent (west) to route F-97. It was clearcut during the spring of 1979, at which time the dominant jack pine was 55 to 60-years-old. Widely scattered red pine (*Pinus resinosa*) were left standing. This area was surveyed as a 0-year clearcut on 7/17/79 and later that day the area was prescribe burned. During the 1980 and 1981 field seasons this area was resurveyed as a 1-year-old and 2-year-old burn (site 7C80-81). No other disturbance information is known

*The number 79, 80, and 81 following the alphanumerical site designation refers to the 1979, 1980, and/or 1981 growing seasons when the sites were surveyed, for sites surveyed in more than one growing season.

for this site.

Site 1B80-81. This area surveyed was part of a larger clearcut located at the southeast junction of 4-Mile Road and Staley Lake Road. The 57-year-old jack pine on this site was clearcut during the winter and spring of 1980, and the site was surveyed in 1980 and 1981 as a 0-year-old and 1-year-old clearcut. Scattered intermediate sized oak (northern red group, Quercus spp.) and black cherry (Prunus serotina) were present. No other previous disturbance to this stand is known.

Site 2. In 1961 and 1974 this area was selectively cut for jack pine logs exceeding 20 cm d.b.h. In 1978 the 55 to 60-year-old jack pine was clearcut and the site was surveyed in 1979 as a 1-year-old clearcut. Subsequent to that survey, the site was planted and not used for further study. Scattered 3- to 5-m-tall jack pine and mature red pine were left standing after harvesting. This site was gently undulating, as opposed to near total flatness of most of the other sites.

Site 3A. The southern border of this area lies north of 4-Mile Road. The site was clearcut in 1978, and surveyed in 1980 as a 2-year-old clearcut. The age of the dominants ranged from 48 to 57 at the time of clearcutting. Scattered intermediate-sized oaks and black cherry, along with suppressed 3- to 5-m jack pine were present.

Site 3B79-80-81. This area lies directly west of Muskrat Lake Road. The 50 to 55-year-old jack pine on this site were clearcut in 1977, the site was surveyed in 1979, 1980, and 1981 as a 2-, 3-, and 4-year-old clearcut. In 1961 and 1964, the site was selectively logged for jack pine logs. An overgrown trail road ran through the center of the site. A ¼ ha clone of 7 to 10 m tall aspen (*Populus tremuloides*) was also located in the center of the site.

Site 4A79-80-81. This area is found directly east of Richardson Road. In 1957 there was selective cutting for jack pine pulp logs, and in 1976 the area was clearcut. At the time of harvesting, the age of the dominants ranged from 54 to 72 years. In 1979, 1980, and 1981 this area was surveyed as a 3-, 4-, and 5-year-old clearcut. Scattered sapling sized jack and red pine and a few mature red pine were found. Topography of the site was gently rolling, characteristic of a till plain.

Site 5A79-80-81. This area lies directly north of Airport Road, and is part of a larger research area directed by the U. S. Forest Service. This area was clearcut in 1975, with no previous disturbance to the stand reported. The dominants ranged from 57 to 66 years at the time of cutting. The area was surveyed in 1979, 1980, and 1981 as a 4-, 5-, and 6-year-old clearcut. Regularly spaced dense oak and cherry sprouts were found throughout.

Site 6. This area lies directly south of Emery Road. No other disturbance to the stand was reported prior to clearcutting in 1974. Dominant jack pine ranged from 57 to 63 years at the time of harvest. Dense oak and cherry sprouts were found throughout the area, and thick stands of 20 m tall jack pine surrounded this site on the east, west, and south borders.

Burned areas

Site 7A80-81. This lies directly west of county road 13, and is part of a large research area directed by the Michigan DNR. A large wildfire swept through this entire research area in 1946. Some oak, red pine, and jack pine survived the fire; those individuals of financial maturity were logged in 1975 and 1976. What remained was a variable age and density jack pine stand, representing postfire regeneration and emergents that survived the 1946 fire and subsequent logging. The emergents ranged from 40- to 45-years-old and intermediates from 22- to 35-years-old. However, there also were present a substantial number of jack pine in the 0-5 year, 5-10 year, and

10-20 year age classes.

On 7/12/79 the site was prescribe burned with residual trees left standing. The fire was severe enough to kill nearly all the pines and above-ground parts of the hardwoods. The hardwoods have subsequently sprouted from the base or produced root suckers. Patchy and scattered intermediate-sized snags are distributed throughout the site. The area was surveyed in 1980 and 1981 as a 1-year and 2-year-old burn. Burned sites 7B79-80-81 and 9A79-80-81 and 35-year-old jack pine stands 12A and 12B are part of this same research area.

Site 7B79-80-81. This site was prescribe burned on 8/8/78. See site 7A80-81 for stand history. A unique aspect of this site is a 2 ha heath bog in the northeast portion. The site gently slopes towards the bog, but is level on the upland areas. Only the level upland areas away from the bog were surveyed. Patchy and scattered intermediate-sized snags were found throughout. The site was surveyed in 1979, 1980, and 1981 as a 1-year, 2-year, and 3-year-old prescribed burn.

Site 9A79-80-81. This area was prescribe burned on 8/17/76. See site 7A80-81 for stand history. This site is somewhat unique due to the large number of oak, black cherry, and red and jack pine that survived the fire. The remaining canopy, although patchy, created an unusual microhabitat for a recently burned site. Surveys took place in 1979, 1980, and 1981 as a 3-, 4-, and 5-year-old prescribed burn, respectively.

Site 7C8081. This site was surveyed as a 0-year clearcut in 1979 and a 1-year and 2-year-old prescribed burn in 1980 and 1981. See unburned site 1A for site history.

Site 7D79-80-81. This area is located directly south of Penn Road, and originated as a jack pine plantation (800 trees/acre), established in 1930. The area was clearcut from the spring of 1976 to spring 1978. However, nearly all harvesting was done in 1977, and this is used as the reference date. On 9/26/78, the area was prescribed burned as a 1-year-old clearcut. Surveys were made in 1979, 1980, and 1981 as a 1-year, 2-year, and 3-year-old prescribed burn. The recorded stump age at the time of clearcutting ranged from 31 to 49 years, with most ages falling between 40 and 47 years. This area is surrounded by dense stands of mixed red and jack pine and a large clearcut to the north and west. The mixed red and jack pine stands had a much sparser understory than usually seen in pure jack pine stands; blueberry (*Vaccinium* spp.) was conspicuously reduced.

Site 8A79-80-81. This area was burned by wildfire on 7/2/77, and is located directly east and west of Roll Road. The forest at the time of burning was a well stocked jack pine stand, with dominants ranging from 40 to 52 years-old. Most of the individuals were left standing as charred snags. Because of their density, they greatly increased the shading to the forest floor compared to other burned areas. The topography is gently rolling slopes with larger flat areas. Surveys were conducted in 1979, 1980, and 1981 as a 2-year, 3-year, and 4-year-old burn, respectively.

Site 9B79-80-81. This area, burned by wildfire on 8/23/76, is located directly north of 4-Mile Road. The age of the dominants at the time of burning was highly variable, ranging from 48 to 66 years. The area was apparently well-stocked, as indicated by the remaining charred snags and stumps, and the high density of the adjacent jack pine stands. The topography was gently rolling throughout. This area was surveyed in 1979, 1980, and 1981 as a 3-year, 4-year, and 5-year-old burn.

Site 10A79-80-81. This area is located south of the railroad tracks running adjacent to 5-Mile Road. The site was clearcut in the winter and spring of 1973 and prescribe burned as a 2-year clearcut on

10/7/75. At the time of clearcutting the age of the dominants ranged from 42 to 63 years. The area is surrounded on three borders by well-stocked mature jack pine. Hardwoods were apparently an important component of the pre-existing vegetation, as indicated by their current presence as dense sprouts and scattered surviving adults. The area was surveyed in 1979, 1980, and 1981 as a 4-year, 5-year, and 6-year-old burn, respectively.

Site 10B79-80-81. This area is located directly east of Fairview Road. It was clearcut in 1974 and burned as a 1-year-old clearcut on 8/15/75. Previous to this, the area was selectively logged for mature jack pine (exceeding 20 cm d.b.h.) in 1941, 1948, 1950, 1956, 1958, and 1965. The age of the dominants at the time of clearcutting ranged from 44 to 54 years. This area was surrounded by well-stocked mature jack pine with a canopy height of 15 to 20 m. Large areas of dense hardwood sprouts (mainly aspen suckers) up to 4.5 m tall dominated the site. It was surveyed in 1979, 1980, and 1981 as a 4-year, 5-year, and 6-year-old burn.

Site 11. This area is to the southwest of a trail road that runs southeast of Emery Road. It was clearcut in the winter and spring of 1972 and 1973 and on 7/21/73 burned by wildfire. The age of the dominants at the time of cutting ranged from 51 to 60 years. Oak was an important component of the pre-existing vegetation, as exhibited by numerous dense sprouts throughout the area. Mature well-stocked jack pine border the site. The area was surveyed in 1979 as a 6-year burn.

Experimental burn site. Roscommon County, T24N, R2W, sec 8, S½ of SE¼. This 7.2 ha area is located directly west of Airport Road. Clearcutting of this site started in 1976 and continued through the fall and winter of 1977. Most of the harvesting took place in 1976, and this is used as the reference date. When clearcut, the age of the dominants ranged from 55 to 65 years. This area, used to study early plant succession on burned and unburned clearcut blocks, was monitored during the 1979, 1980, and 1981 growing seasons (see Chapter 5 for details of the study).

Intermediate-age jack pine stands

Both stands in this category resulted from a 1946 wildfire in Ogemaw County. Three study sites discussed above (7A80-81, 7B79-80-81, and 9A79-80-81) also originated from the same fire. Although the stand history described in detail for site 7A80-81 applies to these stands, they were not prescribe burned.

Site 12A. This area of 35-year-old jack pine was surveyed in 1981. The jack pine distribution was extremely variable, ranging from impenetrable patches to intermediate-sized openings devoid of trees. The mean basal area of 6.0 m^2/ha, with a standard deviation (S.D.) of 7.46 m^2 (ranging from 0 to 27.6 sq. m), reflects the variability. The patchiness of the stand greatly affected the distribution of light reaching the forest floor. The open areas appeared hot and dry and the shaded areas cool and moist. The open areas were dominated by low-growing grasses, sedges, and forbs, and the shaded understory was dominated by small trees and shrubs. Along with the patchy distribution of jack pine, the canopy height was extremely variable. This reflected the wide range of age classes represented here.

Site 12B. This area was also surveyed in 1981. The stand structure was similar to that of site 12; however, mean basal area was somewhat higher (9.7 m^2/ha), with somewhat less variability (S.D. = 6.2 m^2, ranging from 0 to 16.1 sq. m).

Mature jack pine stands

The mature jack pine stands chosen for study were 55 years or older and appeared free from recent disturbance. These mature stands were well-stocked with evenly distributed dominants. The canopy was fairly regular, but light gaps, created from recent blowdown, was a common feature. The height of the dominants on all sites ranged from 15 to 20 m. Intermediate and sapling-sized individuals were generally present.

Site 13A. This area is directly south of the experimental burn area off of Airport Road. The mean basal area was 17.0 m^2/ha (S.D. = 4.4). The stand age was considered 68 years; dominants ranged from 55 to 68 years.

Site 13B. This area is situated directly north of Airport Road and is located 1.6 km south of site 13A The mean basal area was 15.6 m^2/ha (S.D. = 3.9). The dominants ranged in age from 55 to 68 years; as on site 13A the stand age was considered 68 years. Most probably this site and site 13A originated from fire, based on their close proximity, age of dominants, and stand structure.

Site 13C. This area is located directly south of county road 26. The mean basal area was 22.1 m^2/ha (S.D. = 3.9 sq. m). The age of the dominants ranged from 47 to 55 years, stand age was considered 55 years. The site was selectively logged (diameter cuts greater than 20 cm d.b.h. as well as salvage cuts) in 1946, 1949, 1956, and 1961. Twenty years lapsed between the last cutting and the present survey of the site. This apparently vigorous, healthy stand in no way appeared disturbed or degraded from logging.

Site 13D. This stand, directly east of Staley Lake Road, was left from a large area that was clear-cut in 1980 (see site 1B80-81). The mean basal area was 19.8 m^2/ha (S.D. = 4.3). The age of the dominants ranged from 47 to 57 years; the stand was considered to be 57-years-old.

CHAPTER III

EARLY REVEGETATION OF BURNED AND UNBURNED JACK PINE CLEARCUTS IN NORTHERN LOWER MICHIGAN

INTRODUCTION

The importance of fire as an ecological factor and its use as a management tool in the Lake States is well documented (Eyre and LeBarron 1944, Cayford 1970, Vogl 1970, Heinselman 1973, Ahlgren 1974). A large portion of this previous work focuses on the ecology and management of jack pine (*Pinus banksiana* Lamb.). Jack pine is a typical postfire pioneer species whose present distribution is directly related to wildfires following early pine logging (Benzie 1977). Throughout most of its range, jack pine produces serotinous cones and requires a mineral seedbed for optimum germination. Therefore, most attempts to manage this species have utilized prescribed burning.

Studies of prescribed burning have mainly focused on slash reduction, seedbed preparation, and response of seedlings to various environmental factors (Eyre and LeBarron 1944, Beaufait 1962). Limited detailed work, however, has been conducted on plant succession on jack pine sites following logging and/or burning in the Lake States (Ahlgren 1960, Vogl 1970, Krefting and Ahlgren 1974, Ohmann and Grigal 1979). Thus a study was undertaken to characterize early revegetation of burned and unburned clearcuts in northern lower Michigan where jack pine is a predominant component of the tree vegetation on sandy soils. The main objective of this chapter is to discuss the differences between burned versus unburned jack pine clearcuts and the variation that results from these disturbances. A discussion of successional patterns within and between burned and unburned sequences will be presented in Chapter 4.

METHODS

Unburned clearcut sites 1A, 1B80-81, 2, 3A, 3B79-80-81, 4A79-80-81, 5A79-80-81 and 6, and burned clearcut sites 7C79-80-81, 7D79-80-81, 10A79-80-81, and 10B79-80-81 were used for comparison in this chapter (see Chapter 2 for site descriptions). On each site all vascular plants, including grasses, sedges, ferns, herbs, shrubs, and trees were characterized by frequency and cover measurements. Frequency was determined using a 1 m^2 circular plot randomized along transects. Transects were oriented to best include the entire area to be surveyed. Cover determinations were made by summing the distance intersected by each species along randomly placed 20 m transects. Thirty frequency plots and 3 cover transects (60 m total) were used to characterize each site. Deviation from this method occurred on site 1A where, due to time constraints, only 20 frequency plots and 40 m cover were included. On all sites a 10% or less increase in the number of species resulted from the final 10% increase in sample area (Cain 1938). Nomenclature follows Voss (1972) for gymnosperms and monocots and Fernald (1950) for all other taxa.

RESULTS

The data presented are from sites sampled annually once, twice, or three times during the 1979, 1980, and 1981 growing seasons (Table 3.1 and 3.2). The age of these sites make up a sequence ranging from 0-year (clearcut the winter and spring previous to summer sampling) to 6-year clearcuts (Table 3.1) and 1-year (burned the summer previous to sampling) to 6-year burns (Table 3.2). Caution is advised in inferring that these sites are typical or sufficient to represent average conditions for those ages. Although sites were rigorously selected, the severity and timing of the disturbance on each site varied. Therefore each site is unique in many aspects, making direct comparisons difficult. Nonetheless, I do feel that certain

TABLE 3.1

RELATIVE COVER (C), RELATIVE FREQUENCY (F), AND SPECIES RICHNESS (R) FOR VEGETATIONAL GROUPS ON UNBURNED CLEARCUTS

Site[a] Number	Years Since Treatment	Area	Annuals & Biennials			Grasses & Sedges			Perennial Herbs			Trees & Shrubs			Total R	Total Cover
		ha	C	F	R	C	F	R	C	F	R	C	F	R		per 60 m
1A	0	16	-	.7	1	32.5	26.1	6	15.0	31.2	9	52.5	42.0	10	26	36.0
1B80	0	16	.49	-	2	12.9	20.4	7	29.9	33.3	9	56.7	46.3	13	31	61.5
1B81	1	16	-	.5	1	27.2	22.5	5	34.3	26.7	8	38.5	50.4	9	23	61.5
2	1	24	-	-	-	24.7	27.6	5	7.1	23.2	12	68.2	49.2	7	24	27.6
3A	2	16	-	-	-	49.6	43.8	9	21.6	21.6	9	29.1	34.6	9	27	50.7
3B79	2	16	-	1.9	1	36.5	24.8	5	13.6	32.2	10	49.6	41.1	9	25	37.1
3B80	3	16	-	-	-	53.1	32.0	7	4.3	26.0	7	42.5	42.0	8	22	46.9
4A79	3	32	.1	-	1	83.4	52.7	7	5.1	16.4	6	11.4	30.9	6	20	37.7
3B81	4	16	-	1.5	1	45.7	30.4	6	1.6	23.9	6	52.7	44.2	9	22	64.4
4A80	4	32	-	-	-	68.8	50.0	6	.3	10.3	5	30.9	39.5	8	19	64.5
5A79	4	4	-	-	-	77.2	35.7	2	2.2	14.3	1	20.7	50.0	7	10	41.7
4A81	5	32	-	-	-	81.8	51.6	6	.1	9.5	5	18.0	39.0	7	18	58.9
5A80	5	4	-	-	-	67.3	37.1	5	2.9	19.3	4	29.8	43.5	5	14	44.7
6	5	16	-	-	-	77.3	45.6	3	.2	2.9	3	22.5	51.5	10	16	30.1
5A81	6	4	-	-	-	65.6	35.0	4	5.7	18.0	4	28.7	47.0	7	15	46.8

[a]Site numbers starting with the same combination of number and letter represent the same site surveyed twice; the numbers 79, 80, and 81 indicate the year surveyed (1979, 1980, and 1981), for sites surveyed in more than one growing season.

TABLE 3.2

RELATIVE COVER (C), RELATIVE FREQUENCY (F), AND SPECIES RICHNESS (R)
FOR VEGETATIONAL GROUPS ON BURNED CLEARCUTS

Site[a] Number	Years Since Treatment	Area	Annuals & Biennials			Grasses & Sedges			Perennial Herbs			Trees & Shrubs			Total R	Total Cover
		ha	C	F	R	C	F	R	C	F	R	C	F	R		per 60 m
7C80	1	16	18.3	7.1	4	35.8	32.0	9	2.8	26.1	15	43.1	34.8	7	35	26.9
7D79	1	24	.1	2.8	3	73.5	44.6	9	8.5	24.3	12	17.8	28.1	10	34	30.6
7C81	2	16	-	-	-	45.7	38.4	8	1.1	13.2	10	53.2	48.3	7	25	52.6
7D80	2	24	-	-	-	71.6	56.3	9	12.4	21.1	8	15.8	22.5	8	25	48.5
7D81	3	24	-	-	-	66.7	52.5	8	14.3	25.1	8	19.1	22.7	8	24	48.7
10A79	4	26	-	1.6	1	71.8	35.7	13	15.2	39.3	13	13.0	23.3	9	36	58.2
10B79	4	23	.2	3.9	1	53.5	40.0	14	22.9	23.3	10	23.4	32.8	14	39	45.4
10A80	5	26	.1	1.7	2	57.3	38.2	11	18.5	32.9	16	24.1	27.2	7	36	75.7
10B80	5	23	.8	5.4	3	57.3	37.3	10	8.0	23.5	8	33.8	33.9	14	35	61.6
10A81	6	26	.2	.6	2	66.4	39.3	8	8.9	34.9	14	24.5	25.2	8	32	74.4
10B81	6	23	.8	2.3	1	50.3	38.3	9	12.2	21.4	10	36.7	38.0	14	34	74.8

[a]See Table 3.1.

consistent differences in burned versus unburned clearcuts can be discerned from this study.

A comparison of three different measures of diversity, total species richness (combined total number of species recorded in frequency and cover measurements), average richness per plot, and Shannon Index[2], of sites averaged within years for a 6-year progression is shown in Figure 3.1. Species were grouped into annuals and biennials, grasses and sedges, perennial herbs, and trees and shrubs. Relative cover, relative frequency, and richness data for each surveyed area by vegetational group is shown in Tables 3.1 and 3.2 for unburned and burned clearcuts, respectively. Relative cover and relative frequency data for each species surveyed on unburned clearcut and burned clearcut sites during 1979, 1980, and 1981 are shown in Appendices A and B.

Species richness, a diversity index in which rare and dominant species contribute equally, was higher on burned clearcuts compared to unburned clearcuts for each year except year 2. Average frequency per plot and Shannon Index, which reflect number of species and equitability, initially were higher for the unburned clearcuts. Later in the sequence (years 4, 5, and 6),

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[2]Shannon Index of Diversity (H) = Σ Pi log Pi, where Pi = relative cover (Odum 1971).

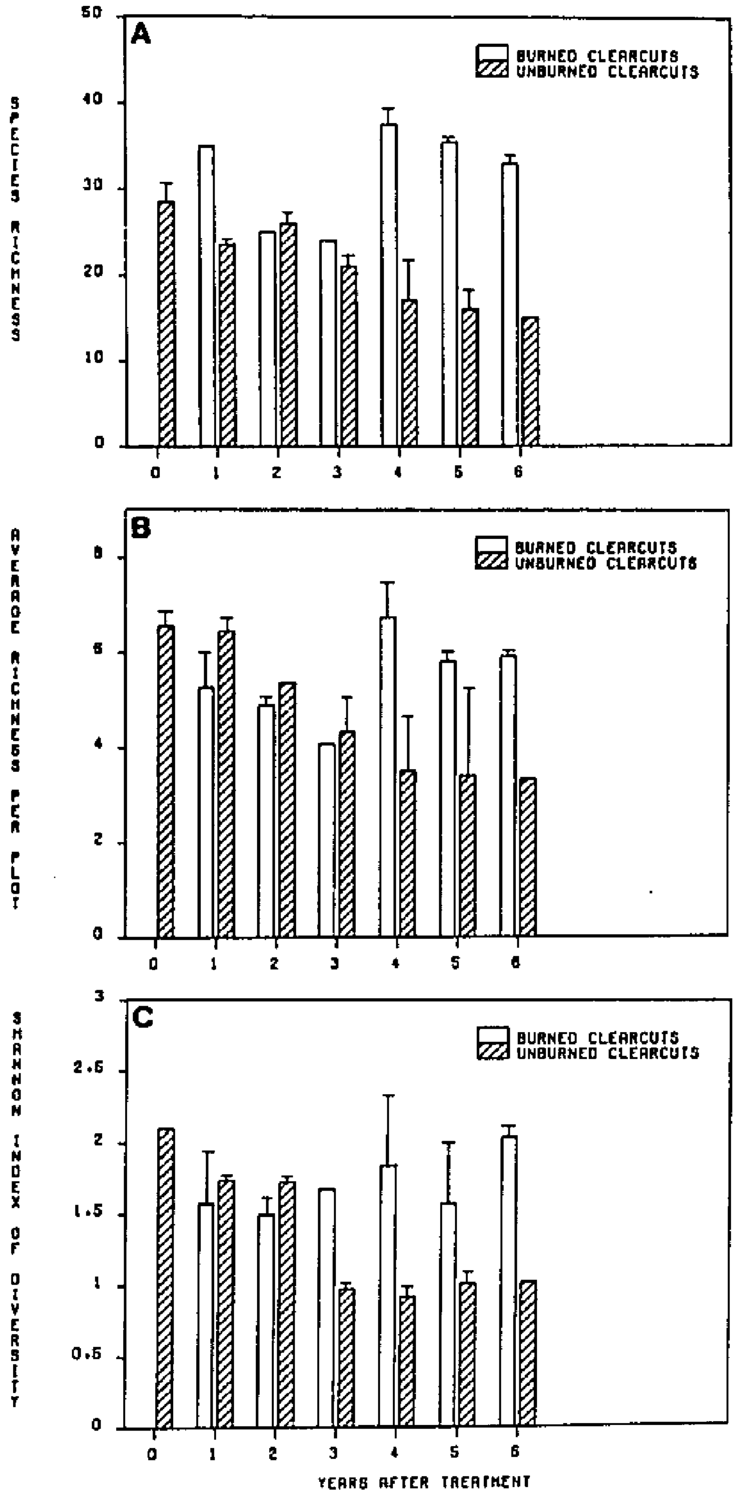

Fig. 3.1 A) Species richness, B) average richness per 1 m² plot, and C) Shannon index of diversity versus years after treatment on burned and unburned sites. Vertical bars equal one standard deviation (SD). Only one observation at year 3 burned and year 6 unburned.

however, values of this indice were much higher on the burned areas, compared to unburned areas. Although the average frequency per plot and the Shannon Index were lower on certain burned sites, compared to unburned sites, these sites had a greater number of species, mostly rare, contributing to these indices, whereas fewer, but more common, species were contributing on the unburned clearcuts.

As shown in Table 3.3, 73 different species were recorded on burned clearcuts compared to 49 on unburned clearcuts. Twenty-eight species were exclusive to burned areas, whereas only 4 species were exclusive to unburned areas. Three of the 7 annuals and biennials, 12 of the 20 grasses and sedges, 18 of the 30 perennial herbs, and 16 of the 23 trees and shrubs recorded on all sites were present on unburned clearcuts. In contrast, burned sites contained all 7 annuals and biennials, all 19 grasses and sedges, 24 of the 28 perennial herbs, and all 23 trees and shrubs.

Figure 3.2 shows that cover was much lower on burned sites, compared to unburned sites, during year 1. By year 2, however, cover on burned clearcuts was higher than on unburned clearcuts. Over the temporal sequence, burned areas showed a general increase in cover through year 6, whereas cover values on unburned sites varied little. However, nearly all sites surveyed

TABLE 3.3

PLANT SPECIES ENCOUNTERED ON BURNED AND UNBURNED CLEARCUT SITES IN NORTHERN LOWER MICHIGAN

Species Exclusive to Burned Areas
(28 species total)

Annuals and Biennials
(4 species)

Cirsium sp.
Corydalis sempervirens L.
Geranium bicknellii Britt.
Erigeron canadensis L.

Grasses and Sedges
(7 species)

Agropyron trachycaulum Link
Carex rugosperma Mack.
Festuca sp.
Muhlenbergia mexicana L.
Panicum xanthophysum Gray
Poa pratensis L.
Sorghastrum nutans L.

Perennial Herbs
(13 species)

Aster saggitifolius Wedemeyer
Convolvulus spithamaeus L.
Hieracium canadense Michx.
Helianthemum canadensis Michx.
Lechea minor L.
Polygala polygama Walt.
Polygonum cilinode Michx.
Potentilla arguta Pursh.
Potentilla simplex Michx.
Potentilla tridentata Ait.
Rumex acetosella L.
Senecio tomentosus Michx.
Viola adunca Sm.

Trees and Shrubs
(4 species)

Acer rubrum L.
Ceanothus ovatus Desf.
Gaylussacia baccata (Wang.) C. Koch
Symphoricarpos albus L.

Species Exclusive to Unburned Areas
(4 species)

Perennial Herbs

Antennaria neglecta Greene
Asclepias syriaca L.
Spiranthes gracilis (Bigel.) Beck
Viola pedatifida G. Don.

TABLE 3.3 (Continued)

Species Common to Both Burned and Unburned Clearcuts
(45 species total)

Annuals and Biennials
(3 species)

Arabis glabra L.
Lactuca canadensis L.
Melampyrum lineare Lam.

Grasses and Sedges
(12 species)

Agrostis hyemalis Walt.
Andropogon gerardii Vitman
Bromus kalmii Gray
Carex pensylvanica Lam.
Danthonia spicata (L.) Beauv.
Deschampsia flexuosa L.
Dichanthelium depauperatum Muhl.
Koeleria macrantha Pers.
Panicum columbianum Scribn.
Oryzopsis asperifolia Michx.
Oryzopsis pungens Torr.
Schizachne purpurascens Torr.

Perennial Herbs
(14 species)

Apocynum androsaemifolium L.
Anemone quinquefolia L.
Aster laevis L.
Campanula rotundifolia L.
Fragaria virginiana Duchesne
Gaultheria procumbens L.
Hieracium aurantiacum L.
Hieracium venosum L.
Helianthus occidentalis Ridd.
Liatris novae-angliae Lunell
Maianthemum canadensis Desf.
Physalis virginiana Mill.
Pteridium aquilinum Desf.
Solidago sp.

Trees and Shrubs
(16 species)

Amelanchier sp.
Arctostaphylos uva-ursi L.
Comptonia peregrina L.
Crataegus sp.
Diervilla lonicera Mill.
Epigea repens L.
Pinus banksiana Lamb.
Populus tremuloides Michx.
Prunus pumila L.
Prunus serotina Ehrh.
Prunus virginiana L.
Quercus spp. (red oak group)
Rosa blanda Ait.
Rubus pensilvanicus Poir.
Salix glaucophylloides Fern.
Vaccinium spp.

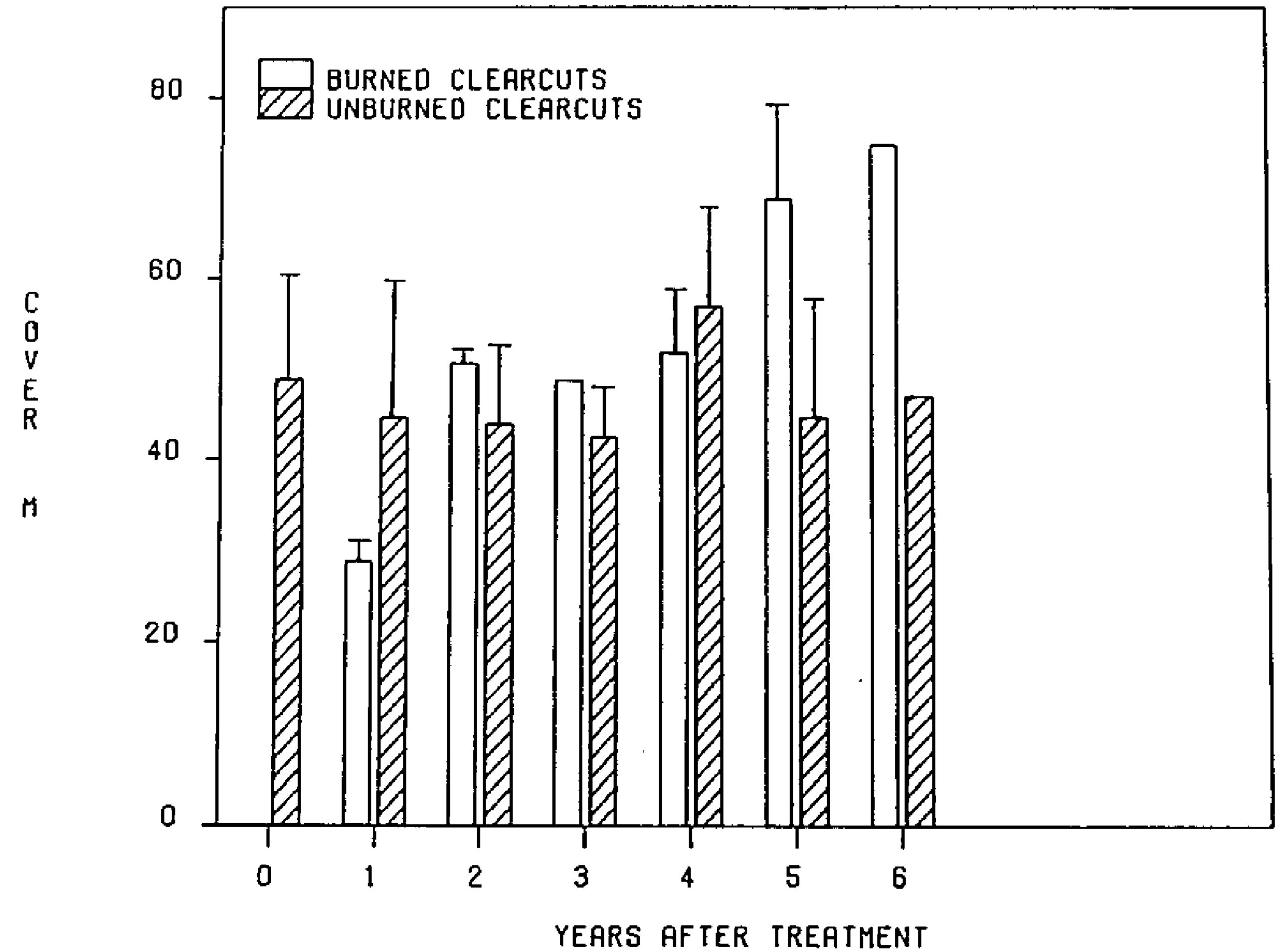

Fig. 3.2. Total vegetational cover (m) versus years after treatment on burned and unburned sites. Vertical bars equal one SD. Only one observation at year 3 burned and year 6 unburned.

during two or more growing seasons showed increased cover from that of the previous year.

Trends in relative cover and frequency of annuals and biennials over the temporal sequence are shown in Tables 3.1 and 3.2. On unburned sites, species in this group are virtually absent, except for _Melampyrum lineare_ Lam. (cow wheat) which is common in the understory of mature jack pine stands. On burned sites the relative cover of this species group varied greatly between the two sites surveyed as first year burns. Very high levels of cover (18.3%) of annuals and biennials were seen on site 7C80, whereas on site 7D79 only 0.1% cover for this species group was recorded (Table 3.2). On site 7C80, _Geranium bicknellii_ Britt. (geranium) and _Corydalis sempervirens_ L. (rock-harlequin) dominated this species group. Heat stimulated germination of these species is indicated by their drastic reduction from years 1 to 2 following fire on site 7C80-81 (see Chapter 7).

Perennial grasses and sedges were dominant on both burned and unburned clearcuts (Tables 3.1 and 3.2). The richness of this group, however, was due to the many species of grasses. Burned sites from years 1 to 6 showed greater species richness of grasses than analogous unburned sites (Fig. 3.3A). The burned clearcuts retained high levels of richness of grass

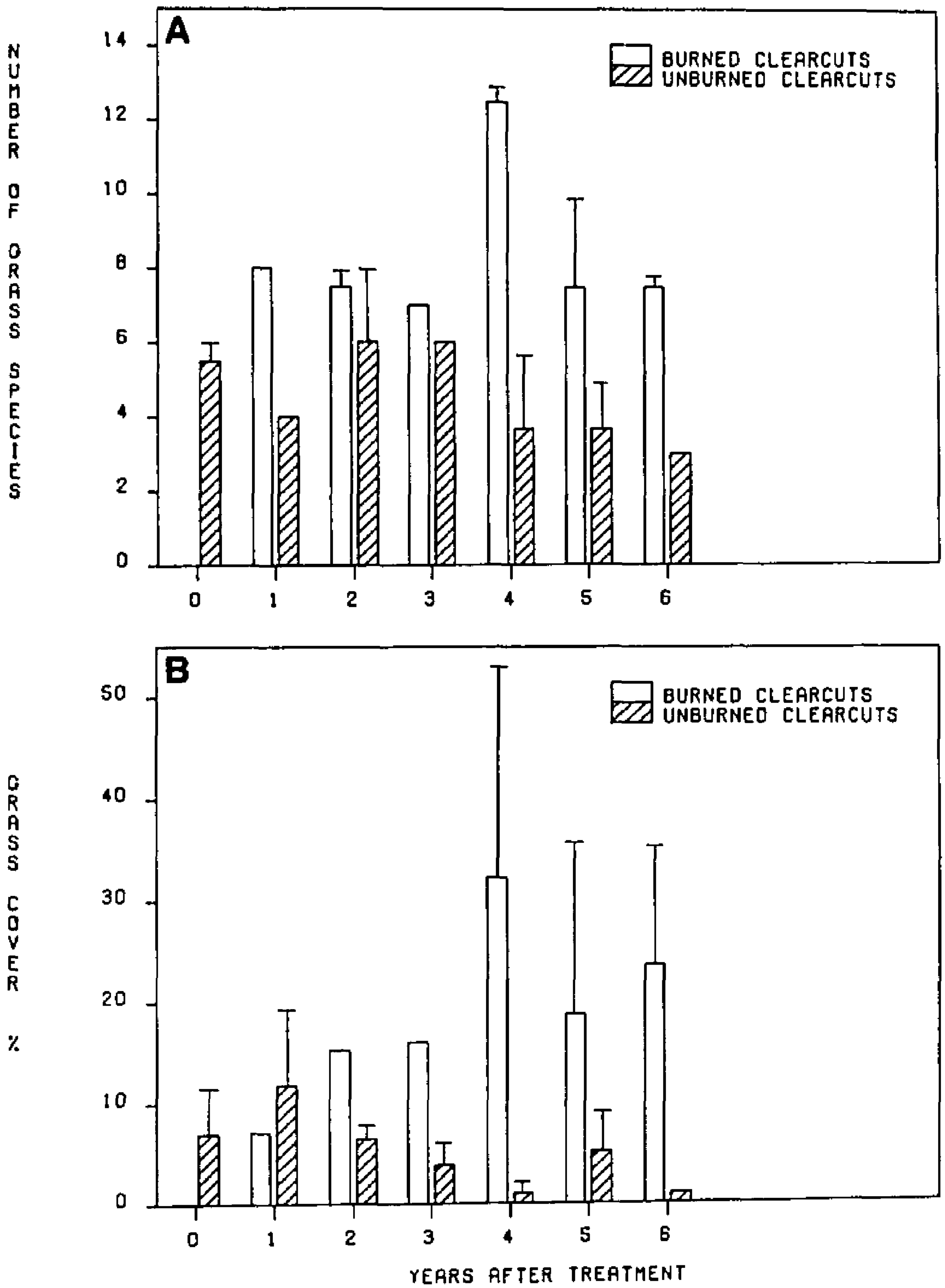

Fig. 3.3. A) Number of grass species and B) percent cover of grasses versus years after treatment on burned and unburned sites. Vertical bars equal one SD. Only one observation at year 3 burned and year 6 unburned.

species throughout the temporal sequence, whereas unburned clearcuts showed a decline in richness in the latter part of the sequence. From years 2 to 6 grass cover on the burned sites greatly exceeded that of the unburned sites of the same age (Fig. 3.3B). Dominant grass species occupying the burned sites include Oryzopsis asperifolia Michx., O. pungens Torr., and Schizachne purpurascens Torr. In contrast, the cover of grasses on unburned sites was negligible.

The relative cover of sedges on unburned clearcuts is shown in Fig. 3.4. Only two species of sedge, Carex pensylvanica Lam. and C. rugosperma Mack., were observed on the study sites, which were characterized as Carex spp. and given a richness value of 1. Sedges comprised the majority of the cover of the grass and sedge species group, and only on burned site 10A79-80-81 (years 4, 5, and 6) and unburned site 1B81 (year 1) did the relative cover of grasses exceed that of sedges. On unburned clearcuts Carex cover initially (years 0 and 1) was low. By year 2, however, Carex cover dramatically increased and by year 5 Carex covered an average 70% of the unburned sites. Initially, Carex relative cover increased to a greater extent on burned clearcuts compared to unburned clearcuts. In contrast to the unburned sites, Carex relative cover did not increase in the latter part of the

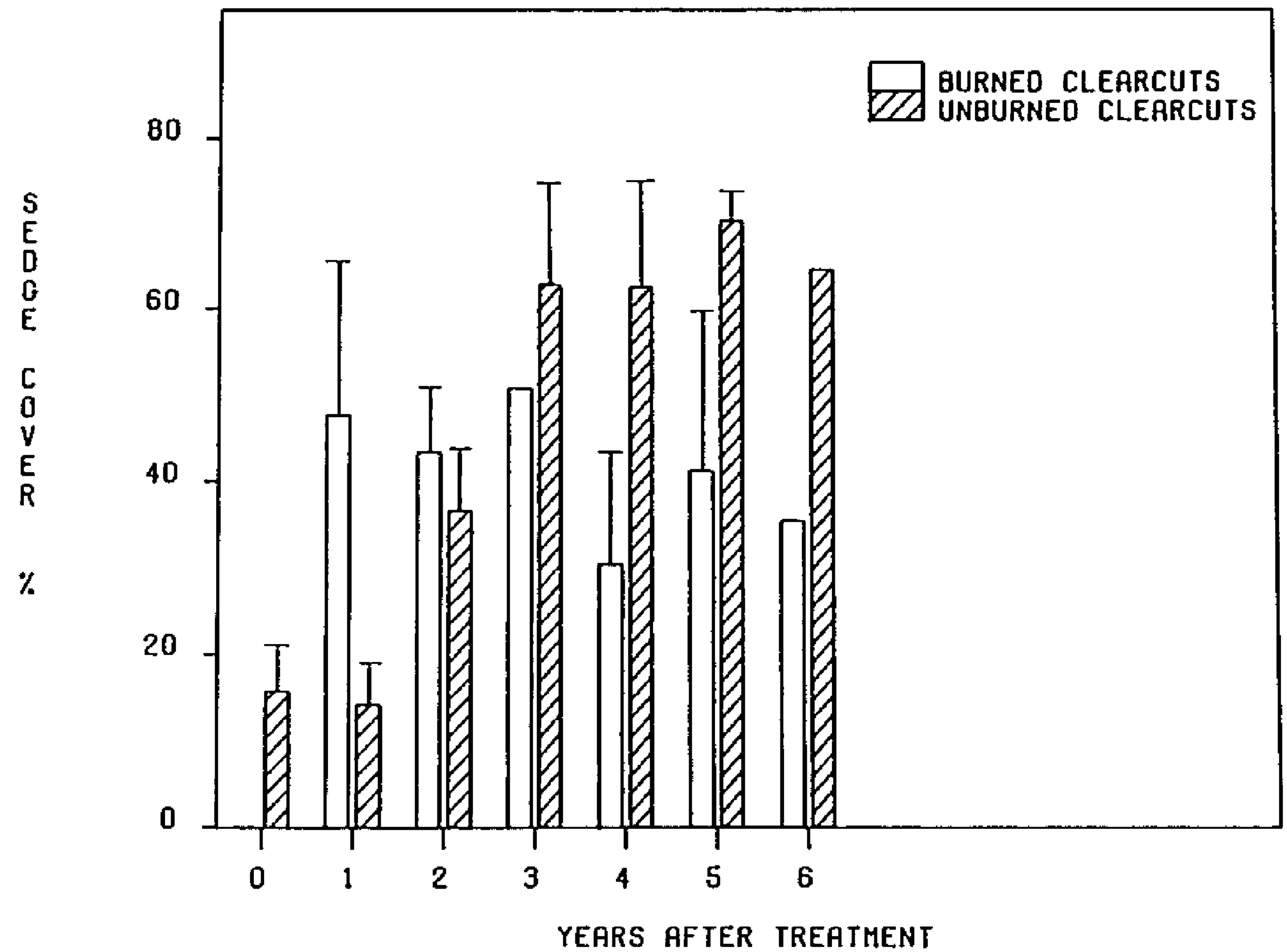

Fig. 3.4. Percent cover of sedge versus years after treatment on burned and unburned sites. Vertical bars equal one SD. Only one observation at year 3 burned and year 6 unburned.

burned sequence. In fact, on the burned sites, Carex showed a general decrease in relative cover between years 3 and 6.

Bracken fern (Pteridium aquilinum Desf.) and wintergreen (Gaultheria procumbens L.), included as perennial herbs in this study, were the dominant contributors to the relative cover of this species group. All other perennial herbs contributed little to relative cover of this species group but added greatly to species richness on all sites, especially those which had been burned (Tables 3.1 and 3.2). A steady decrease in the number of herbs was seen on the unburned sequence, whereas burned sites showed an initial decline (years 1 through 3) but later exhibited high richness (years 4 through 6). Some frequently occurring perennial herbs exclusive to burned clearcuts include Hieracium canadense Michx. (Canadian hawkweed), Rumex acetosella L. (sheep sorrel), and Senecio tomentosus Michx. (groundsel).

The number of species of trees and shrubs differed little between burned and unburned clearcuts of the same age (Tables 3.1 and 3.2). Of the four major species groups, trees and shrubs showed the least increase in species richness after fire. Relative cover of these species was on the average higher on unburned clearcuts during years 1 through 4, but slightly lower during years 5 and 6. Unburned clearcuts showed a general decrease in relative cover over time, whereas burned sites showed a decline from year 2 to years 3 and 4, but increased during years 5 and 6. The species dominating this group on both burned and unburned sites included *Vaccinium* spp. (blueberry), *Populus tremuloides* Michx. (aspen), *Quercus* spp. (oak), *Prunus serotina* Ehrh. (black cherry), and *Rubus* spp. (dewberry).

DISCUSSION

A major effect of fire on vegetation is the addition and loss of species through mechanisms involving both site factors and characteristics of the preburn vegetation (including propagules). These mechanisms include creation of large openings in the forest canopy and forest floor, increased nutrient availability (Ahlgren 1960, St. John and Rundel 1976, Wells 1979), increased soil temperatures and soil moisture (Ahlgren and Ahlgren 1960, Wells 1979), stimulation of sprouting of preexisting vegetation and germination of buried seed (Sweeney 1956, Muller *et al.* 1968, Christensen and Muller 1975, Tredici 1977), volatilization of allelopathic chemicals (Muller *et al.* 1968, Christensen and Muller 1975) and increased soil microbial activity (Ahlgren and Ahlgren 1960, Wells 1979).

The increase in species richness and dominance of certain plant groups occurring after fire seen in this study is a phenomenon which has been described in a variety of ecosystems (Little and Moore 1949, Ahlgren and Ahlgren 1960, Dyrness 1973, Shafi and Yarranton 1973, Christensen and Muller 1975, Purdie and Slatyer 1976). This increased diversity is usually temporary, lasting only a few years. A shift is typically seen in plant composition and dominance away from invading species, which establish themselves by seed initially after fire, to those species present before the fire which reestablish themselves largely by vegetative means.

The postfire successional trends previously reported from the Lake States, however, do not always follow this pattern. For example, Ohmann and Grigal (1979) studied early revegetation of the Little Sioux wildfire in northeastern Minnesota but did not find an abundance of disturbance species. Except for the presence of a few "fire followers", such as geranium and rock-harlequin, species composition before and after fire were nearly identical. Vogl (1970), working in the northern Wisconsin pine barrens, found that the frequency of occurrence of barren species did not show a significant response to burning. Changes in understory balsam fir and paper birch vegetation following timber harvest in northern Minnesota were reported by Outcalt and White (1981). They showed decreased diversity of nearly all species groups on logged and burned sites compared to unburned logged sites; however, high densities of geranium and rock-harlequin after fire were found. Ahlgren (1959) grouped vegetational data from 11 series of plots in the northern coniferous forests of Minnesota and found 60 species exclusive to burned areas, 4 species exclusive to unburned areas, and 35 species common to both areas. These data indicate that large increases in species richness follow fire. Krefting and Ahlgren (1974), however, reported changes in species composition from this same study area, specifically by site, and showed that burning resulted in either no significant change or decreased species richness compared to unburned controls.

The above studies report data from prescribed burns and wildfires that took place during the spring (Ahlgren 1960, 1974, Vogl 1970, Ohmann and Grigal 1979) and summer (Ahlgren 1960, 1974, Outcalt and White 1981), but none reported a large site-specific increase in species diversity after fire as seen in this study. I found, as did Ahlgren, that burning clearly promotes the establishment of a large variety of species not typical to unburned areas. A total of 73 different species were recorded on burned sites compared to 49 on unburned sites. However, nearly all burned sites in this study showed greater species richness compared to analogous unburned sites (Fig. 3.1). Increases in the number of annuals and biennials, grasses, and perennial herbs following fire were found. The establishment of new species following fire results from viable seed stored in the forest floor or transported by wind and animal vectors. Studies have shown that viable seed from species of all successional ages are ubiquitous in the floor under forest stands (Livingston and Allessio 1968, Tredici 1977, Ahlgren 1979a).

The longevity of many fire-followers is short; two years after fire many are gone (note decreased species richness in burned sites between years 1 and 2, Table 3.2 and Fig. 3.1). In the latter years after fire, species that were probably members of the pre-existing vegetation and which establish and perpetuate themselves mainly by vegetative means dominate. Four, 5, and 6-year-old burned sites (sites 10A79-80-81 and 10B79-80-81) retained a high level of diversity comprising a mixture of fire-stimulated grasses and herbs, whose presence appears to be waning, and trees and shrubs, whose dominance appears to be increasing (Table 3.2).

These findings represent important contrasts in the early successional development on the burned and unburned clearcuts in this study. Major differences in dominance and diversity of all species groups during the early revegetation process is seen on the burned and unburned clearcuts. The most important contrast, and certainly the most observable in the field, is the different pathways of vegetational development characterized on these sites. On all burned and unburned clearcut areas jack pine regeneration is failing to become established, and these sites are dominated by other vegetation. The unburned clearcuts are being converted to essentially *Carex* "meadows" (Plate 3.1). The only other vegetation of any consequence are oak and cherry stump sprouts and blueberry growing in and around the shade of slash piles (logging debris). In contrast, burned clearcuts are being converted to early successional hardwoods such as aspen, oak, and black cherry. Shrub species, such as blueberry, willow, *Ceanothus*, and *Amelanchier* are also important on these sites (Plate 3.2). *Carex* is also a dominant member of the older burned sites, but there is little indication that these sites will be converted to a *Carex* "meadow." In fact, the dominance of *Carex* is being checked by tree and shrub species mentioned above and graminoids such as *Oryzopsis asperifolia* and *Schizachne purpurascens*.

An increase in sedges following fire has been

Plate 3.1. *Carex* meadow established on a 5-year-old unburned clearcut site.

Plate 3.2. Shrubs and early successional hardwoods dominating a 5-year-old prescribed burn site.

previously documented (Ahlgren 1960, Vogl 1970, Outcalt and White 1981). However, the overwhelming dominance of Carex observed in this study seems to be unique to jack pine sites in northern lower Michigan. A Carex "meadow", once established, appears capable of excluding tree and shrub seedling reproduction for many years (Niering and Goodwin 1974, Noble 1980). The dominance of Carex on unburned clearcuts prevented the establishment of a multilayered canopy, as observed on the burned clearcuts. The monolayered Carex canopy on unburned clearcuts was responsible for the lack of increase in total cover over the temporal sequence. By years 5 and 6 after treatment, burned clearcuts had 47% and 63% more vegetation cover, respectively, than unburned clearcuts.

There are several possible mechanisms that explain the dominance of Carex pensylvanica. One possibility may be Carex's ability to exploit nutrients and space made available following a perturbation such as clearcutting and/or burning. Recent studies involving disturbances have shown that certain exploitative species, due to their life-history characteristics, can monopolize resources liberated by disturbance and suppress or exclude other species. Marks's work (1974) on New Hampshire clearcuts has shown pin cherry (Prunus pensylvanica L.) to be such an exploitative species. Bakelaar and Odum (1978) concluded that a few opportunistic species already established on abandoned fields in Georgia were able to expand their niches after fertilization by pre-empting certain subordinates, thus reducing overall diversity. Ahlgren (1960) showed that nutrients released following fire have fertilizing effects that stimulate the growth of certain species. The results of a study initiated in May to test this hypothesis are discussed in Chapter 6. A second explanation for the dominance of *Carex*, although untested, is its possible release of a chemical inhibitor (allelochem).

At this time I cannot fully explain the contrasting successional pathways followed on burned and unburned jack pine clearcuts. However, from the formal characterization of early revegetation of these sites and my own personal observations, the following points are probably important in answering this question. Canopy removal without subsequent burning results in the rapid formation of a near monoculture of *Carex pensylvanica*. Canopy removal followed by fire also promoted the spread of sedges, but in addition promoted the establishment of a large variety of new species and the rapid spread of many species that were probably members of the preexisting vegetation. These dramatic effects of fire on species composition and species relative dominance altered the competitive abilities of *Carex*. Following fire there was the establishment and continued development of a multilayered canopy consisting of graminoids, herbs, shrubs, and small trees. The shade provided by the canopy appeared to check the further spread of *Carex*. Further proof that the competitiveness of *Carex* is lowered in shaded situations is its high frequency but very low relative cover under a mature jack pine canopy. Also, a consistent pattern observed on unburned clearcuts was the vigorous growth of blueberry in and around the shade of the slash piles, while *Carex* dominated the larger open areas.

CHAPTER IV

MULTIPLE PATHWAYS IN EARLY SUCCESSIONAL DEVELOPMENT FOLLOWING DISTURBANCE TO JACK PINE STANDS IN NORTHERN LOWER MICHIGAN

Introduction

Of all the anthropogenic and natural disturbances, fire has been the most widely studied. Secondary plant succession has been a major theme in the fire ecology literature, and numerous terms and models have been proposed to describe it. Godwin (1929) used "deflected succession" to describe successional development following burning, grazing, and cutting, which differed from the "normal succession" in the absence of disturbance. Egler (1954) hypothesized an "initial floristic composition" (IFC) model for old-field vegetation development which has been similarly used to describe community development following fire (Purdie and Slatyer 1976). According to Egler, a field receives many different propagules up to the time of abandonment; after abandonment development unfolds from this initial flora, without additional increments by further invasions. Egler recognized that several equilibria may exist on a given site, and succession could be arrested if the woody plant species that would dominate the mature community were killed at some intermediate stage. Richards (1955) termed different secondary successions "progressive" if, following clearing, a young secondary forest rapidly establishes which eventually leads to a forest like the original, or "regressive" if a savanna develops with few or no trees. Loucks (1970) concluded there is a natural tendency in forest systems toward periodic perturbation that recycles the system and maintains a periodic wave of peak diversity. Connell and Slatyer (1977) outlined the "inhibition model", which describes a postdisturbance successional process where earlier colonists secure space and/or other resources and inhibit the invasion of subsequent colonists, or suppress or exclude the growth of those already present. Their model outlines the apparent mechanism involved in arrested or regressive succession.

In the Lake States, limited detailed work has been conducted on the characterization of plant succession following fire (Ahlgren 1960, Vogl 1970, Krefting and Ahlgren 1974, Ohmann and Grigal 1979, Outcalt and White 1981, Scheiner and Teeri 1981) and logging (Outcalt and White 1981). However, similar studies on jack pine sites in Michigan have not been published.

In this chapter, detailed comparisons of species composition and species dominance are made between disturbed sites (clearcut and/or burned) and undisturbed jack pine stands. Conclusions are drawn concerning the direct effects of clearcutting and/or burning on these jack pine communities and subsequent early successional trends. Comparisons among sites show that multiple successional pathways are evident soon after disturbance.

Methods

On each site, all vascular plants were characterized by frequency and cover measurements as described in Chapter 3. In the mature and 35-year-old jack pine stands, only the understory vegetation (plants $\leq$ 1.5 m tall) were characterized.

Results

Unburned Clearcut Sites Versus Mature Jack Pine Stands

All unburned clearcut sites included for study were formerly mature jack pine. The four mature jack pine stands surveyed were used, therefore, as representative of the predisturbance condition. Each site, although rigorously selected, was unique, in that they varied to some extent in predisturbance species composition and dominance, seed pool composition, nearby sources of invading propagules, and severity and timing of the disturbance. However, certain overall successional trends can be discerned.

Relative cover and relative frequency data for each species on unburned and burned clearcut sites, as well as burned 35-year-old jack pine sites, intermediate-age and mature jack pine stands are shown in Appendices A, B, and C, respectively.

Clearcut sites initially had increased total species richness compared to the undisturbed forested stands. However, species richness generally decreased on clearcut sites over the six year sequence, resulting in most older clearcut sites having lower species richness than mature jack pine understories (Fig. 4.1 and Table 4.1). Similar trends in average richness per plot and the Shannon index were found.

As shown in Table 4.2, 51 different species were recorded on clearcut sites compared to 41 species on mature jack pine sites. Increases in grass and perennial herb species on clearcut sites are evident; in fact, increases in these species groups were responsible for the initial rise in species richness on recent clearcut sites (Fig. 4.1 and Table 4.1).

It appears that total vegetational cover on clearcut sites varied little from that of the understory of forested stands (Fig. 4.2). However, when sites are examined individually, clearcutting did, in fact, cause changes in the total plant cover and cover of individual

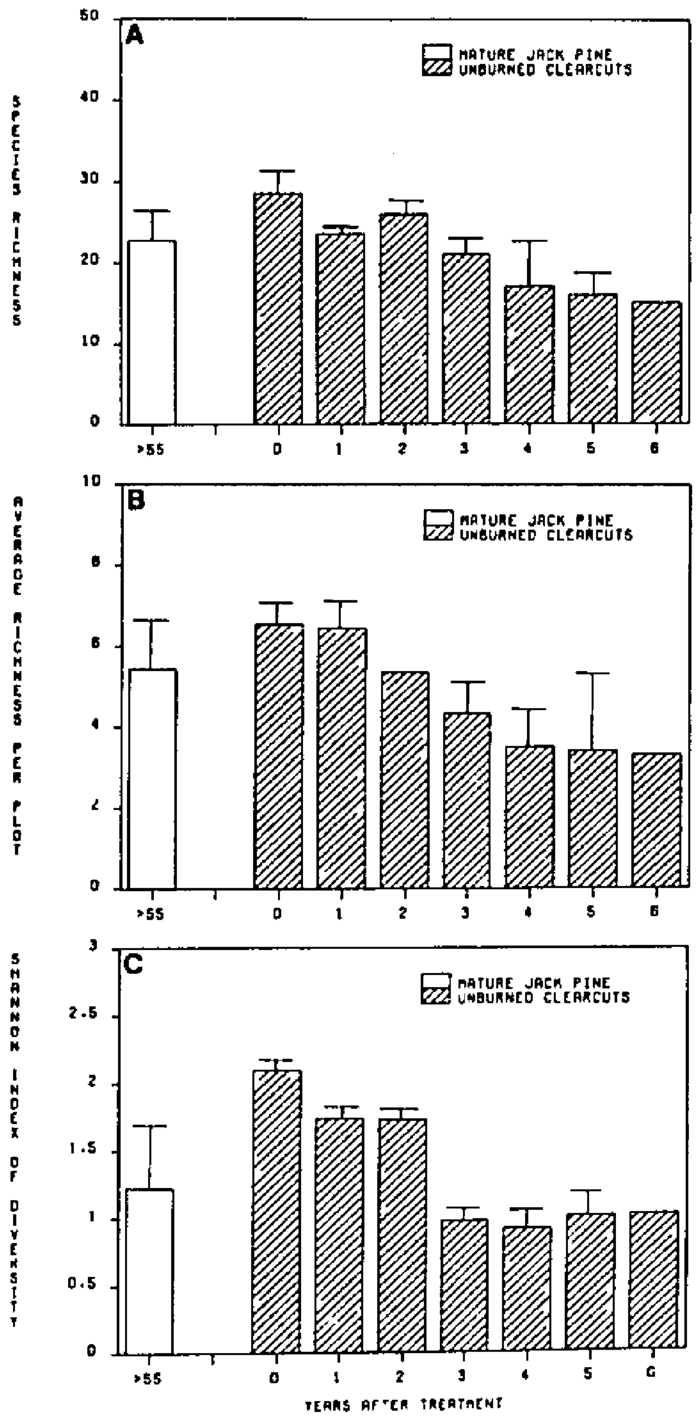

Fig. 4.1. A) Species richness (total number of species), B) average richness per plot, and C) Shannon index of diversity, of sites averaged within years, for mature jack pine stands and unburned clearcut jack pine sites comprising a 6-year sequence following logging. Vertical bars equal one standard deviation (SD).

TABLE 4.1

RELATIVE COVER (C), RELATIVE FREQUENCY (F), AND SPECIES RICHNESS (R)
FOR VEGETATIONAL GROUPS ON MATURE JACK PINE STANDS
AND UNBURNED CLEARCUTS

Site Number[a]	Years Since Treatment	Area	Annuals & Biennials			Grasses & Sedges			Perennial Herbs			Trees & Shrubs			Total R	Total Cover per 60 m
		ha	C	F	R	C	F	R	C	F	R	C	F	R		
13A	≥ 55	12	2.1	11.6	1	3.5	25.6	3	.3	11.6	5	94.1	51.3	9	18	30.7
13B	≥55	4	1.2	14.9	1	15.7	28.4	6	8.5	14.9	7	75.0	41.9	7	21	32.1
13C	≥55	8	.8	9.8	1	13.7	17.5	4	28.8	25.8	7	56.7	46.9	11	23	42.7
13D	≥55	3	.6	7.4	1	9.7	18.4	4	41.2	30.5	8	48.4	43.7	14	27	71.6
1A	0	16	-	.7	1	32.5	26.1	6	15.0	31.2	9	52.5	42.0	10	26	30.0
1B80	0	16	.49	-	2	12.9	20.4	7	29.9	33.3	9	56.7	46.3	13	31	61.5
1B81	1	16	-	.5	1	27.2	22.5	5	34.3	26.7	8	38.5	50.4	9	23	61.5
2	1	24	-	-	-	24.7	27.6	5	7.1	23.2	12	68.2	49.2	7	24	27.6
3A	2	16	-	-	-	49.6	43.8	9	21.6	21.6	9	29.1	34.6	9	27	50.7
3B79	2	16	-	1.9	1	36.5	24.8	5	13.6	32.2	10	49.6	41.1	9	25	37.1
3B80	3	16	-	-	-	53.1	32.0	7	4.3	26.0	7	42.5	42.0	8	22	46.9
4A79	3	32	.1	-	1	83.4	52.7	7	5.1	16.4	6	11.4	30.9	6	20	37.7
3B81	4	16	-	1.5	1	45.7	30.4	6	1.6	23.9	6	52.7	44.2	9	22	64.4
4A80	4	32	-	-	-	68.8	50.0	6	.3	10.3	5	30.9	39.5	8	19	60.5
5A79	4	4	-	-	-	77.2	35.7	2	2.2	14.3	1	20.7	50.0	7	10	41.7
4A81	5	32	-	-	-	81.8	51.6	6	.1	9.5	5	18.0	39.0	7	18	58.9
5A80	5	4	-	-	-	67.3	37.1	5	2.9	19.3	4	29.8	43.5	5	14	44.7
6	5	16	-	-	-	77.3	45.6	3	.2	2.9	3	22.5	51.5	10	16	30.1
5A81	6	4	-	-	-	65.6	35.0	4	5.7	18.0	4	28.7	47.0	7	15	46.8

[a]Site numbers starting with the same combination of number and letter represent the same site surveyed twice; the number 79, 80, and 81 indicate the year surveyed (1979, 1980, and 1981), for sites surveyed in more than one growing season.

TABLE 4.2

PLANT SPECIES ENCOUNTERED ON UNBURNED CLEARCUT SITES AND MATURE JACK PINE (>55 YEARS) STANDS IN NORTHERN LOWER MICHIGAN

Species Exclusive to Unburned Clearcut Sites
(18 species total)

Annuals and Biennials
(2 species)

Arabis glabra L.
Lactuca canadensis L.

Grasses and Sedges
(5 species)

Agrostis hyemalis Walt.
Deschampsia flexuosa L.
Dichanthelium depauperatum Muhl.
Oryzopsis asperifolia Michx.
Panicum columbianum Schribn.

Perennial Herbs
(7 species)

Antennaria neglecta Greene
Asclepias syriaca L.
Hieracium aurantiacum L.
Liatris novae-angliae Lunell
Physalis virginiana Mill
Spiranthes gracilis (Bigel.) Beck
Viola pedatifida G. Don.

Trees and Shrubs
(4 species)

Diervilla lonicera Mill.
Prunus virginiana L.
Rosa blanda Ait.
Salix glaucophylloides Fern.

Species Exclusive to Mature Jack Pine Stands
(8 species total)

Grasses and Sedges
(1 species)

Muhlenbergia mexicana L.

Perennial Herbs
(3 species)

Chimaphila umbellata (L.) Nutt
Potentilla tridentata Ait.
Viola adunca Sm.

Trees and Shrubs
(4 species)

Acer rubrum L.
Ceanothus ovatus Desf.
Pinus strobus L.
Rubus hispidus L.

TABLE 4.2 (Continued)

Species Common to Both Unburned Clearcuts and Mature Jack Pine Stands (33 species total)

Annuals and Biennials (1 species)

Melampyrum lineare Lam.

Grasses and Sedges (7 species)

Andropogon gerardii Vitman
Bromus kalmii Gray
Carex pensylvanica Lam.
Danthonia spicata (L.) Beauv.
Koeleria macrantha Pers.
Oryzopsis pungens Torr.
Schizachne purpurascens Torr.

Perennial Herbs (11 species)

Apocynum androsaemifolium L.
Anemone quinquefolia L.
Aster laevis L.
Campanula rotundifolia L.
Fragaria virginiana Duchesne
Gaultheria procumbens L.
Helianthus occidentalis Ridd.
Hieracium venosum L.
Maianthemum canadense Desf.
Pteridium aquilinum Desf.
Solidago spp.

Trees and Shrubs (14 species)

Amelanchier sp.
Arctostaphylos uva-ursi L.
Comptonia peregrina L.
Crataegus sp.
Epigea repens L.
Pinus banksiana Lamb.
Populus tremuloides Michx.
Prunus pumila L.
Prunus serotina Ehrh.
Quercus spp. (red oak)
Rubus pensilvanicus Poir.
Vaccinium angustifolium Ait.
Vaccinium myrtilloides Michx.
Vaccinium vacillans Torr.

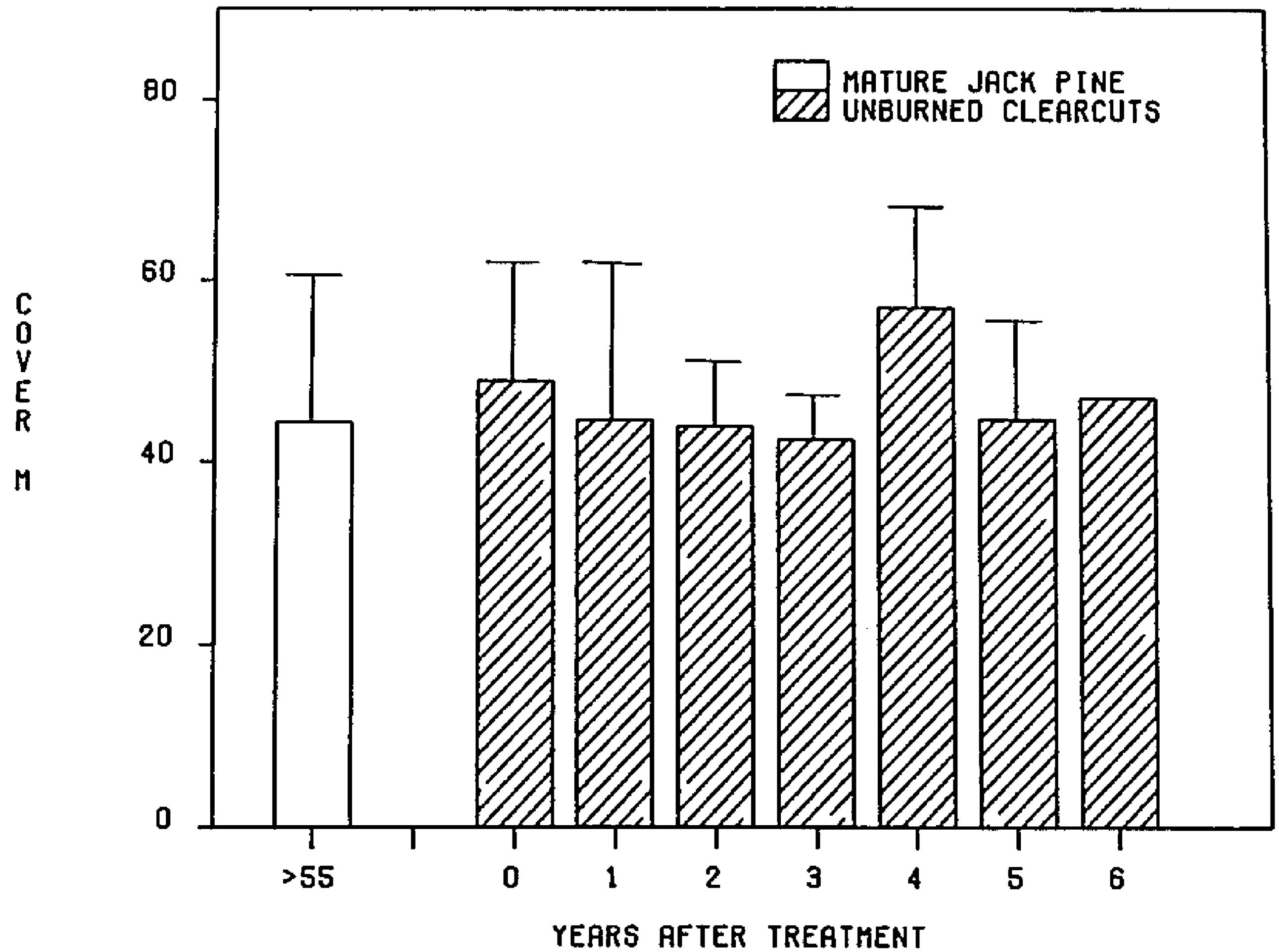

Fig. 4.2. Total vegetational cover (m), of sites averaged within years, for mature jack pine stands and unburned clearcut jack pine sites comprising a 6-year sequence following logging. Vertical bars equal one SD.

species (Table 4.1). For example, on site 1B80 (0-year clearcut) a large drop in cover is seen when compared to site 13D (an adjacent mature jack pine stand) due to decreased bracken fern cover. A large drop in blueberry was also seen on site 1B80, but this was offset by an increase in Amelanchier sp. (serviceberry). Mature jack pine site 13B lies adjacent to site 5A79 (4-year-old clearcut). Increased cover on site 5A79 was due to the extraordinary increases in Carex cover, which more than compensated for the drastic decrease in blueberry. In general, cover increased from one year to the next, based on data from sites surveyed over more than one growing season.

Cover of annuals and biennials was negligible in the mature forests and all clearcut sites (Fig. 4.3). However, cow wheat (Melampyrum lineare Lam.) was quite frequent on mature jack pine sites (Table 4.1). The grass and sedge species group showed extraordinary increases in dominance after clearcutting. This group dominated by Carex pensylvanica Lam., represented 10% of the cover in the mature jack pine understory and 75% of the cover by the fifth year after clearcutting. Perennial herb cover increased sharply initially following clearcutting, but was drastically reduced as the dominance of Carex increased. Tree and shrub species (e.g. blueberry) dominated mature jack pine stands, but showed

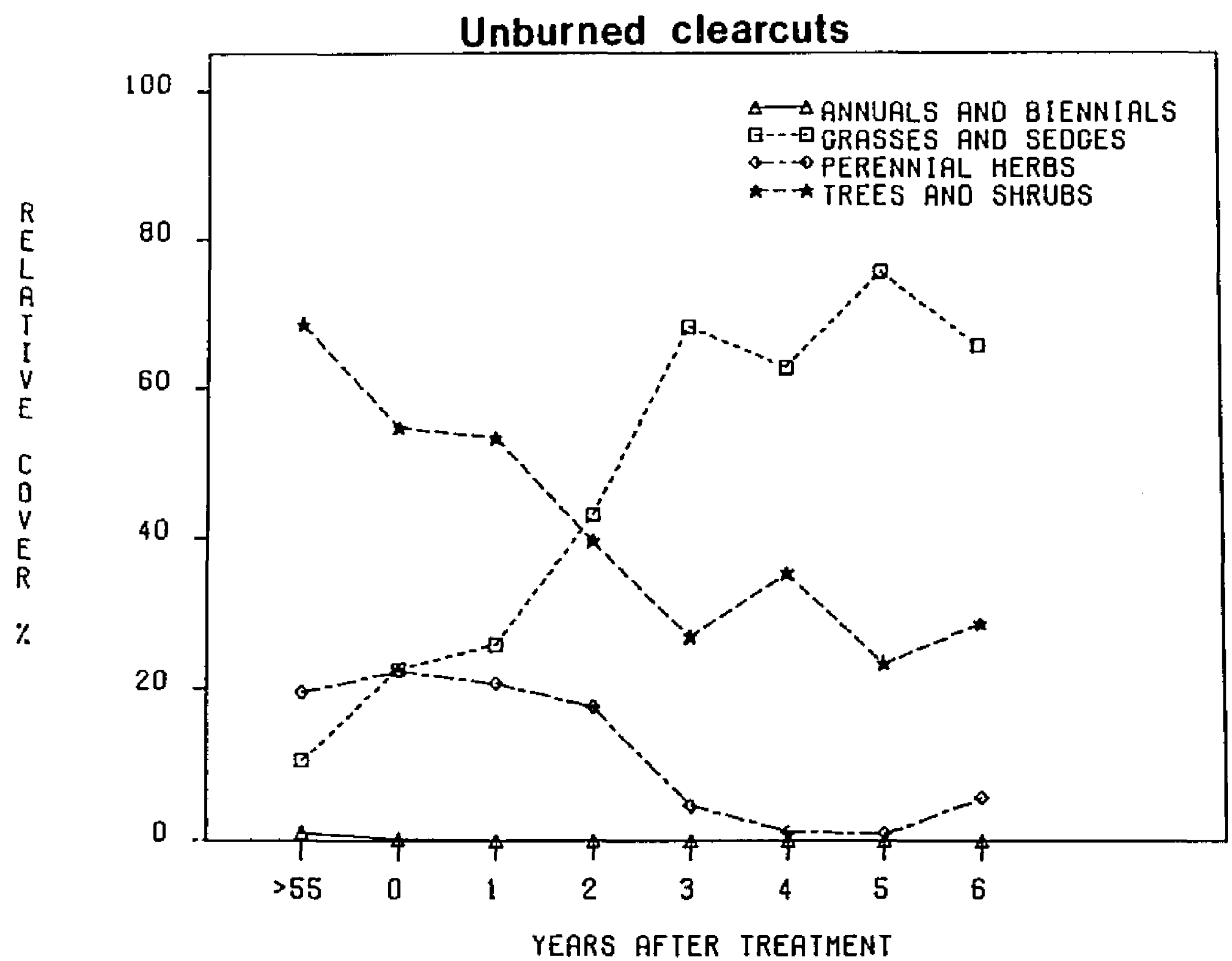

Fig. 4.3. Relative cover for each species group, of sites averaged within years, for mature jack pine stands and unburned clearcut sites comprising a 6-year sequence following logging.

a rapid decrease following clearcutting.

Burned Clearcuts Versus Mature Jack Pine Stands

All burned clearcut sites were of mature jack pine origin. The four mature jack pine stands surveyed in this study were considered representative of the predisturbed condition.

During the first year following burning, clearcuts showed greatly increased levels of species richness compared to mature jack pine stands (Fig. 4.4), but species richness on these sites (7C80-81 and 7D79-80-81) dropped drastically 2 and 3 years after burning. High levels of species richness, similar to that at year one, were also seen on sites 10A79-80-81 and 10B79-80-81, 4, 5, and 6 years after burning (Table 4.3). Different trends developed in the average richness per plot and Shannon index. One-year-old burned sites and mature jack pine sites were similar in average richness, but showed considerable variation in this index. A gradual drop in average richness per plot occurred during years 2 and 3. On sites 10A and 10B the highest levels of this index were seen during years 4, 5 and 6. All burned clearcuts, averaged within age classes, had higher levels of the Shannon index compared to mature jack pine sites. Trends in this index did not show any pattern, but

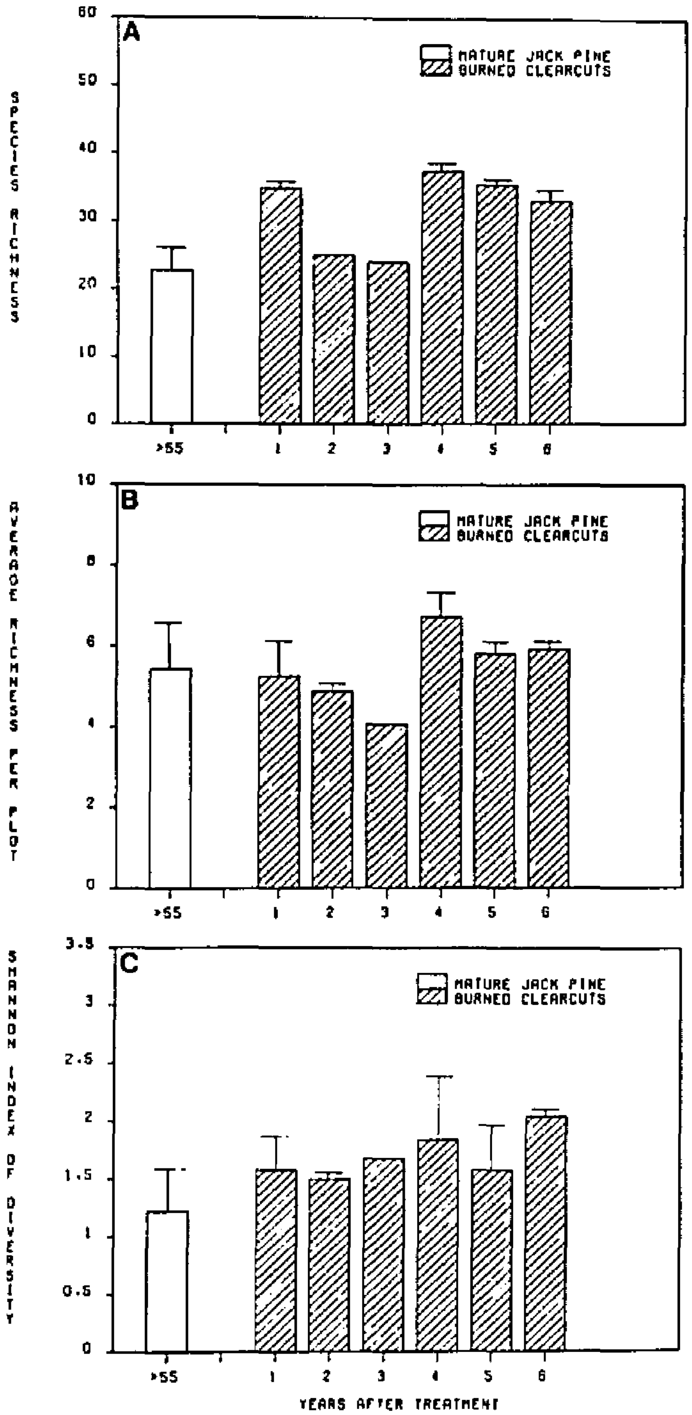

Fig. 4.4. A) Species richness (total number of species), B) average richness per plot, and C) Shannon index of diversity, of sites averaged within years, for mature jack pine stands and burned clearcut sites comprising a 6-year sequence following burning. Vertical bars equal one SD.

TABLE 4.3

RELATIVE COVER (C), RELATIVE FREQUENCY (F), AND SPECIES RICHNESS (R) FOR VEGETATIONAL GROUPS ON MATURE JACK PINE STANDS AND BURNED CLEARCUTS

Site[a] Number	Years Since Treatment	Area	Annuals & Biennials			Grasses & Sedges			Perennial Herbs			Trees & Shrubs			Total R	Total Cover per 60 m
		ha	C	F	R	C	F	R	C	F	R	C	F	R		
13A	≥55	12	2.1	11.6	1	3.5	25.6	3	.3	11.6	5	94.1	51.3	9	18	30.7
13B	≥55	4	1.2	14.9	1	15.7	28.4	6	8.5	14.9	7	75.0	41.9	7	21	32.1
13C	≥55	8	.8	9.8	1	13.7	17.5	4	28.8	25.8	7	56.7	46.9	11	23	42.7
13D	≥55	3	.6	7.4	1	9.7	18.4	4	41.2	30.5	8	48.4	43.7	14	27	71.6
7C80	1	16	18.3	7.1	4	35.8	32.0	9	2.8	26.1	15	43.1	34.8	7	35	26.9
7D79	1	24	.1	2.8	3	73.5	44.6	9	8.5	24.3	12	17.8	28.1	10	34	30.6
7C81	2	16	-	-	-	45.7	38.4	8	1.1	13.2	10	53.2	48.3	7	25	52.6
7D80	2	24	-	-	-	71.6	56.3	9	12.4	21.1	8	15.8	22.5	8	25	48.5
7D81	3	24	-	-	-	66.7	52.5	8	14.3	25.1	8	19.1	22.7	8	24	48.7
10A79	4	26	-	1.6	1	71.8	35.7	13	15.2	39.3	13	13.0	23.3	9	36	58.2
10B79	4	23	.2	3.9	1	53.5	40.0	14	22.9	23.3	10	23.4	32.8	14	39	45.4
10A80	5	26	.1	1.7	2	57.3	38.2	11	18.5	32.9	16	24.1	27.2	7	36	75.7
10B80	5	23	.8	5.4	3	57.3	37.3	10	8.0	23.5	8	33.8	33.9	14	35	61.6
10A81	6	26	.2	.6	2	66.4	39.3	8	8.9	34.9	14	24.5	25.2	8	32	74.4
10B81	6	23	.8	2.3	1	50.3	38.3	9	12.2	21.4	10	36.7	38.0	14	34	74.8

[a]See Table 4.1.

highest levels were attained 6 years after burning.

Burning stimulated the establishment of a large variety of species not present in mature jack pine stands (Table 4.4). Seventy-six different species were recorded on burned clearcut sites compared to 41 species on mature jack pine sites. Thirty-nine species were exclusive to burned clearcut sites, whereas only 4 species were exclusive to mature jack pine sites.

One year after fire, burned clearcut sites had greatly decreased vegetational cover compared to mature jack pine sites (Fig. 4.5). However, large increases in cover occurred by year 2, with further increases during years 5 and 6. Generally, cover increased from one year to the next on sites surveyed over more than one growing season. Different species contributed to these increases in cover. For example, on site 7C80-81, Carex, Vaccinium, Prunus pumila L. (sand cherry), and Oryzopsis pungens Torr. were important; whereas on site 7D79-80-81, Pteridium aquilinum L. (bracken fern) and Dichanthelium depauperatum Muhl. contributed most to the cover. On site 10A79-80-81 large increases were noted in Carex, Vaccinium, Pteridium aquilinum, Schizachne purpurascens Torr., and Prunus serotina Ehrh. (black cherry), while on site 10B79-80-81 increased cover was due to Carex,

TABLE 4.4

PLANT SPECIES ENCOUNTERED ON BURNED CLEARCUT SITES AND MATURE JACK PINE (≥ 55 YEARS) STANDS IN NORTHERN LOWER MICHIGAN

Species Exclusive to Burned Clearcut Sites
(39 species total)

Annuals and Biennials
(7 species)

Arabis glabra L.
Cirsium sp.
Corydalis sempervirens L.
Erigeron canadensis L.
Geranium bicknellii Britt.
Lactuca canadensis L.
Lithospermum arvense L.

Grasses and Sedges
(12 species)

Agropyron trachycaulum Link
Agrostis hyemalis Walt.
Bromus kalmii Gray
Deschampsia flexuosa L.
Dichanthelium depauperatum Muhl.
Festuca sp.
Koeleria macrantha Pers.
Oryzopsis asperifolia Michx.
Panicum columbianum Scribn.
Panicum xanthophysum Gray
Poa pratensis L.
Sorghastrum nutans L.

Perennial Herbs
(12 species)

Aster sagittifolius Wedemeyer
Convolvulus spithamaeus L.
Helianthemum canadense Michx.
Hieracium aurantiacum L.
Hieracium canadense Michx.
Lechea minor L.
Liatris novae-angliae Lunell
Polygala polygama Walt.
Polygonum cilinode Michx.
Physalis virginiana Mill.
Rumex acetosella L.
Senecio tomentosus Michx.

Trees and Shrubs
(8 species)

Diervilla lonicera Mill.
Gaylussacia baccata (Wang.) C. Koch
Potentilla arguta Pursh.
Prunus virginiana L.
Rosa blanda Ait.
Symphoricarpos albus L.

Species Exclusive to Mature Jack Pine Stands
(4 species)

Grasses and Sedges
(1 species)

Andropogon scoparius Michx.

Perennial Herbs
(1 species)

Chimaphila umbellata (L.) Nutt.)

Trees and Shrubs
(2 species)

Pinus strobus L.
Rubus hispidus L.

TABLE 4.4 (Continued)

Species Common to Both Burned Clearcuts and Mature Jack Pine Stands (37 species total)

Annuals and Biennials (1 species)

Melampyrum lineare Lam.

Grasses and Sedges (7 species)

Andropogon gerardii Vitman
Bromus kalmii Gray
Carex pensylvanica Lam.
Danthonia spicata (L.) Beauv.
Muhlenbergia mexicana L.
Oryzopsis pungens Torr.
Schizachne purpurascens Torr.

Perennial Herbs (13 species)

Anemone quinquefolia L.
Apocynum androsaemifolium L.
Aster laevis L.
Campanula rotundifolia L.
Fragaria virginiana Duchesne
Gaultheria procumbens L.
Helianthus occidentalis Ridd.
Hieracium venosum L.
Maianthemum canadense Desf.
Potentilla tridentata Ait.
Pteridium aquilinum Desf.
Solidago sp.
Viola adunca Sm.

Trees and Shrubs (16 species)

Acer rubrum L.
Amelanchier sp.
Arctostaphylos uva-ursi L.
Ceanothus ovatus Desf.
Comptonia peregrina L.
Crataegus sp.
Epigea repens L.
Pinus banksiana Lamb.
Populus tremuloides Michx.
Prunus pumila L.
Prunus serotina Ehrh.
Quercus spp. (red oak)
Rubus pensilvanicus Poir.
Vaccinium angustifolium Ait.
Vaccinium myrtilloides Michx.
Vaccinium vacillans Torr.

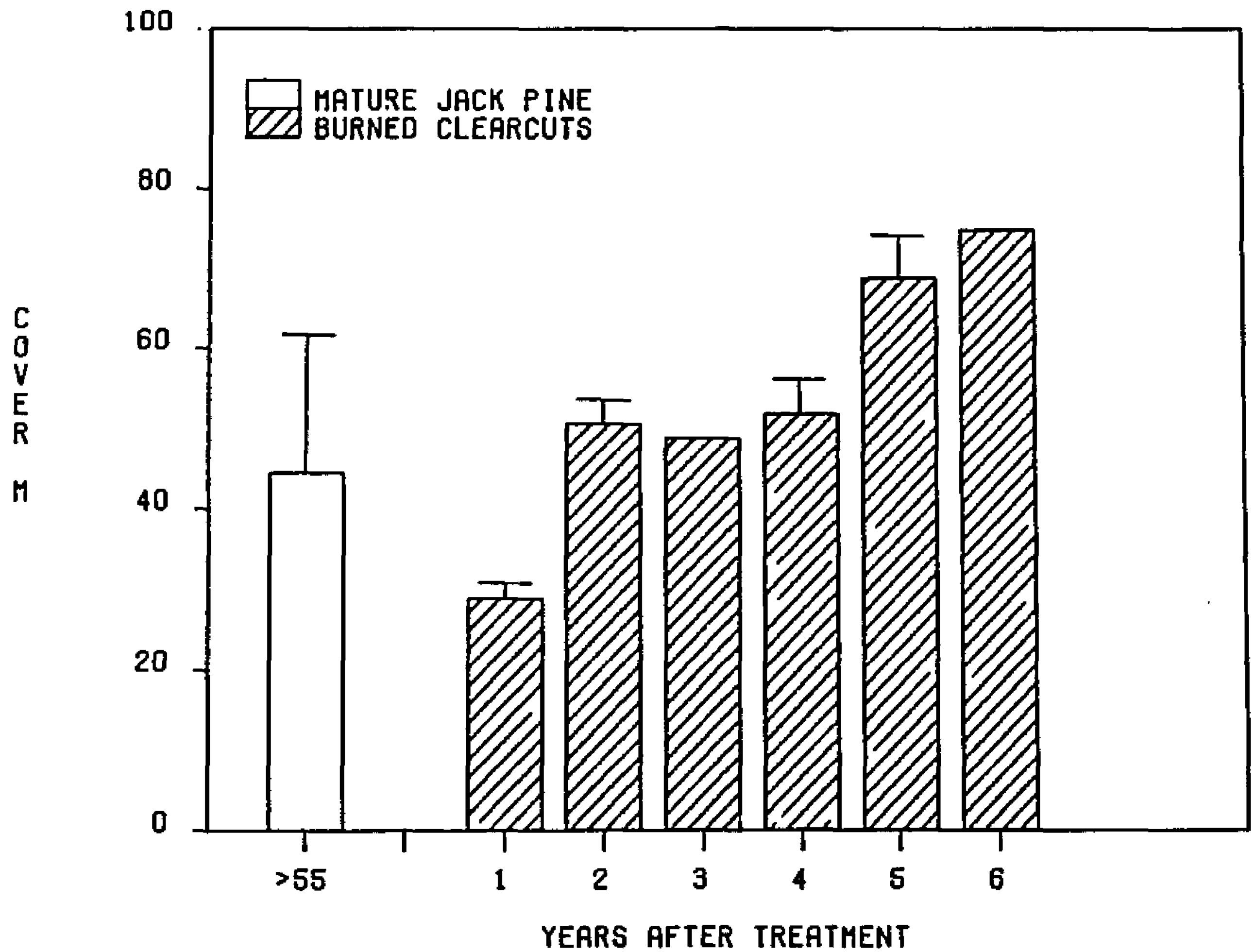

Fig. 4.5. Total vegetational cover (m), of sites averaged within years, for mature jack pine stands and burned clearcut sites comprising a 6-year sequence following burning. Vertical bars equal one SD.

Vaccinium, and Populus tremuloides Michx. (trembling aspen).

Whereas cover of annuals and biennials was negligible under mature jack pine, a sharp increase in cover of this group occurred one year after fire (Fig. 4.6). The presence of annuals and biennials, however, was different on the two sites (7C80 and 7D79) in this age class. The cover of these species, mainly Geranium bicknellii Britt. and Corydalis sempervirens L. (rock-harlequin), was exceptionally high (18.3%) on site 7C80, whereas it was negligible (.1%) on site 7D79. Species in this group were either absent or reduced to scattered individuals on the 2- to 6-year old burned clearcuts. Dramatic increases in grasses and sedges were seen on the burned clearcuts. For example, on 3-year-old sites, this species group represented an average 66% of the total vegetational cover. The grass and sedge species group was not entirely dominated by Carex, as seen on the unburned clearcut sites. This was especially true on the older burned sites (10A79-80-81 and 10B79-80-81), where grasses (e.g. Oryzopsis asperifolia Michx. and Schizachne purpurascens) represented 38% to 51% of the species group cover. In contrast, grasses represented only 1% to 5% cover of the grass and sedge species group on unburned clearcuts.

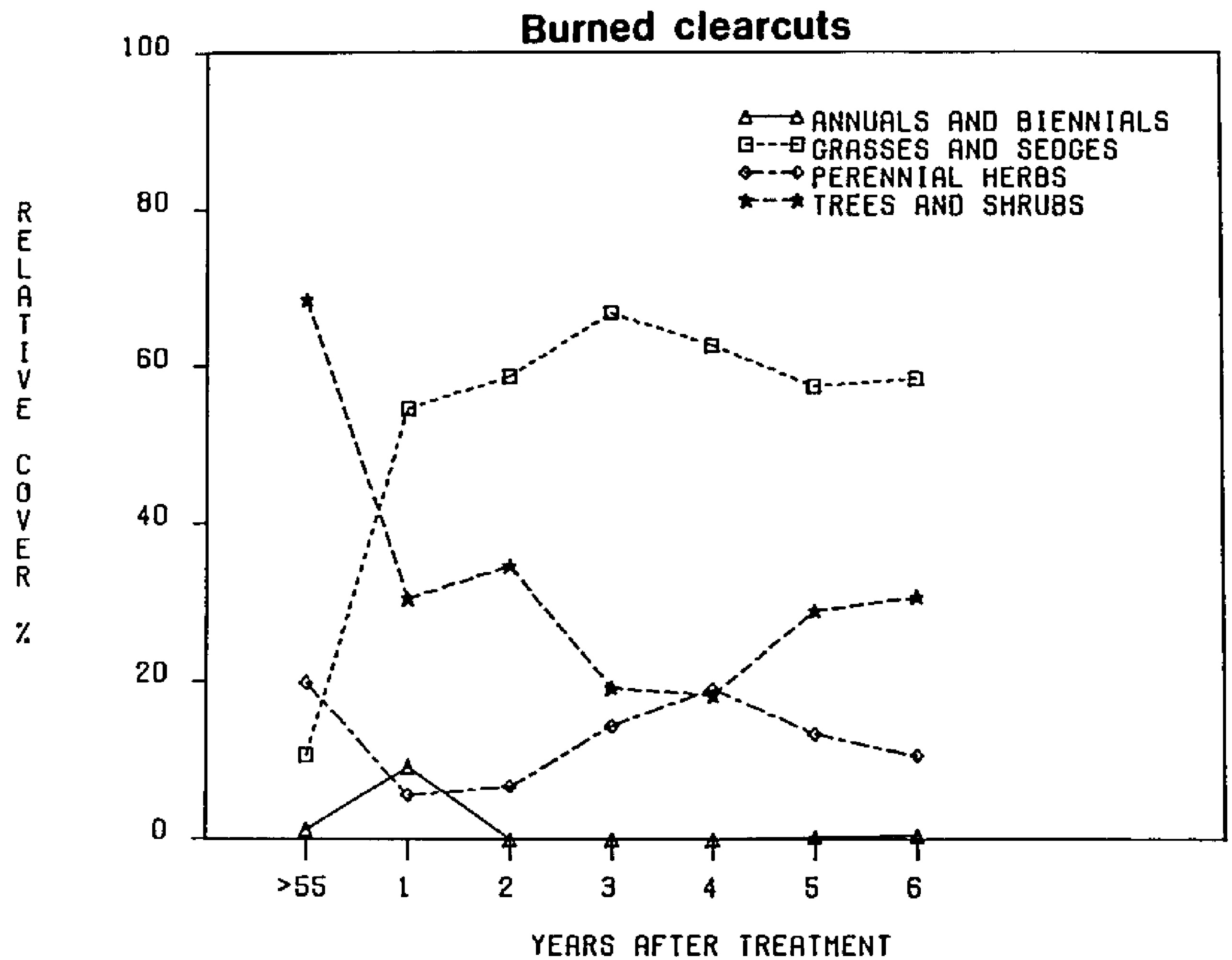

Fig. 4.6. Relative cover for each species group, of sites averaged within years, for mature jack pine stands and burned clearcut jack pine sites comprising a 6-year sequence following burning.

A sharp decline in cover of perennial herbs, mainly due to decreased cover of bracken fern, was seen when comparing mature jack pine sites to 1-year-old burned clearcuts (Fig. 4.6). The subsequent increase (years 1 to 4) and decrease (years 4 to 6) in perennial herb cover was also due to variation in bracken fern cover. Other perennial herb species, although contributing substantially to site richness, contributed little to total cover. A very large drop in tree and shrub cover, due to the loss of blueberry, was also noted in 1-year-old burned clearcuts. Cover of this species group generally declined through year 4, but sharply increased at year 5 due to increases in aspen, black cherry, blueberry, and dewberry (*Rubus pensilvanicus* Poir.).

Burned Versus Unburned 35-Year-Old Jack Pine

All burned and unburned areas were part of a larger area consumed by wildfire in 1946. The forest that subsequently developed was logged in 1975 and 1976 of financially mature jack pine, red pine, and oak. This area, dominated by intermediate-aged jack pine (representing postfire regeneration), was divided into blocks; some of these blocks were prescribe burned and others have remained unburned (see Chapter 2, site 7A80-81 for complete details). Five blocks, 3 burned and 2 unburned, have been surveyed and are used to contrast differences in unburned and burned stands, making up a postfire sequence of 1 to 5 years (Table 4.5).

Burned jack pine stands were considerably richer in species one year after fire than the unburned stands (Fig. 4.7), but a large drop in species richness occurred between years 1 and 2 (sites 7A80-81 and 7B79-80). Site 7B dropped from 45 to 30 species between years 1 and 2, although site 7A remained essentially unchanged (Table 4.5). A steady increase in species richness occurred from years 2 to 5, mainly due to site 9A79-80-81 (3-, 4-, and 5-year old burn). A drop in average richness per plot occurred during years 1 and 2, followed by increased levels of this index during years 3, 4, and 5. The Shannon index was higher the first year after fire, but lower during years 2, 3, and 4, followed by a sharp increase at year 5. Sixty-seven species were recorded on the burned sites compared to 43 species on the unburned stands (Table 4.6).

A large drop in cover occurred as a result of burning (Fig. 4.8), but the openings created by fire were very rapidly reoccupied, resulting in large increases in cover during years 2 and 3. Cover increased yearly on each site surveyed over more than one growing season.

TABLE 4.5

RELATIVE COVER (C), RELATIVE FREQUENCY (F), AND SPECIES RICHNESS (R) FOR VEGETATIONAL GROUPS ON UNBURNED 35-YEAR-OLD JACK PINE STANDS AND BURNED 35-YEAR-OLD JACK PINE STANDS

Site[a] Number	Years Since Treatment	Area	Annuals & Biennials			Grasses & Sedges			Perennial Herbs			Trees & Shrubs			Total R	Total Cover per 60 m
		ha	C	F	R	C	F	R	C	F	R	C	F	R		
12A	35	16	.1	.9	1	20.5	33.1	10	1.8	24.1	14	77.6	42.0	11	36	52.7
12B	35	24	-	2.6	1	26.1	36.5	9	3.5	21.9	11	70.4	39.1	8	29	51.4
7A80	1	19	14.2	13.3	4	30.5	34.4	10	2.5	13.3	12	52.8	39.0	10	36	35.8
7B79	1	26	25.6	12.0	5	27.0	34.8	13	8.1	18.0	13	38.7	34.8	14	45	28.7
7A81	2	19	.1	2.3	3	47.6	37.4	10	.9	12.4	11	51.4	47.8	10	34	49.8
7B80	2	26	-	1.1	2	60.8	44.0	10	12.9	14.7	10	26.3	40.1	8	30	43.7
7B81	3	26	.1	2.2	3	58.8	48.9	11	4.8	12.4	10	36.2	36.5	9	33	60.9
9A79	3	31	.6	-	2	63.7	41.0	12	1.2	14.9	12	34.4	44.2	12	38	54.9
9A80	4	31	-	.5	1	62.7	40.7	11	1.2	18.0	13	36.0	40.7	11	36	56.7
9A81	5	31	.15	.51	3	49.2	37.2	10	3.6	20.4	13	47.1	41.8	13	39	65.6

[a]See Table 4.1

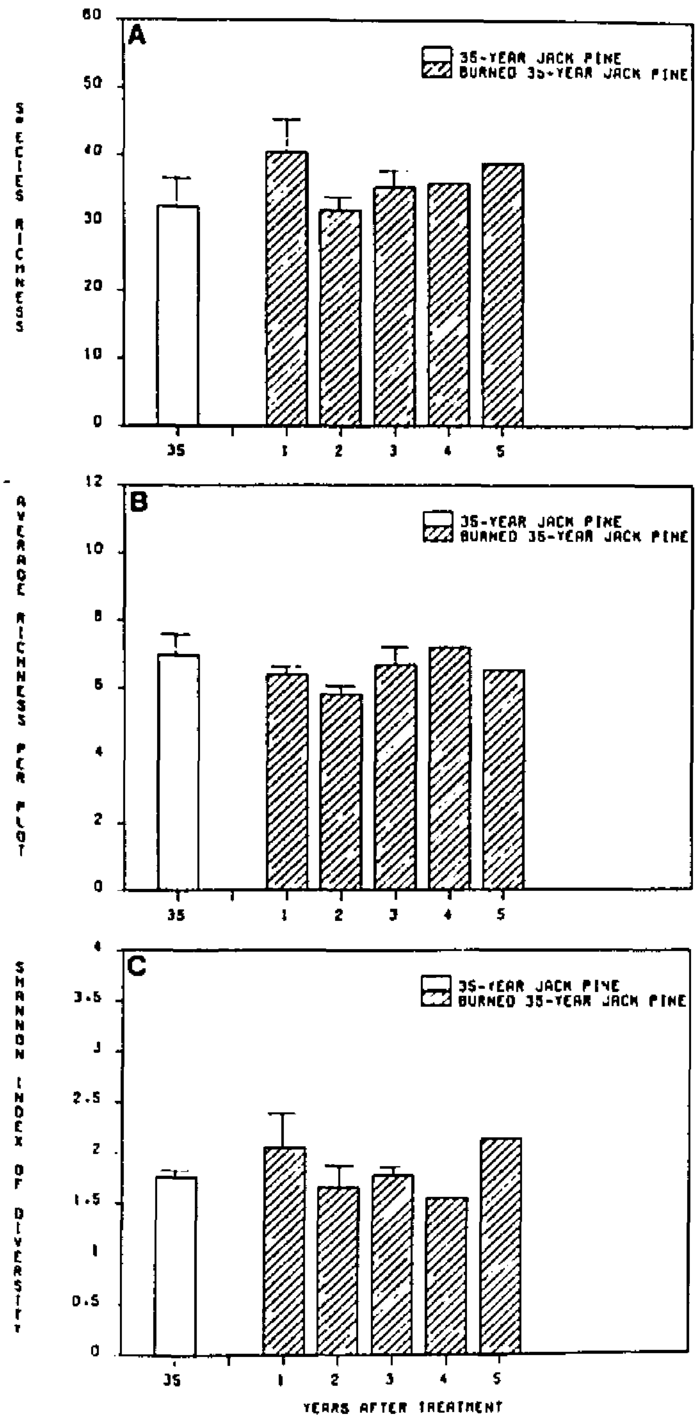

Fig. 4.7. A) Species richness, B) average richness per plot, and C) Shannon index of diversity, of sites averaged within years, for unburned 35-year-old jack pine stands and burned 35-year-old jack pine stands comprising a 5-year sequence following burning. Vertical bars equal one SD.

TABLE 4.6

PLANT SPECIES ENCOUNTERED ON BURNED AND UNBURNED 35-YEAR-OLD JACK PINE STANDS IN NORTHERN LOWER MICHIGAN

Species Exclusive to Burned Areas
(28 species total)

Annuals and Biennials
(7 species)

Cirsium sp.
Corydalis sempervirens L.
Erigeron canadensis L.
Geranium bicknellii Britt.
Krigia virginica L.
Lactuca canadensis L.
Silene antirrhina L.

Grasses and Sedges
(5 species)

Agropyron trachycaulum Link
Carex rugosperma Mack.
Festuca sp.
Koeleria macrantha Pers.
Sorghastrum nutans L.

Perennial Herbs
(11 species)

Anemone quinquefolia L.
Anemone riparia Fern.
Antennaria neglecta Greene
Campanula rotundifolia L.
Convolvulus spithamaeus L.
Equisetum hymale L.
Hieracium aurantiacum L.
Lechea minor L.
Maianthemum canadense Desf.
Polygonum cilinode Michx.
Viola pedatifida G. Don.

Trees and Shrubs
(5 species)

Crataegus sp.
Rosa blanda L.
Salix glaucophylloides Fern.
Symphoricarpos albus L.

Species Exclusive to Unburned Areas
(4 species)

Perennial Herbs
(4 species)

Cypripedium acaule Ait.
Gaultheria procumbens L.
Polygala polygama Walt.
Spiranthes gracilis (Bigel.) Beck

TABLE 4.6 (Continued)

Species Common to Both Burned and Unburned 35-Year-Old Jack Pine
(39 species total)

Annuals and Biennials
(1 species)

Melampyrum lineare Lam.

Grasses and Sedges
(12 species)

Andropogon gerardii Vitman
Andropogon scoparius Michx.
Bromus kalmii Gray
Carex pensylvanica Lam.
Danthonia spicata (L.) Beauv.
Deschampsia flexuosa L.
Dichanthelium depauperatum Muhl.
Muhlenbergia mexicana L.
Oryzopsis asperifolia Michx.
Oryzopsis pungens Torr.
Panicum columbianum Scribn.
Schizachne purpurascens Torr.

Perennial Herbs
(13 species)

Apocynum androsaemifolium L.
Aster junciformis Rydb.
Aster laevis L.
Fragaria virginiana Duchesne
Helianthemum canadense Michx.
Helianthus occidentalis Ridd.
Hieracium venosum L.
Liatris novae-angliae Lunell
Potentilla tridentata Ait.
Pteridium aquilinum Desf.
Senecio tomentosus Michx.
Solidago sp.
Viola adunca Sm.

Trees and Shrubs
(13 species)

Arctostaphylos uva-ursi L.
Amelanchier sp.
Ceanothus ovatus Desf.
Comptonia peregrina L.
Pinus banksiana Lamb.
Prunus pumila L.
Prunus serotina Ehrh.
Prunus virginiana L.
Quercus spp. (red oak)
Rubus pensilvanicus Poir.
Vaccinium angustifolium Ait.
Vaccinium myrtilloides Michx.
Vaccinium vacillans Torr.

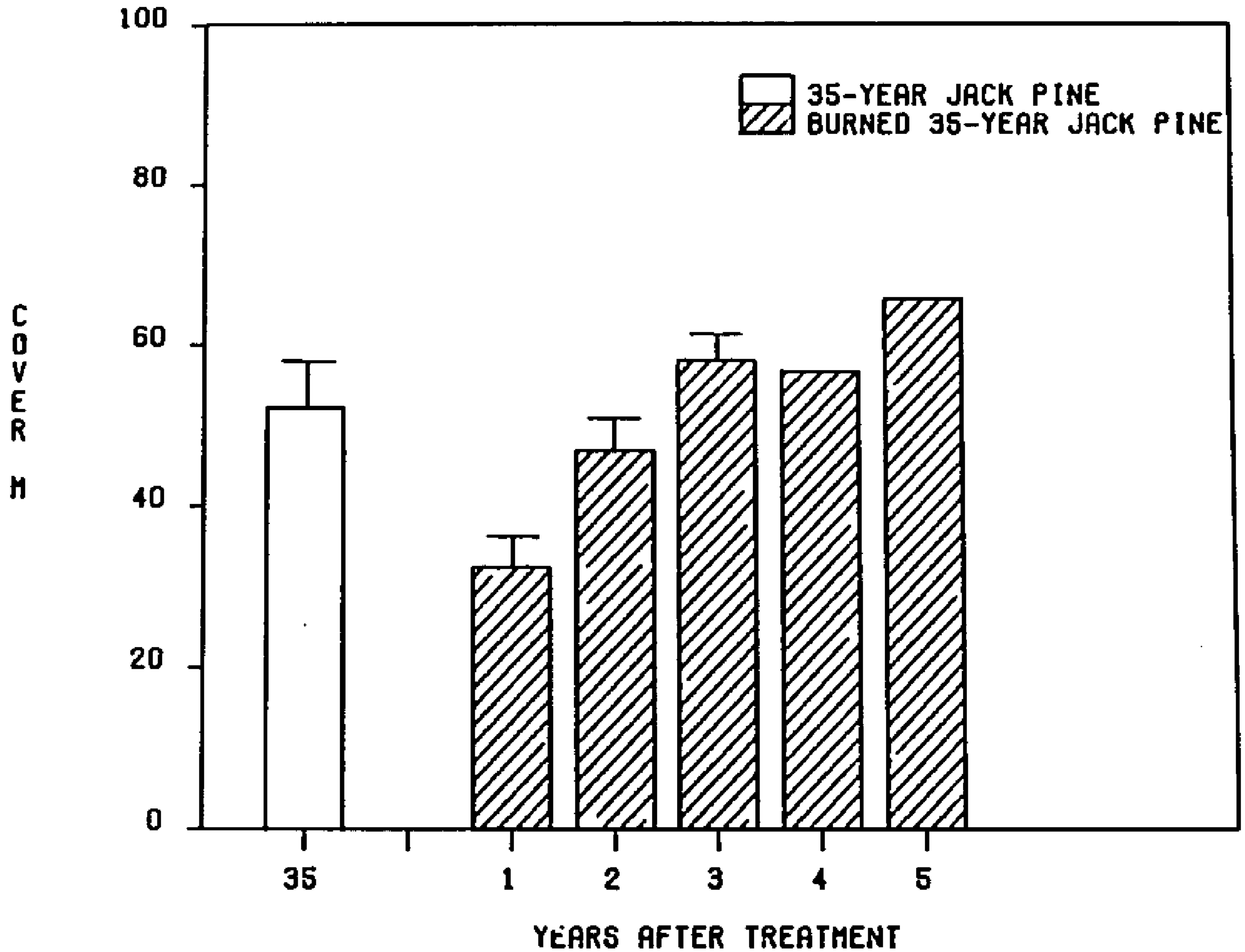

Fig. 4.8. Total vegetational cover (m), of sites averaged within years, for unburned 35-year-old jack pine stands and burned 35-year-old jack pine stands comprising a 5-year sequence following burning. Vertical bars equal one SD.

A large increase in cover of annuals and biennials occurred during the first year on burned sites (Fig. 4.9). This species group, dominated by geranium and rock harlequin, averaged 20% cover on the 1-year-old burns, with a maximum of 25% on site 7B79. A drastic reduction in these species was seen by year 2. Large increases in grasses and sedges occurred in the early postfire sequence (e.g. sites 7A80-81 and 7B79-80, surveyed as 1- and 2-year-old burns). Grasses and sedges represented approximately 60% of the vegetational cover 3 and 4 years after fire, but their cover dropped between years 4 to 5 (site 9A80-81). Perennial herbs contributed little to the total vegetational cover on the sites. The cover of tree and shrub species, such as blueberry, sand cherry, and sweet fern (*Comptonia peregrina* L.) was drastically reduced through year 4 on the burn sites. By the fifth year increases in this group, attributed to black cherry, sand cherry, oak, willow (*Salix glaucophylloides* Fern.) and dewberry, had occurred.

Geranium was a dominant contributor to the cover on first year burns, but was absent or reduced to scattered individuals on these sites thereafter. To characterize the specific vegetational changes between years 1 and 2 on patches dominated by geranium, 3 permanent 20 m cover transects were established on site

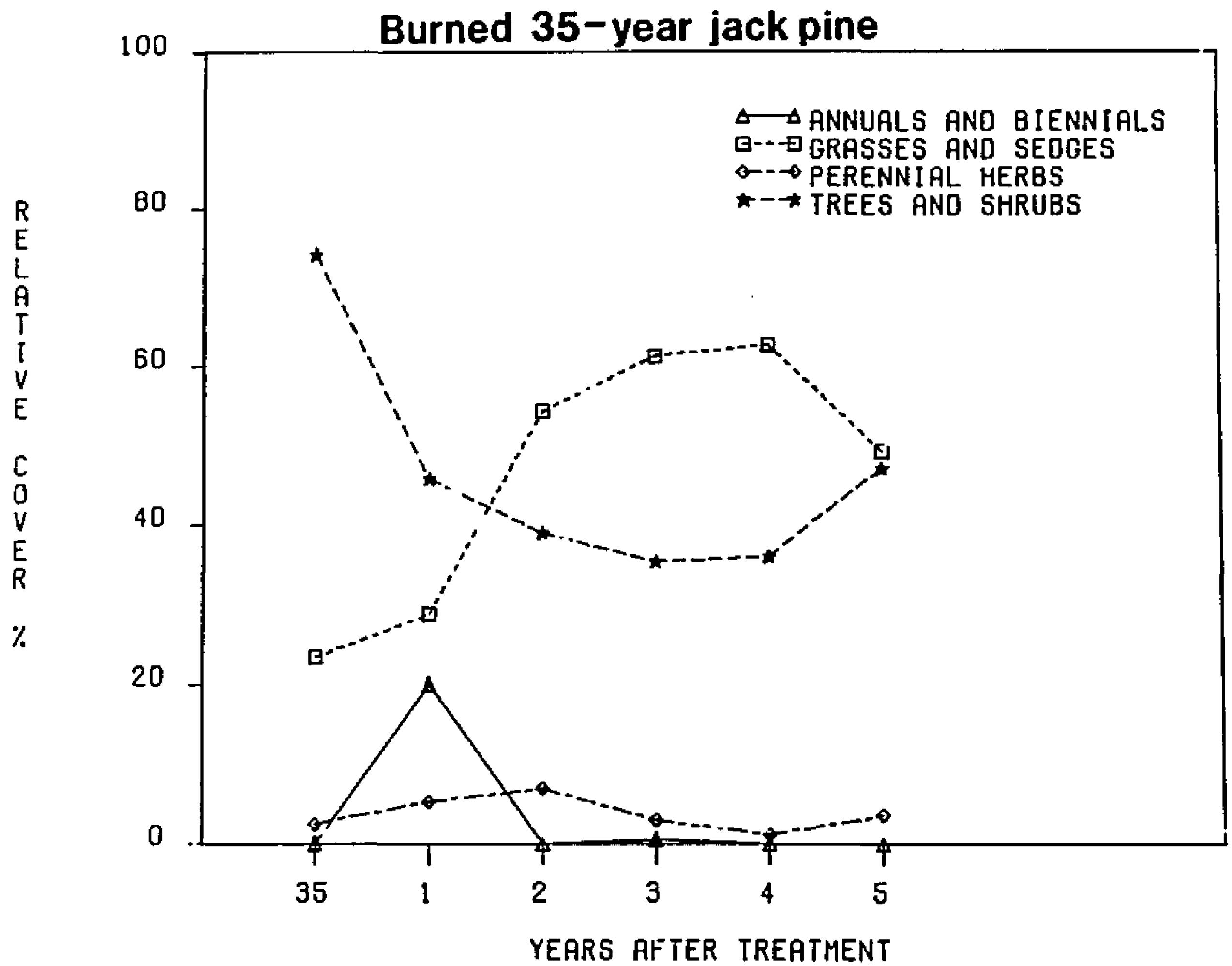

Fig. 4.9. Relative cover for each species group, of sites averaged within years, for unburned and burned 35-year-old jack pine stands comprising a 5-year sequence following burning.

7A80. Table 4.7 shows the total and relative cover, totalled for 60 m, during 1980 (1-year-old burn) and 1981 (2-year-old burn). In 1980, a total of 14 species comprised the 50.6 m cover on the 3 transects (Plate 4.1). Geranium represented 74% of the cover, followed by blueberry (10%), sand cherry (6%), and _Carex_ (3%). In 1981, a large decrease in vegetation cover (33.8 m) occurred on these transects; this was accompanied by a large increase in species richness (24 species) (Plate 4.2). Geranium was reduced to under 1% cover, whereas sedge and blueberry increased to 41% and 34% cover, respectively. Three species, _Symphoricarpos albus_ L. (snowberry), _Prunus virginiana_ L. (choke cherry), and rock harlequin were present in 1980 but were missing from the 1981 survey. New species present in 1981 on these transects included 1 annual, 5 grasses, 5 perennial herbs, and 2 shrubs, but none of these species represented more than 2% of the total cover.

Areas Burned By Wildfires

The sites included for this study were 2 areas of standing mature jack pine and 1 clearcut area (1-year-old of mixed jack pine and oak) burned by wildfire. These 3 sites displayed a wide range in species composition and dominance (Table 4.8). For example, site 8A79-80-81 showed the highest species richness

TABLE 4.7

COMPOSITE DATA FROM 1980 AND 1981 SURVEY OF 3 PERMANENT COVER TRANSECTS (60m) ESTABLISHED IN GERANIUM (GERANIUM BICKNELLII) PATCHES ON SITE 7A

	Cover[1] 1980		Cover 1981	
Species	Total(m)	Relative(%)	Total(m)	Relative(%)
Species present in 1980 and 1981				
Geranium bicknellii	37.6	74.2	.2	.6
Prunus pumila	3.0	6.0	2.7	8.2
Vaccinium spp.[2]	5.3	10.4	11.2	33.9
Carex spp.[3]	1.7	3.3	13.5	41.0
Ceanothus ovatus	.2	.4	.2	.7
Aster laevis	.1	.2	.1	.2
Amelanchier sp.	.2	.4	.5	1.6
Dichanthelium depauperatum	.3	.7	1.2	3.7
Lithospermum arvense	.2	.4	.1	.4
Cirsium sp.	1.0	1.9	.5	1.6
Campanula rotundifolia	-	.2	-	-
Species present in 1980 but absent in 1981				
Symphoricarpos albus	.6	1.2		
Prunus virginiana	.3	.6		
Corydalis sempervirens	.1	.2		
Species present in 1981 only				
Senecio tomentosus			.5	1.4
Oryzopsis pungens			.4	1.1
Koeleria macrantha			.1	.4
Comptonia peregrina			-	-
Fragaria virginiana			-	-
Solidago sp.			.2	.6
Arctostaphylos uva-ursi			.1	.3
Andropogon gerardii			.6	1.9
Hieracium venosum			-	.2
Lechea minor			.3	.8
Panicum columbianum			-	.2
Danthonia spicata			.3	.8
Melampyrum lineare			-	.2
Totals	50.6		33.8	

[1] - indicates a cover value (total or relative) less than .05.

[2] Includes V. angustifolium, V. myrtilloides, and V. vacillans.

[3] Includes C. pensylvanica and C. rugosperma.

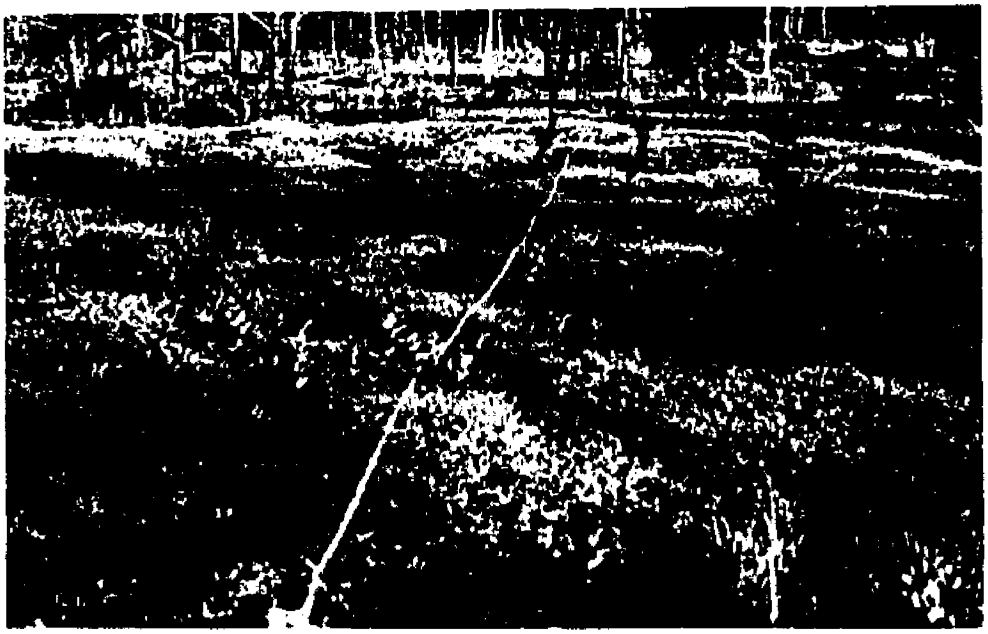

Plate 4.1. Cover transect (20 m) through a geranium patch on 1-year-old prescribed burn site.

Plate 4.2. Above cover transect at year 2 after fire; note disappearance of geranium.

TABLE 4.8

RELATIVE COVER (C), RELATIVE FREQUENCY (F), AND SPECIES RICHNESS (R) FOR VEGETATIONAL GROUPS ON AREAS BURNED BY WILDFIRE

Site[a] Number	Years Since Fire	Area	Annuals & Biennials			Grasses & Sedges			Perennial Herbs			Trees & Shrubs			Total R	Total Cover per 60 m
		ha	C	F	R	C	F	R	C	R	R	C	F	R		
8A79	2	32	.1	1.8	4	44.0	39.9	14	2.8	17.6	16	53.0	40.5	13	47	47.4
8A80	3	32	.1	2.2	2	39.4	33.2	12	6.6	23.1	15	54.2	41.5	11	40	52.8
9B79	3	30	-	-	-	60.2	49.6	7	1.1	3.5	5	38.5	47.6	6	18	42.9
8A81	4	32	.2	1.8	3	43.7	38.6	14	7.6	19.8	15	48.5	39.9	12	44	61.7
9B80	4	30	-	-	-	71.8	50.0	7	.7	9.9	8	27.1	40.1	6	21	54.7
9B81	5	30	-	-	-	62.7	42.9	6	-	2.5	2	37.3	54.6	6	14	56.2
11	6	6	-	-	-	91.8	59.2	6	.5	10.3	1	7.7	30.8	6	13	31.2

[a]See Table 4.1.

of any burned site, including prescribe burned clear-cuts and 35-year-old stands, during years 2, 3, and 4. In contrast, site 9B79-80-81 and site 11 were the least species rich of any burned site during years 3, 4, and 5, and year 6, respectively. It seems, therefore, that comparing these sites along a temporal sequence, with data averaged within years, would be less informative than looking at each site individually.

Site 8A79-80-81 was unique because of the high density of standing snags that increased shading to the forest floor. Also, this site came closer to approaching adequate stocking of jack pine regeneration than any other burned or clearcut site surveyed in this study. In 1980, jack pine regeneration was found in 13 of 30 frequency plots. The total vegetational cover on the site increased from 47.4 m to 61.7 m from years 1 to 3; species contributing to this increase included Carex, blueberry, Oryzopsis pungens, and bracken fern. As seen on other burned sites of similar ages, annuals and biennials and perennial herbs contributed little to the vegetation cover. However, this site was especially rich in perennial herbs. Frequently occurring species in this group were bracken fern, Aster laevis L. (smooth aster), Senecio tomentosus (wooly ragwort), and Apocynum androsaemifolium L. (spreading dogbane). Grasses and sedges comprised between 39% and 44% of the cover on this site during the 3 growing seasons. Dominant grass species on this site were Andropogon scoparius Michx., A. gerardii Vitman, Sorghastrum nutans L., and Oryzopsis pungens. Interestingly, Carex cover on this site was among the lowest of any burned site of analogous age. Trees and shrubs represented 48% to 53% cover on this site during the 1979, 1980, and 1981 growing seasons; the dominant species included blueberry, sand cherry, and sweet fern.

On site 9B79-80-81 and site 11, Carex pensylvanica represented from 60% to 86% cover, respectively. For all practical purposes these sites became Carex "meadows", on which other vegetation was suppressed or excluded.

Successional Trends on Unburned Clearcut Sites, Burned Clearcut Sites, and Burned 35-Year-Old Sites

The index of similarity is used here to test differences in species composition between site pairs, including the same site surveyed more than once as well as different sites within the same age class and between different age classes. The index of similarity (S) is computed as follows:

$$S = \frac{2C}{A + B}$$

where A is the number of species in sample A, B is the number of species in sample B, and C is the number of species common to both samples (Odum 1971). The index of similarity ranges from 0 to 1; 1 indicates identical species composition on the sites.

Table 4.9 shows that the degree of similarity among unburned clearcut sites within an age-class was often less than that of sites within different age classes. For example, the average S value among the 2-year-old sites is 0.65, whereas the average S value for 2-year-old sites compared to 3-year-old sites is 0.70. Even more striking is that the average S value among 4-year-old sites is 0.56, whereas it is 0.64 for 4- and 5-year-old site comparisons and 0.69 for 4- and 6-year old comparisons. This pattern also occurs in the 3- and 5-year sequence.

When comparisons were made between consecutive years, intrasite (same site) similarities among unburned clearcut sites were much greater than intersite (different sites) similarities (Table 4.9). For example, site 1B80-81 was surveyed as a 1- and 2-year-old unburned clearcut and had an S value of 0.74 when the data from two years were compared. In contrast, different sites compared within 1- and 2-year age classes had an average S value of 0.59. This relationship was found for almost all intrasite and intersite comparisons between consecutive years. Overall,

TABLE 4.9

YEAR-BY-YEAR COMPARISONS OF THE MEAN INDEX OF SIMILARITY (S) FOR UNBURNED CLEARCUT SITES COMPRISING A 6-YEAR SEQUENCE, AND THE MEAN INTERSITE (DIFFERENT SITES) AND MEAN INTRASITE (SAME SITE) INDEX OF SIMILARITY OF SITES COMPARED AT CONSECUTIVE YEARS

Year	0	1	2	3	4	5	6
0	.74						
1	.62	.64					
2	.67	.63	.65				
3	.60	.61	.70	.62			
4	.56	.59	.63	.62	.56		
5	.53	.57	.60	.61	.64	.59	
6	.53	.60	.58	.61	.69	.63	-

Intersite versus intrasite differences in the index of similarity at consecutive years.

Year 0 - 1

mean intersite = .59
mean intrasite = .74

Year 1 - 2

mean intersite = .63
mean intrasite = -

Year 2 - 3

mean intersite = .71
mean intrasite = .68

Year 3 - 4

mean intersite = .56
mean intrasite = .75

Year 4 - 5

mean intersite = .61
mean intrasite = .77

Year 5 - 6

mean intersite = .53
mean intrasite = .83

the mean S value for all intrasite and intersite comparisons between consecutive years was 0.75 and 0.60, respectively. Therefore, successional data collected from different sites over a temporal sequence will show a greater disparity in species composition by virtue of site differences than would similar data collected over time on the same site.

These data show that each site, regardless of its disturbance age, has a unique species composition. The S value of the same site compared at different ages was greater than that of different sites of the same disturbance age. To illustrate, the mean intrasite S value for years 3-4 is 0.75, whereas the within-year S value for year 3 and year 4 was 0.62 and 0.56, respectively. This relationship existed on unburned clearcut sites for every year of the sequence. In fact, the mean within year S value for these sites was 0.63, compared to a mean intrasite value of 0.75.

Burned clearcut sites of the same age were generally not as similar to each other as burned clearcut sites of different ages (Table 4.10). This relationship can be seen in years 1, 2, 4, and 5. Also, intrasite similarity was consistently higher than intersite similarity when site comparisons were made between consecutive years. The mean intrasite S value (0.73) for burned clearcut sites was much higher than the

TABLE 4.10

YEAR-BY-YEAR COMPARISONS OF THE MEAN INDEX OF SIMILARITY (S) FOR BURNED CLEARCUT SITES COMPRISING A 6-YEAR SEQUENCE, AND THE MEAN INTERSITE (DIFFERENT SITES) AND MEAN INTRASITE (SAME SITE) INDEX OF SIMILARITY OF SITES COMPARED AT CONSECUTIVE YEARS

Year	1	2	3	4	5	6
1	.58					
2	.58	.60				
3	.60	.67	-			
4	.54	.53	.49	.68		
5	.51	.47	.47	.69	.54	
6	.52	.55	.49	.67	.65	.65

Intersite versus intrasite differences in the index of similarity at consecutive years.

<u>Year 1 - 2</u>

mean intersite = .52
mean intrasite = .64

<u>Year 2 - 3</u>

mean intersite = .57
mean intrasite = .78

<u>Year 3 - 4</u>

mean intersite = .49
mean intrasite = -

<u>Year 4 - 5</u>

mean intersite = .62
mean intrasite = .76

<u>Year 5 - 6</u>

mean intersite = .55
mean intrasite = .74

mean within year S value (0.60).

Although not shown, index of similarity relationships among burned 35-year-old sites were similar to that of burned and unburned clearcuts.

Discussion

Fire has long been a recurring factor in shaping forest communities in the Lake States (Heinselman 1973, Swain 1973). Even before the appearance of the abundant disturbance literature generated since the early 1970's, periodic fire was recognized as a normal event influencing the structure and maintenance of Lake States forest communities (Cooper 1913, Graham 1941, Maissurow 1941, Stearns 1949). Whereas fire history has been well documented in areas such as the Boundary Waters Canoe Area in Minnesota, it is scarce in Michigan. Simard and Blank (1981), in one of the few such studies, counted fire scars on red pine trees killed by the Mack Lake fire, which occurred on May 5, 1980, in Oscoda county Michigan, and found that fire occurred on a specific site with an average interval of 23 years since 1830.

Trends in species diversity during early postfire succession have been reported from widely varying communities. Certain authors have reported that fire did not greatly alter the species composition or richness of the site (Dix 1960, Vogl 1970, Krefting and Ahlgren 1974, Purdie 1977, Ohmann and Grigal 1979). In contrast, there is a documentation that fire greatly increases species richness (i.e. alters species composition) of the site (Gashwiler 1970, Dyrness 1973, Parsons 1976, Bell and Koch 1980, Trabaud and Lepart 1980, Abrams and Dickmann 1982). The data from this study show that species richness and total number of unique species, with a few exceptions, was greater on the burned sites than either unburned clear-cuts or unburned jack pine stands.

Denslow (1980) suggests that plant communities which evolved with recurring large-scale clearing disturbances such as fire, should be most diverse initially following the disturbance, but species diversity should decrease during succession. Documentation supporting this hypothesis does exist (Christensen and Kimber 1975, Parsons 1976, Purdie and Slatyer 1976, Trabaud and Lepart 1980). Much of the literature supporting Denslow's ideas also support Egler's IFC model, in that nearly all members of the predisturbance community were present directly following fire.

It is difficult to generalize about the pattern of succession following burning on jack pine sites used in this study. The rapid conversion and domination of all but possibly one burned site by vegetation other than jack pine is the main difficulty. However, the formation of Carex meadows on many of the disturbed sites can be labelled a "regressive succession", in the terminology of Richards (1955); because of the apparent stability of these meadows, they may be involved in arresting or inhibiting succession (Egler 1954, Connell and Slatyer 1977). Early successional trends in species richness and composition on many of the sites are consistent with Denslow's hypothesis and Egler's IFC model. That burned sites had nearly every species found on the undisturbed sites (Tables 4.2, 4.4, and 4.6), supports the IFC model. Evidence supporting Denslow's hypothesis includes the decreasing richness that generally occurs in a sequence going from recently burned areas to 35-year-old stands to mature stands (Tables 4.3 and 4.9). However, two areas burned by wildfires, which were dominated by Carex, had species richness levels lower than that of intermediate-aged or mature jack pine stands. Also, the fact that 35-year-old and mature jack pine stands each had a substantial number of species not surveyed in the other age class is inconsistent with the IFC model. To support this model, mature stands should have essentially no species not present in an earlier successional stage. However, this discrepancy may be due to the small number of sites surveyed and/or using a sampling technique that was not designed to uncover every species on the site.

The domination of disturbed sites by vegetation, usually early successional species, other than the previous dominants has been reported for a variety of plant communities. Williams et al. (1969) reported that Lantana thickets which effectively suppress normal succession can form following clearcutting of rain forests in Queensland. Ahlgren (1976) showed that without adequate seed sources, logged red and white pine sites in northeastern Minnesota were converted to brushland. Recently, Cattelino et al. (1979) recognized that many disturbed communities do not follow a single regeneration pathway. The conversion of a plant community to a certain dominant vegetation represents one pathway in a multiple pathway succesional scheme that apparently exists in frequently disturbed communities. Models have been developed based on inter-fire period (Cattelino et al. 1979, Kessell and Fischer 1981), scorch height (Kessell and Potter 1980), and vital attributes of individual species and the community (Noble and Slatyer 1980) to predict successional changes in plant communities subject to recurrent disturbances.

The data presented in this study support the hypothesis that various developmental pathways are possible during early post-disturbance succession. A partial explanation for this successional divergence is that jack pine failed to reproduce on these sites with any consistency following disturbance. Unburned clearcut sites very quickly converted to *Carex* meadows (see Plate 3.1). This same pathway was followed by two areas burned by wildfires and two prescribe-burned areas. Other burned areas, apparently following a different developmental pathway, were being converted to shrubs and early successional hardwoods such as aspen, oak, cherry, and willow (see Plate 3.2). Another pathway was the reestablishment of a jack pine dominated site (Plate 4.3). *Carex* cover on this site was among the lowest of any of the disturbed sites. Partial shade, provided by the high density of standing snags, apparently provided suitable conditions for the survival and growth of jack pine reproduction and controlled the spread of *Carex*, a proven competitor in open situations.

The specific factors determining successional pathways followed on burned sites are unknown. Certainly species composition and dominance of the predisturbed flora, buried seed pools, adjacent seed sources, soils differences, burn intensity, and disturbance history are important. Unfortunately, very little information about the sites prior to burning is available. But, even a little information may

Plate 4.3. Vigorous jack pine reproduction on a 4-year-old site burned by wildfire.

provide some valuable clues about the response of a community to disturbance. For example, clearcut and burned site 10B had scattered areas of aspen within the site before logging and burning. It now appears that this site is being converted to aspen-dominated early successional hardwoods. Also, older standing individuals or stumps of hardwood species with sprouting or suckering capabilities are often present on newly disturbed sites. These relict species often have a profound localized or widespread effect in shaping the post-disturbance community.

In many instances sites of the same disturbance age were less similar to each other than to different sites of another age. This, too, can be explained by multiple successional pathways, because sites following the same pathway (e.g. *Carex* meadows or domination by early successional hardwoods) were more similar to themselves than to sites following different pathways. However, even sites following the same successional pathway were highly unique; a site was consistently more similar to itself, even over a three year period, than to other sites of the same disturbance age. It was also noted that a unique set of species were responsible for the increased cover on each site. Therefore, the individualistic (Gleason 1926) nature of each site, rather than age following disturbance, becomes the dominant aspect in discerning successional relationships in the communities. This conclusion is consistent with Bell and Koch (1980), who found that geographic area was more important than time-since-last-burn in determining similarity of sites in the jarrah forests of Western Australia.

The unique community on each site makes it very difficult, or even inappropriate to compare these sites along temporal sequences. For example, site 7B81 (burned clearcut) showed strong indications of being converted to a Carex meadow; this site had a species richness of 24 at year 3. Sites 10A and 10B (4-, 5-, and 6-year-old prescribed burns) were being converted to shrub and early successional hardwoods and were richer in species (36 and 39 species, respectively at year 4). There is no way site 7B at age 4 will resemble sites 10A79 and 10B79. The developmental processes on these sites are too varied. Also, data was collected from two sites comprising years 1, 2, and 3 and two different sites comprising years 4, 5, and 6 following fire to establish the burned clearcut sequence. This explains the anomalous increase in species richness and average richness per plot that occurred between years 3 and 4 (Fig. 4.4).

It is generally thought that disturbance sets back community succession to an earlier developmental stage (Clements 1916, Margalef 1963, Odum 1971). Jack pine is among the most shade intolerant Lake States species, and historically needed periodic fire to perpetuate itself. In the absence of fire, jack pine stands will eventually be replaced by more tolerant hardwoods and conifers, which are in turn followed by later successional associations (Eyre and LeBarron 1944, Heinselman 1973). In this study, however, burning on certain sites accelerated the replacement of jack pine to early successional hardwoods. This resulted because the jack pine overstory was destroyed, jack pine reproduction failed, and species such as aspen, cherry, oak, and willow survived the fire and spread vegetatively or became established after the fire by seed.

I have not identified older burned or clearcut areas on which jack pine did not become adequately established immediately following the disturbance. I, therefore, cannot say what the ultimate fate of the clearcut and/or burned areas used in this study will be. Jack pine, although rare, was present on every site used in this study. If these individuals and adjacent sources provide enough seed, and the seed find adequate "safe sites" (Harper 1977) for germination, jack pine, over a long time period, may again dominate the site. There is documentation that jack pine can become reestablished in areas it once dominated but failed to reinvade initially following disturbance (Thomson 1943, Vogl 1964, Marshall 1980). This situation, if in fact possible on these sites, appears more likely to occur on the sites coverted to Carex meadows. These sites are not developing a stratified plant canopy and, therefore, the forest floor, even 6 years after logging or burning, is still highly exposed to full sunlight. In contrast, it is unlikely that jack pine, because of its extremely low shade tolerance, will become established under a canopy of early successional hardwoods. Succession on these sites may be arrested at a shrub-early hardwood stage, or may progress to later successional associations. However, later associations developing on these sites will be limited by the extreme edaphic conditions imposed by the Grayling sand series, which represents the most depauperate of the sandy soil types in northern lower Michigan, in terms of nutrient and moisture holding capabilities. A sugar maple- basswood or spruce-fir association, said to eventually replace jack pine in the absence of fire (Eyre and LeBarron 1944), seems unlikely on these sites; northern red oak, red maple, and black cherry, or white pine represent stronger possibilities. Also, any intermediate or long-range successional development on these sites will depend on future disturbance events, which occur frequently in northern lower Michigan, and are the factors that ultimately shape the vegetation in the area.

CHAPTER V

FLORISTIC COMPOSITION BEFORE AND AFTER FIRE ON A JACK PINE CLEARCUT SITE IN NORTHERN LOWER MICHIGAN

Introduction

There exist three broad strategies in data collection used to characterize postfire succession and/or compare disturbed sites to other sites that have not been recently disturbed. One strategy is to survey many sites (usually once) that together represent a temporal sequence ranging from newly disturbed to long-since disturbed (Vogl 1970, Hanes 1971, Shafi and Yarranton 1973, Parsons 1976, Bell and Koch 1980). A second strategy, generally limited to early successional studies, involves establishing permanent plots soon after a fire and then surveying these sites, usually annually, for varying lengths of time (Ahlgren 1960, Lyon and Stickney 1976, Ohmann and Grigal 1979, Trabaud and Lepart 1980). These types of studies may include data from adjacent stands that are representative of the pre-disturbed condition (Ahlgren 1960, Ohmann and Grigal 1979, Uhl *et al.* 1981). A third strategy, also used in early successional studies, is to establish permanent plots in an area prior to burning. Data is then collected from the pre-disturbed community and from the disturbed community for varying lengths of time following disturbance. This strategy eliminates the confounding effects of many different aged sites in establishing successional trends. Fewer authors have utilized the latter approach (Gashwiler 1970, Dyrness 1973, Purdie and Slatyer 1976). To my knowledge this third strategy has not been previously used in fire succession studies in the Lake States.

In 1979, a clearcut area on Michigan Department of Natural Resources (DNR) land was designated to characterize fire-induced vegetational changes using the third strategy. On this area it was possible to 1) monitor blocks before and after burning, 2) evaluate fire intensity to determine its effects on vegetational changes, 3) characterize vegetational development on unburned clearcut blocks, and 4) compare burned and unburned clearcut blocks with an adjacent mature jack pine stand.

Methods

The experimental burn area was clearcut in 1976 from mature jack pine (65-years-old), and was untreated thereafter. See Chapter 2 for a more detailed description of the experimental burn area and mature jack pine site 13A used in this study.

In 1979 the experimental burn site was divided into 6 blocks ranging from 1.0 to 1.5 ha. Three blocks (1, 3, 6) were randomly designated to be burned and the three remaining blocks (2, 4, 5) were to be left unburned. During July 1979, 15 permanent 1 m^2 frequency plots and 2 permanent 20 m cover transects were randomly located in each block; at that time the vegetation was recorded. On September 19, 1979, the three designated blocks were burned by personnel of the Michigan DNR. However, block 6 was not completely burned; this resulted in only 6 frequency plots and 1 cover transect being included in the burned area. Therefore, only these burned plots from block 6 were included in the data analyses. The burned and unburned blocks were resurveyed during the 1980 and 1981 growing seasons.

Burn intensity was evaluated using a method modified from that described by Ahlgren (1960). During July 1979, a steel duff pin was placed at a randomly chosen cardinal direction adjacent to 10 randomly chosen frequency plots in blocks 1 and 3. The pins were located such that their collar was exactly level with the top of the litter layer (unaltered or only slightly decomposed plant material). The day after the area was burned, the duff pins were located and the amount of consumed organic matter was measured. Also noted at each duff pin was whether 1) the litter layer was still present (i.e. low intensity burn), 2) the litter layer was consumed but part of the duff layer (moderate-to well decomposed organic matter) was still intact (i.e. moderate intensity burn), or 3) all organic matter was consumed, exposing mineral soil (i.e. high intensity burn).

The understory (vascular vegetation ≤ 1.5 m) of the adjacent, mature, uncut jack pine site was surveyed during the summer of 1981 using 30 frequency plots and three 20 m cover transects as described in Chapter 3.

Results

Table 5.1 shows the relative cover and relative frequency of each species, by species group (annuals and biennials, grasses and sedges, perennial herbs, and trees and shrubs), surveyed in 1979, 1980, and 1981 (3-, 4-, and 5-year-old clearcut) as a composite of the 3 unburned blocks. Trends in diversity on the unburned blocks show the mean total richness increased from 1979 to 1980 and decreased in 1981 (Table 5.2). The increased richness seen in 1980 was mainly due to the increase in the number of grass species, including *Danthonia spicata* (L.) Beauv., *Dichanthelium depauperatum* Muhl., *Andropogon gerardii* Vitman, and *Oryzopsis pungens* Torr. (Table 5.1). The mean average richness per plot on the blocks did not change, and

TABLE 5.1

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES, BY SPECIES GROUP, SURVEYED IN 1979, 1980, AND 1981 (3-, 4-, AND 5-YEAR-OLD CLEARCUT, RESPECTIVELY), AS A COMPOSITE OF THE 3 UNBURNED BLOCKS

	Year of Survey					
	1979		1980		1981	
Species	Cover(%)	Freq(%)	Cover(%)	Freq(%)	Cover(%)	Freq(%)
Annuals and Biennials						
Melampyrum lineare	-	-	-	1.4	-	.7
Grasses and Sedges						
Carex pensylvanica	65.3	30.0	70.3	29.0	76.7	30.4
Andropogon gerardii	.1	.5	-	1.3	-	1.1
Danthonia spicata	-	.5	.1	2.7	-	1.5
Oryzopsis pungens	.1	.5	.2	.5	.2	3.6
Oryzopsis asperifolia	-	1.0	-	1.1	.1	1.1
Dichanthelium depauperatum	-	-	.3	1.3	.1	2.0
Perennial Herbs						
Pteridium aquilinum	3.3	10.6	.3	6.2	-	5.7
Gaultheria procumbens	.3	4.4	-	3.6	-	3.0
Potentilla tridentata	-	1.0	-	1.1	-	-
Apocynum androsaemifolium	.1	1.2	-	1.2	-	-
Campanula rotundifolia	-	.5	-	-	-	-
Aster laevis	.1	-	.1	-	-	-
Trees and Shrubs						
Vaccinium spp.[1]	22.7	28.3	23.8	28.4	18.3	29.2
Prunus pumila	1.8	8.8	1.3	10.9	.9	12.0
Comptonia peregrina	.2	1.2	.1	1.2	-	.8
Arctostaphylos uva-ursi	5.1	3.9	2.4	3.9	2.0	3.0
Pinus banksiana	.1	3.7	.2	2.7	.5	2.8
Epigea repens	-	1.0	-	1.1	-	1.1
Rubus hispidus	-	.5	-	.5	-	1.1
Quercus spp. (red oak)	1.0	-	.7	.5	.7	-
Prunus serotina	-	2.4	.5	1.5	.5	-
Amelanchier sp.	-	-	-	-	.1	-

[1]Includes V. angustifolium, V. myrtilloides, and V. vacillans.

TABLE 5.2

DIVERSITY TRENDS OVER THE 1979, 1980, AND 1981 GROWING SEASONS, EXPRESSED AS TOTAL SPECIES RICHNESS, RICHNESS OF EACH SPECIES GROUP, AVERAGE RICHNESS PER 1 m^2 PLOT, AND SHANNON INDEX, AVERAGED AMONG THE UNBURNED CLEARCUT BLOCKS

	Year of Survey		
Diversity	1979	1980	1981
Total Species Richness	12.4	14.7	12.4
Richness - Annuals and Biennials	-	.3	.7
- Grasses and Sedges	2.7	4.7	4.0
- Perennial Herbs	3.7	3.0	1.7
- Trees and Shrubs	6.0	6.7	6.0
Average Richness per Plot	3.4	3.4	3.4
Shannon Index	.95	.81	.70

a slight decline in the Shannon Index was seen over the 1979, 1980, and 1981 surveys. However, all changes in these diversity indices over the three growing seasons were nonsignificant.

Significant increases ($P < .01$) in total cover occurred over the three growing seasons (Fig. 1) due to the spread of Carex pensylvanica Lam. on all unburned blocks (Plate 5.1). Annuals and biennials produced no cover while the relative cover of perennial herbs was negligible on all unburned blocks. Relative cover of grasses and sedges increased significantly ($P < .01$) whereas trees and shrubs declined significantly ($P < .01$) over the three years.

Table 5.3 summarizes additions and losses of species, as a composite of the three unburned blocks, during 1979, 1980, and 1981. Seven species disappeared from plots between the 1979-1980 growing seasons. Bracken fern was most frequently lost from the unburned plots. A total of 9 species were added to unburned plots between 1979 and 1980, Prunus pumila L. (sand cherry) and Dichanthelium depauperatum being the most common additions. From 1980 to 1981, 10 species were lost from the plots, whereas 9 species were added. Oryzopsis pungens and Melampyrum lineare Lam. (cow-wheat) were the most common additions to the plots in 1981.

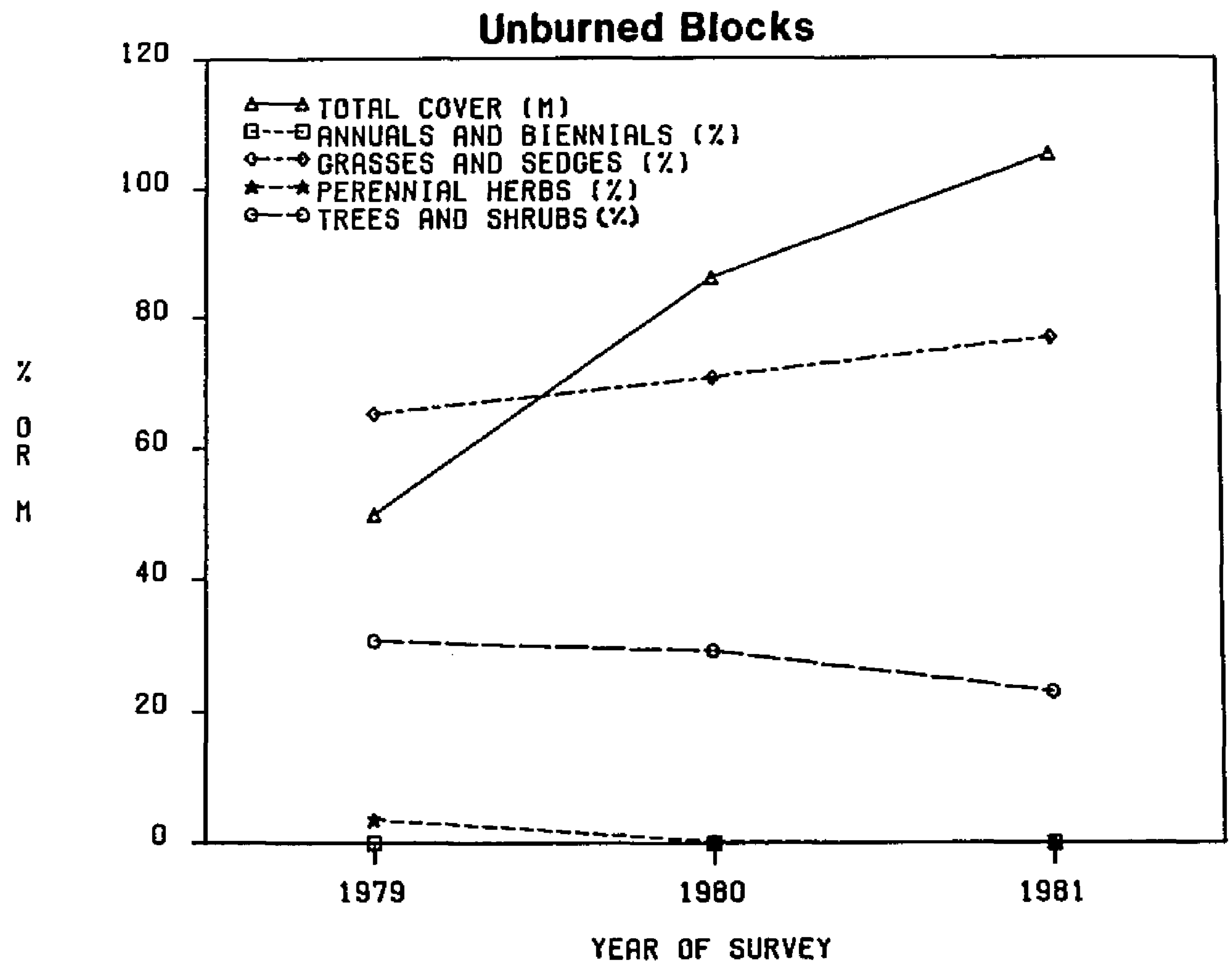

Fig. 5.1. Total cover (m) and relative cover (%) for each species group, as a composite of the 3 unburned blocks, surveyed in 1979, 1980, and 1981.

Plate 5.1. Carex pensylvanica dominating unburned blocks at year 4 after clearcutting.

TABLE 5.3.

ADDITIONS AND LOSSES OF SPECIES, AS A COMPOSITE OF THE 3 UNBURNED BLOCKS, SURVEYED IN 1979, 1980, AND 1981. VALUES FOR LOSSES OF SPECIES ARE EXPRESSED AS A RATIO OF NUMBER OF PLOTS IN WHICH A SPECIES WAS LOST IN A SURVEY, OVER THE NUMBER OF PLOTS IT WAS PRESENT IN THE PREVIOUS YEAR SURVEY

Species Lost Between 1979-1980 Survey	Number of Plots Lost / Total Present	Species Added Between 1979-1980 Survey	Number of Plots
Pteridium aquilinum	8/17	*Quercus* spp. (red oak)	1
Prunus pumila	1/13	*Prunus pumila*	3
Campanula rotundifolia	1/1	*Dichanthelium depauperatum*	3
Vaccinium spp.	1/42	*Vaccinium* spp.	2
Oryzopsis asperifolia	1/2	*Pteridium aquilinum*	1
Prunus serotina	1/3	*Danthonia spicata*	2
Gaultheria procumbens	1/7	*Andropogon gerardii*	1
		Melampyrum lineare	2
		Apocynum androsaemifolium	1

Species Lost Between 1980-1981 Survey	Number of Plots Lost / Total Present	Species Added Between 1980-1981 Survey	Number of Plots
Quercus spp. (red oak)	1/1	*Andropogon gerardii*	1
Danthonia spicata	1/3	*Oryzopsis pungens*	4
Potentilla tridentata	1/2	*Comptonia peregrina*	1
Gaultheria procumbens	1/6	*Melampyrum lineare*	3
Arctostaphylos uva-ursi	1/6	*Rubus hispidus*	1
Prunus serotina	1/2	*Pteridium aquilinum*	2
Andropogon gerardii	1/2	*Gaultheria procumbens*	1
Melampyrum lineare	2/2	*Prunus pumila*	1
Pteridium aquilinum	2/8	*Carex pensylvanica*	1
Apocynum androsaemifolium	1/2		

Table 5.4 shows the relative cover and relative frequency of each species, by species group, surveyed in 1979 (3-year-old clearcut), and 1980 and 1981 (1- and 2- year-old prescribed burn, respectively), as a composite of the 3 burned blocks. Substantial changes in the relative frequency of all species groups were induced by burning. Over the three growing seasons both perennial herbs and trees and shrubs decreased significantly ($P < .05$) in relative frequency, with bracken fern, wintergreen (*Gaultheria procumbens* L.), and kinnick kinick (*Arctostaphylos uva-ursi* L.) showing the largest decreases during this interval. In spite of the lowered frequency of *Carex* following burning, the grass and sedge species group significantly increased ($P < .01$) in relative frequency due to increases in *Dichanthelium depauperatum*, *Panicum columbianum* Scribn., and *Oryzopsis pungens*.

There was a nonsignificant decrease in mean total richness on the burned blocks the first year after burning, but a significant increase ($P < .05$) during year 2 (Table 5.5). Decreased richness between 1979 and 1980 was mostly due to the loss of many tree and shrub species on blocks 3 and 5, and the loss of 3 perenennial herb species on block 3. The mean richness per plot decreased slightly at year 1 following burning, but increased at year 2. The

TABLE 5.4

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES, BY SPECIES GROUP, SURVEYED IN 1979 (3-YEAR-OLD CLEARCUT), AND 1980 AND 1981 (1- AND 2-YEAR-OLD PRESCRIBED BURN, RESPECTIVELY), AS A COMPOSITE OF THE 3 BURNED BLOCKS

	Year of Survey					
	1979		1980		1981	
Species	Cover(%)	Freq(%)	Cover(%)	Freq(%)	Cover(%)	Freq(%)
Grasses and Sedges						
Carex pensylvanica	57.2	28.9	21.8	17.9	23.7	19.6
Andropogon gerardii	.2	4.3	-	-	-	-
Oryzopsis asperifolia	.6	4.7	-	2.2	-	2.9
Oryzopsis pungens	.1	1.4	.3	.6	2.6	7.8
Dichanthelium depauperatum	-	.6	14.3	24.1	20.3	20.7
Panicum columbianum	-	-	3.0	9.1	1.1	5.5
Danthonia spicata	-	-	-	-	.1	.5
Perennial Herbs						
Pteridium aquilinum	2.3	8.8	-	2.5	.3	3.5
Aster laevis	-	1.4	-	.6	-	.5
Solidago sp.	-	-	-	.6	-	.5
Gaultheria procumbens	.1	5.3	-	3.8	-	.5
Liatris novae-angliae	-	-	-	.6	-	.5
Apocynum androsaemifolium	-	-	-	1.6	.2	.5
Aster sagittifolius	-	-	-	-	.1	1.5
Polygala polygama	-	-	-	-	.3	-
Hieracium venosum	-	.6	-	-	-	-
Coryspermum hyssopifolium	-	-	-	-	.1	-
Viola adunca	-	-	-	-	-	1.5
Trees and Shrubs						
Vaccinium spp.[1]	30.7	28.3	44.2	29.1	36.7	27.1
Prunus pumila	2.5	2.2	5.6	1.2	2.8	1.1
Prunus serotina	1.3	.6	-	-	-	-
Arctostaphylos uva-ursi	.8	4.0	-	1.0	-	.7
Quercus spp. (red oak)	1.3	.6	1.3	-	1.5	-
Salix glaucophylloides	-	-	-	.6	-	.5
Comptonia peregrina	-	-	-	1.5	.1	.7
Rubus pensilvanicus	.2	.6	-	-	-	-
Rubus hispidus	2.6	2.7	9.6	3.2	10.1	3.6
Epigea repens	-	2.6	-	-	-	-
Populus tremuloides	-	.6	-	-	-	-
Rosa blanda	-	-	-	-	.1	-
Corylus americana	-	1.3	-	-	-	-
Crataegus sp.	.2	-	-	-	-	-

TABLE 5.5

DIVERSITY TRENDS OVER THE 1979, 1980, AND 1981 GROWING SEASONS, EXPRESSED AS TOTAL SPECIES RICHNESS, RICHNESS OF EACH SPECIES GROUP, AVERAGE RICHNESS PER 1 m^2 PLOT, AND SHANNON INDEX, AVERAGED AMONG THE BURNED CLEARCUT BLOCKS

	Year of Survey		
Diversity	1979	1980	1981
Total Species Richness	12.0	9.7	13.3
Richness - Annuals and Biennials	-	-	-
- Grasses and Sedges	3.3	3.7	4.3
- Perennial Herbs	2.7	2.7	5.0
- Trees and Shrubs	6.0	3.3	4.0
Average Richness per Plot	3.4	3.1	3.6
Shannon Index	1.1	1.2	1.4

Shannon Index showed slight increases during the three growing seasons. These changes, however, were not significant.

A significant drop (P < .05) in total cover occurred following burning on the blocks; however by year 2, cover increased significantly (P < .05) to nearly the preburn level (Fig. 5.2) (Plates 5.2 and 5.3). No cover of annuals and biennials was recorded, and relative cover of perennial herbs was negligible for all three growing seasons. The dominance of grasses and sedges, and trees and shrubs was dramatically altered by burning (Table 5.4). Tree and shrub species (mainly blueberry and bristly dewberry, *Rubus hispidus* L.) showed a significant increase (P < .05) in relative cover following burning, whereas grasses and sedges (mainly *Andropogon gerardii*, *Oryzopsis asperifolia* Michx., and *Carex pensylvanica*) decreased significantly (P <.01) during that interval. During the second year after burning, a decrease in relative cover of trees and shrubs occurred, corresponding to an increase in the relative cover of grasses and sedges; these changes, however, were nonsignificant.

Additions and losses of species, as a composite of the three burned blocks, over the three growing seasons is shown in Table 5.6. A total of 17 species were lost from plots during the first year after fire.

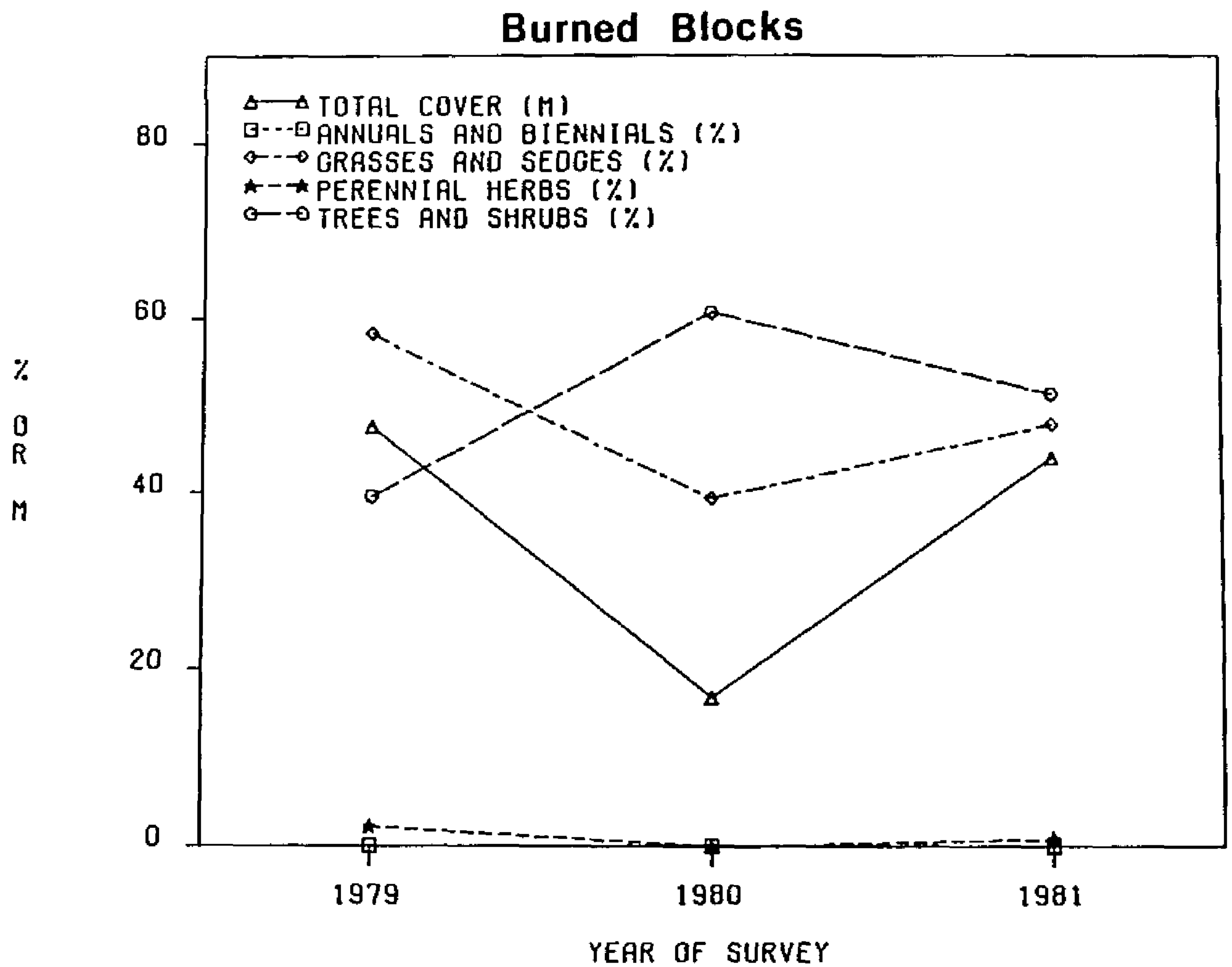

Fig. 5.2. Total cover (m) and relative cover (%) for each species group, as a composite of the 3 burned blocks, surveyed in 1979, 1980, and 1981.

Table 5.2. Large area bared of vegetation one year after fire.

Table 5.3. Overview of burned blocks at year 2 after fire showing rapid revegetation.

TABLE 5.6

ADDITIONS AND LOSSES OF SPECIES, AS A COMPOSITE OF THE 3 BURNED BLOCKS, SURVEYED IN 1979, 1980, AND 1981. VALUES FOR LOSSES OF SPECIES ARE EXPRESSED AS A RATIO OF NUMBER OF PLOTS IN WHICH A SPECIES WAS LOST IN A SURVEY, OVER THE NUMBER OF PLOTS IT WAS PRESENT IN THE PREVIOUS YEAR SURVEY

Species Lost Between 1979-1980 Survey	Number of Plots Lost / Total Present
Prunus pumila	1/3
Pteridium aquilinum	8/11
Carex pensylvanica	13/36
Andropogon gerardii	6/6
Oryzopsis asperifolia	3/4
Vaccinium spp.	5/36
Arctostaphylos uva-ursi	4/6
Rubus pensilvanicus	1/1
Epigea repens	4/4
Gaultheria procumbens	2/4
Oryzopsis pungens	1/2
Hieracium venosum	1/1
Aster laevis	1/2
Populus tremuloides	1/1
Prunus serotina	1/1
Quercus spp. (red oak group)	1/1
Corylus americana	1/1

Species Added Between 1979-1980 Survey	Number of Plots
Dichanthelium depauperatum	23
Panicum columbianum	14
Salix glaucophylloides	1
Liatris novae-angliae	1
Comptonia peregrina	2
Solidago sp.	1
Carex pensylvanica	1
Aster sagittifolius	1
Pteridium aquilinum	1
Apocynum androsaemifolium	1

Species Lost Between 1980-1981 Survey	Number of Plots Lost / Total Present
Panicum columbianum	6/14
Oryzopsis pungens	1/1
Aster sagittifolius	1/1
Vaccinium spp.	1/36
Apocynum androsaemifolium	1/1
Gaultheria procumbens	2/2

Species Added Between 1979-1980 Survey	Number of Plots
Apocynum androsaemifolium	1
Oryzopsis pungens	8
Carex pensylvanica	6
Pteridium aquilinum	3
Vaccinium spp.	4
Danthonia spicata	1
Aster sagittifolius	1
Panicum columbianum	1
Rubus hispidus	1
Oryzopsis asperifolia	1
Viola adunca	1

The species most frequently lost were bracken fern, Carex, Andropogon gerardii, Oryzopsis asperifolia, blueberry, and kinnick kinick. On a percentage basis, however, blueberry showed the lowest losses among the group. Ten species were added to burned plots during this interval. Dichanthelium depauperatum and Panicum columbianum comprised 37 of the 46 instances of species additions to the plots after burning. Two years after fire (1981), 6 species were lost from the plots; P. columbianum comprised half of these losses. During this period 11 species were added to the plots, with Carex, bracken fern, blueberry, and Oryzopsis asperifolia most often added.

In 1981, many differences between unburned blocks (5-year-old clearcut) and burned blocks (2-year-old prescribed burn) were observed (Tables 5.1 and 5.4). Carex cover on the unburned blocks (77%) was significantly greater ($P < .05$) than that on the burned blocks (24%), whereas grass cover on the burned blocks (23%) was significantly greater ($P < .05$) than that on the unburned blocks (1%). A total of 10 perennial herb species were present on the burned blocks, but only 2 were recorded on the unburned blocks. Tree and shrub species comprised significantly more cover ($P < .05$) on the burned blocks (51%) in 1981 than on unburned blocks (23%).

Fire intensity on block 3, with a mean organic reduction of 30 ± 12.5 mm was higher than block 1 where organic matter was reduced 20 ± 9.0 mm. Block 3 had 5 plots of high fire intensity, compared to only 3 plots of high fire intensity on block 1. Postfire species diversity was apparently affected by fire intensity. The 10 plots in block 1 prior to burning had 9 different species present, with an average richness of 3.2 species per 1 m^2 plot. One year after fire, total richness on the plots was 11 species, with an average richness per plot of 3.9. Although block 3 prior to burning had similar diversity to block 1 (10 species with an average richness of 3.2 species per plot), one year after fire only 6 species occurred on these plots with an average richness of 2.2. Two years after burning, block 1 remained more diverse (species richness of 12 and average richness per plot of 4.4) than block 3 (species richness of 8 and average richness per plot of 2.9). Plant cover on block 3 was reduced by 77% one year after fire, whereas plant cover on block 1 was reduced by 50%, providing indirect evidence that fire intensity on block 3 was higher than block 1.

Individual species responded differently to fire intensity. For example, Carex and blueberry were present on all 10 plots on which fire intensity was evaluated in blocks 1 and 3 prior to burning. One year after fire *Carex* was missing from 6 of 10 plots on block 3 (more severely burned), whereas blueberry was missing from only 2 plots. In block 3 *Carex* was lost from all five plots of high fire intensity. In block 1 (less severely burned), *Carex* was lost from 3 of 10 plots (all high intensity), whereas blueberry was lost from only 1 plot (high intensity). Fire intensity also appeared to affect the ability of certain species to become established on a block. *D. depauperatum* became established on all 10 plots in block 1 one year after fire, but only 6 plots in block 3. Also, *P. columbianum* became established on 6 plots in block 1, one year after fire, but only 2 plots in block 3. Year 2 after fire, *O. pungens* was present in 4 plots on block 1 and only 1 plot in block 3.

Table 5.7 shows the relative cover and relative frequency of each species in the understory of the mature jack pine forest (site 13A), adjacent to the experimental burn site. The survey recorded 18 species, with an average richness per plot of 4.0. The Shannon Index of diversity was extremely low (.49) because blueberry represented over 90% of the vegetative cover. *Carex pensylvanica* occurred in 25 of 30 frequency plots, but represented only 3% of the total plant cover. Also, every species surveyed in the mature jack pine

TABLE 5.7

RELATIVE (REL) COVER AND RELATIVE FREQUENCY OF EACH SPECIES IN THE UNDERSTORY OF A MATURE JACK PINE STAND (SITE 13A), ADJACENT TO THE EXPERIMENTAL BURN AREA

Species	Cover (Rel)	Frequency (Rel)
Annuals and Biennials		
Melampyrum lineare	2.1	11.6
Grasses and Sedges		
Andropogon gerardii	.2	3.3
Carex pensylvanica	3.2	20.7
Oryzopsis pungens	.2	1.7
Perennial Herbs		
Apocynum androsaemifolium	-	.8
Campanula rotundifolia	-	.8
Gaultheria procumbens	.3	8.3
Hieracium venosum	-	.8
Pteridium aquilinum	-	.8
Trees and Shrubs		
Amelanchier sp.	.3	.8
Arctostaphylos uva-ursi	1.0	9.9
Comptonia peregrina	1.0	3.3
Epigea repens	-	.8
Pinus banksiana	-	1.7
Prunus pumila	.4	5.0
Prunus serotina	-	.8
Quercus spp. (red oak)	.7	4.1
Vaccinium spp.[1]	90.7	24.8

[1]Includes V. angustifolium, V. myrtilloides, and V. vacillans.

understory was present on either the adjacent unburned or burned clearcut blocks. But the unburned blocks had 5 species and the burned blocks 14 species not found in the mature jack pine stand.

Discussion

Previous postfire successional studies in the Lake States have not characterized the plant community on a specific site before and after burning. However, studies of this type have been conducted in other ecosystems (Gashwiler 1970, Dyrness 1973, Purdie and Slatyer 1976). Dyrness, working in old-growth Douglas-fir forests in the Cascade Mountains of Oregon, reported that clearcutting reduced species richness, compared to old-growth forests, but burning resulted in increased richness through year 5 after fire. Woody tree vegetation was reduced but still present after fire, and species common in the old-growth forests, which showed lowered dominance initially after fire, regained dominance by year 5 after fire. Gashwiler, also working in old-growth Douglas-fir stands in the Cascade Mountains in Oregon, showed that a large number of species not found in the old-growth forests were present after fire. Also, herbaceous plants dominated the site through year 3 after fire; thereafter, woody plant species dominated. From studies in woodland communities in southeastern Australia, Purdie and Slatyer (1976) reported that all species present initially after fire were present as living plants or buried seed prior to fire, and that no new species invaded after burning. They concluded that regeneration of the community closely resembled the initial floristic composition model proposed by Egler (1954).

The present study showed that: 1) clearcutting a mature jack pine stand, with an understory dominated by blueberry, resulted in the formation of a Carex meadow by year 3 after logging, 2) between years 3 and 5 after clearcutting, Carex dominance increased from 65% to 77% relative cover on the unburned blocks, 3) at the conclusion of the experiment, burned blocks were dramatically different, in terms of species composition and dominance, from unburned blocks, 4) Egler's initial floristic composition model is supported by the fact that every species in the mature jack pine understory, plus many unique species, were present on the unburned and burned clearcut blocks, 5) the same fire moving through two adjacent blocks of the same soil type and topography, with similar postfire floristic composition, resulted in variable fire intensities within and between the blocks, 6) fire intensity affects the addition and loss of species and species dominance on the blocks, and 7) higher fire intensity resulted in lower diversity and lower plant cover.

Vegetational development on the study area the first two years after fire differed from the general pattern described on other recently burned jack pine sites (Abrams and Dickmann 1982; Chapters 3 and 4). For example, no annual or biennial species were present at year one after fire. Also, compared to pre-burn levels, total species richness and relative cover of Carex pensylvanica were reduced on the burned blocks. These findings may be related to the extreme severity of the burn, which reduced the fuel loading on the site from 23 to 3 mt/ha and consumed all fuels 6.4 cm or less in diameter (personal communication, Roy Milnes, DNR Area Fire Supervisor). No measurable precipitation occurred for 28 days prior to the burn, resulting in an extremely hot fire.

Research evaluating the effects of fire intensity on postfire plant succession is scarce (Ahlgren 1960, Dyrness 1973, Christensen and Kimber 1975). Ahlgren concluded that fire intensity affected seed germination, vegetative reproduction, plant competition, seedbed quality, and nutrient concentrations on the soil surface. All these factors may act in determining the establishment, perpetuation, and subsequent dominance of species during early postfire succession. Dyrness showed that species richness was greatly reduced on severely burned plots compared to lightly burned plots. Dyrness also found that cover on severely burned plots consistently lagged behind the lightly burned plots for 5 years after fire. Christensen and Kimber reported that hot fires, in addition to promoting seed germination of certain species, destroyed considerable amounts of soil-stored seed. Also, soil temperature during a fire was found to vary greatly within the site; soil temperature recorded at 56 points at the 1 cm and 2 cm depth varied from < 66°C to > 399°C. Floyd (1966, 1976), working in New South Wales, concluded that fire intensity significantly affected the germination (i.e. establishment) of typical postfire species.

The depth of the underground perennating system of understory species is directly related to their survivability during fire (Mclean 1968, Flinn and Wein 1977). The greater fire resistance shown by blueberry compared to sedge and other shallow rooted species is consistent with their individual rooting habits. However, bracken fern, known as a deep-rooted species, was particularly susceptible to burning in this study (lost from 8 of 11 plots).

In the present study fire intensity was highly variable, with two adjacent blocks having markedly different organic matter reduction and mineral soil exposure. I feel the severity of burning was responsible for variability in diversity, total plant cover, survivability of vegetatively reproducing species, and the number of newly established individuals on the burned blocks. Other studies have shown that very different successions can result on similar plant communities following disturbance. On other jack pine sites in northern lower Michigan, early revegetation following burning can be highly variable in terms of species richness, presence of annuals and biennials, and the dominance of grasses and sedges and trees and shrubs (Abrams and Dickmann 1982; Chapters 3 and 4). Multiple successional pathways are apparent on these sites in as little as 5 years after fire.

The concluding points to be made from the data presented here is that each site and each disturbance event is unique. Even when sites are rigorously selected for homogeniety, differences will most certainly exist in pre-disturbance species composition and dominance, edaphic features, buried seed-pools, and adjacent seed sources. Not only is it difficult to compare the effects of different disturbance events, but each event (in this case fire) is highly variable within an area.

CHAPTER VI

RESPONSE OF UNDERSTORY VEGETATION TO FERTILIZATION ON MATURE AND CLEARCUT JACK PINE SITES IN NORTHERN LOWER MICHIGAN

Introduction

In many forested ecosystems, dramatic increases in the dominance of sedges (*Carex* spp.) follow disturbances such as fire (Little and Moore 1949, Buell and Cantlon 1953, Ahlgren 1960, Vogl 1970, Wein and Bliss 1973), atomic radiation exposure (Woodwell 1967), fertilizer application (Noble *et al.* 1979) and transplanting forest soil to a greenhouse (Zavitkovski 1976) have been reported. In our own studies (Abrams and Dickmann 1982), *Carex pensylvanica* Lam. obtained relative cover values of 86% and 71% on recent burned and unburned clearcuts, respectively. We hypothesized that *Carex*, acting as an opportunistic species, exploits resources made available following clearcutting and/or burning, thereby increasing its dominance while reducing the dominance of neighboring vegetation.

Large nutrient reserves stored in the vegetation are made available following clearcutting and burning (Ahlgren 1960, Bormann *et al.* 1968, Debano and Conrad 1978, Likens *et al.* 1978) and result in profound changes in the dominance and diversity of post-disturbance vegetation. Nutrient enrichment studies have been reported from widely varying ecosystems (Willis 1963, Jeffery and Pigott 1973, Stephenson 1973, Harcombe 1977, Bakelaar and Odum 1978). A general finding of these authors is that "A few opportunistic species, already established in the community, expand their niches by preempting some niche space of subordinates, thus reducing overall diversity" (Bakelaar and Odum 1978).

This study was established on jack pine sites in northern lower Michigan to investigate the effects of fertilization on the relative growth of understory vegetation on clearcut and undisturbed sites.

Methods and Materials

A 55-year-old jack pine stand near Grayling, Michigan (Crawford County) was clearcut during the winter and spring of 1979-80. The soil type is a Grayling sand; a nutrient poor, strongly acid, mixed, frigid, typic, udipsamment. A 70 meter-wide border of jack pine of similar age, quality and stocking was left along an adjacent road.

Four blocks (10 m x 11 m) were established in both the standing jack pine and the adjacent clearcut. Each block contained an unfertilized half (control) and a fertilized half, separated by a 1-meter isolation strip. The blocks were established before green-up during the spring of 1980, and were located in areas of seemingly homogeneous vegetation. The blocks were laid out nonrandomly to reduce variability within the blocks, but the fertilization treatment within each block was randomly assigned.

The fertilization rate was 100-60-60 kg/ha N-P-K plus 200 kg/ha Ca as dolomitic limestone. Osmocote, a slow release formulation, was used for 60-60-60 kg/ha N-P-K. The remaining 40 kg/ha of N was ammonium nitrate (quick release). Fertilizer was distributed evenly by hand on May 3, 1980. Response to fertilization was determined at three times during the summer of 1980 (weeks ending June 14, July 21, and August 28) and one time in 1981 (week ending July 24), by sampling biomass from each block in the standing jack pine and clearcut areas. All vegetation under 1.5 m tall was clipped at ground level in 5 randomly located .25 m^2 quadrats within each treatment. The vegetation was sorted by species, cleaned and separated into current-year shoot biomass and residual biomass (the previous years biomass). The samples were dried at 80°C for 48 hours and weighed. Determination of annual and residual biomass was not possible for certain evergreen forbs. Their biomass was included in the residual portion of the total standing biomass. These species usually represented less than 10% of the total biomass.

Biomass data were also collected from a jack pine area that had been prescribe burned in 1978 as part of this study. This area, also on Grayling sand, is located in Ogemaw County, 31 kilometers from the above study area. In 1975 and 1976 the mature jack and red pine was logged, but scattered immature jack pine (about 35-years-old) were left standing. Twenty .25 m^2 biomass samples, randomized along transects, were taken during the same four time intervals, in 1980 and 1981, as indicated above. During the three sampling periods in 1980 all twenty biomass samples were grouped together. In 1981, however, the samples were grouped, in order of collection, into 4 groups of 5 so that a standard deviation could be calculated from the data. Otherwise, the sampling and handling of the vegetation were conducted as described above.

All tests for statistical differences were conducted using Bartlett's test for homogeneity of variance and analysis of variance.

Results

Total live shoot biomass for the prescribed burn area and the fertilized and control plots in the mature and clearcut jack pine are shown in Fig. 6.1. No significant fertilizer effect was detected during sample periods 1 and 2, but total live shoot biomass in the fertilized plots was significantly greater ($P < .05$) than the controls, in both the clearcut and mature jack pine, during sample periods 3 and 4. Total live shoot biomass on the burned site was greater than fertilized and control plots in mature and clearcut jack pine during all four sample periods; however, this difference could not be tested statistically.

In Figures 6.2, 6.3, and 6.4, the total live shoot biomass of three dominant species, sedge (*Carex pensylvanica*), blueberry (*Vaccinium* spp.), and bracken fern (*Pteridium aquilinum* Desf.) is shown for the fertilized and control plots in mature and clearcut jack pine. Fig. 6.2A and 6.2B show that sedge biomass is greatly stimulated by fertilization, but this difference was only significant ($P < .01$) at sample period 4, in both mature and clearcut jack pine. Live shoot biomass of blueberry (Fig. 6.3A and 6.3B) was increased by fertilization in mature and clearcut jack pine; this difference was significant ($P < .05$) during sample period 4 in mature jack pine and period 3 in clearcut jack pine. Significantly increased ($P < .1$) biomass of bracken fern was measured on fertilized

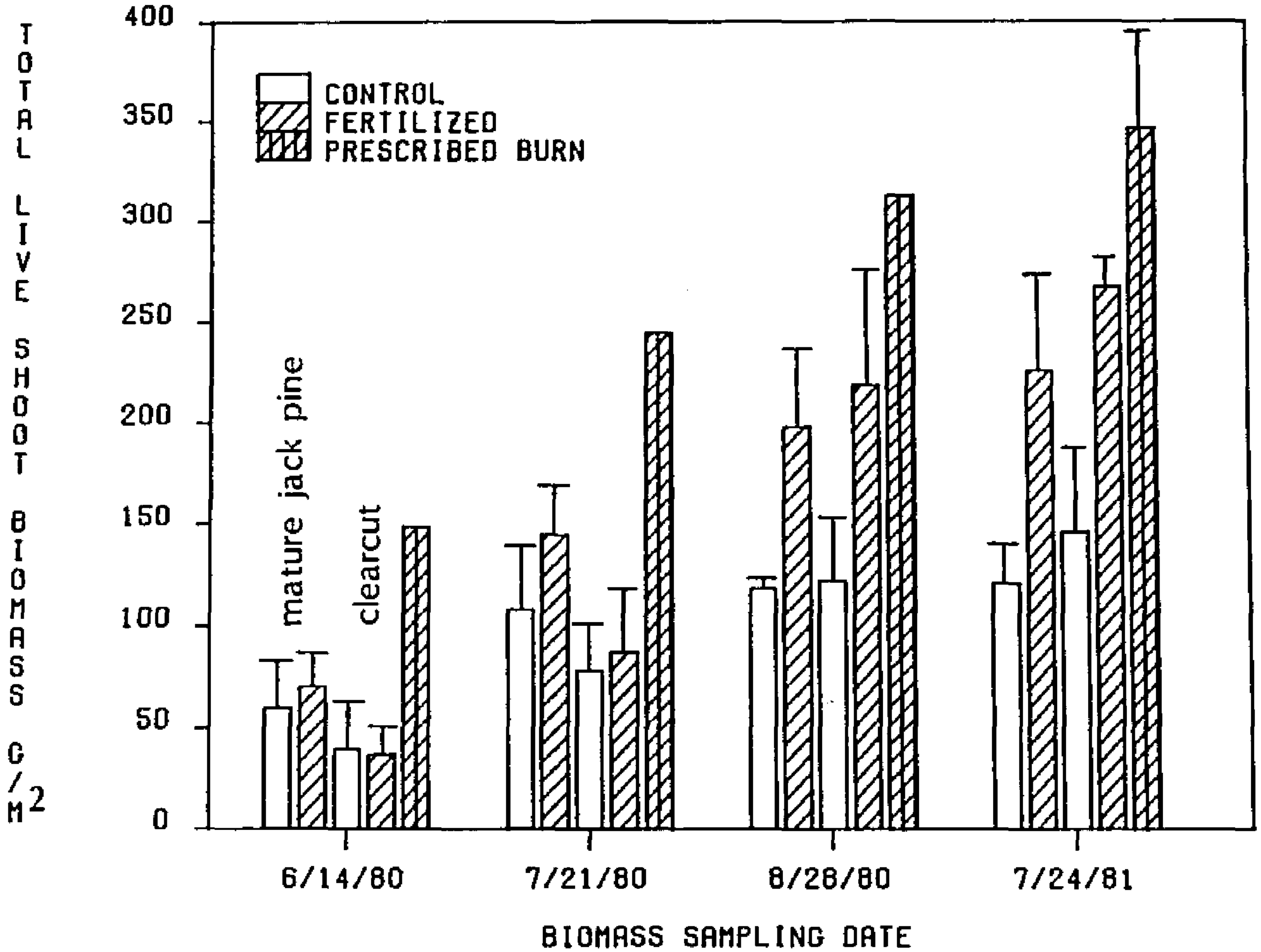

Fig. 6.1. Total live shoot biomass (g/m²) for the fertilized and control plots in the mature and clearcut jack pine, and the prescribed burn area. Vertical bars equal one standard deviation (SD).

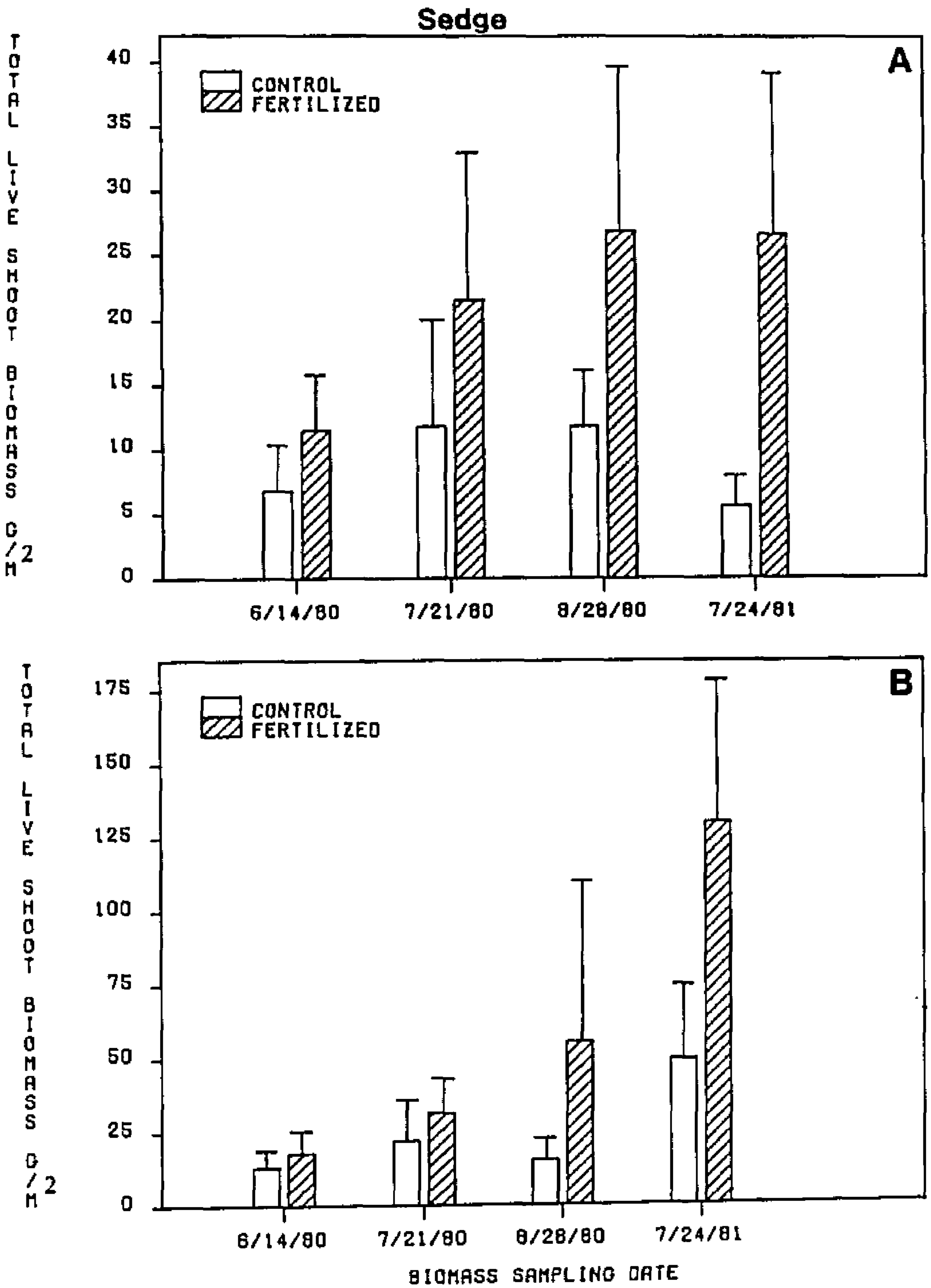

Fig. 6.2. Total live shoot biomass (g/m^2) of sedge (Carex pensylvanica) for the fertilized and control plots in A) mature jack pine and B) clear-cut jack pine. Vertical bars equal one SD.

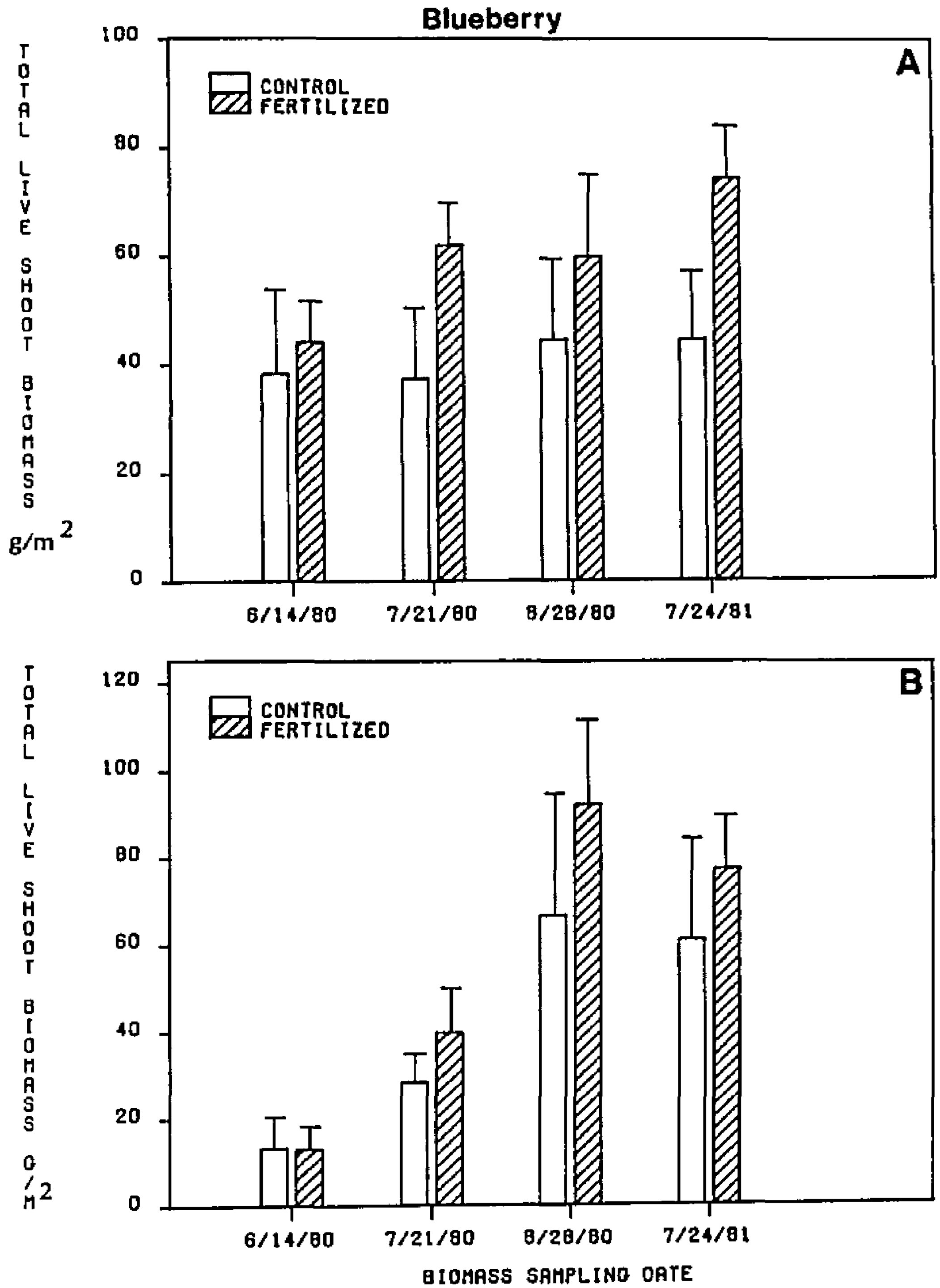

Fig. 6.3. Total live shoot biomass (g/m^2) for blueberry (Vaccinium spp.) for the fertilized and control plots in A) mature jack pine and B) clearcut jack pine. Vertical bars equal one SD.

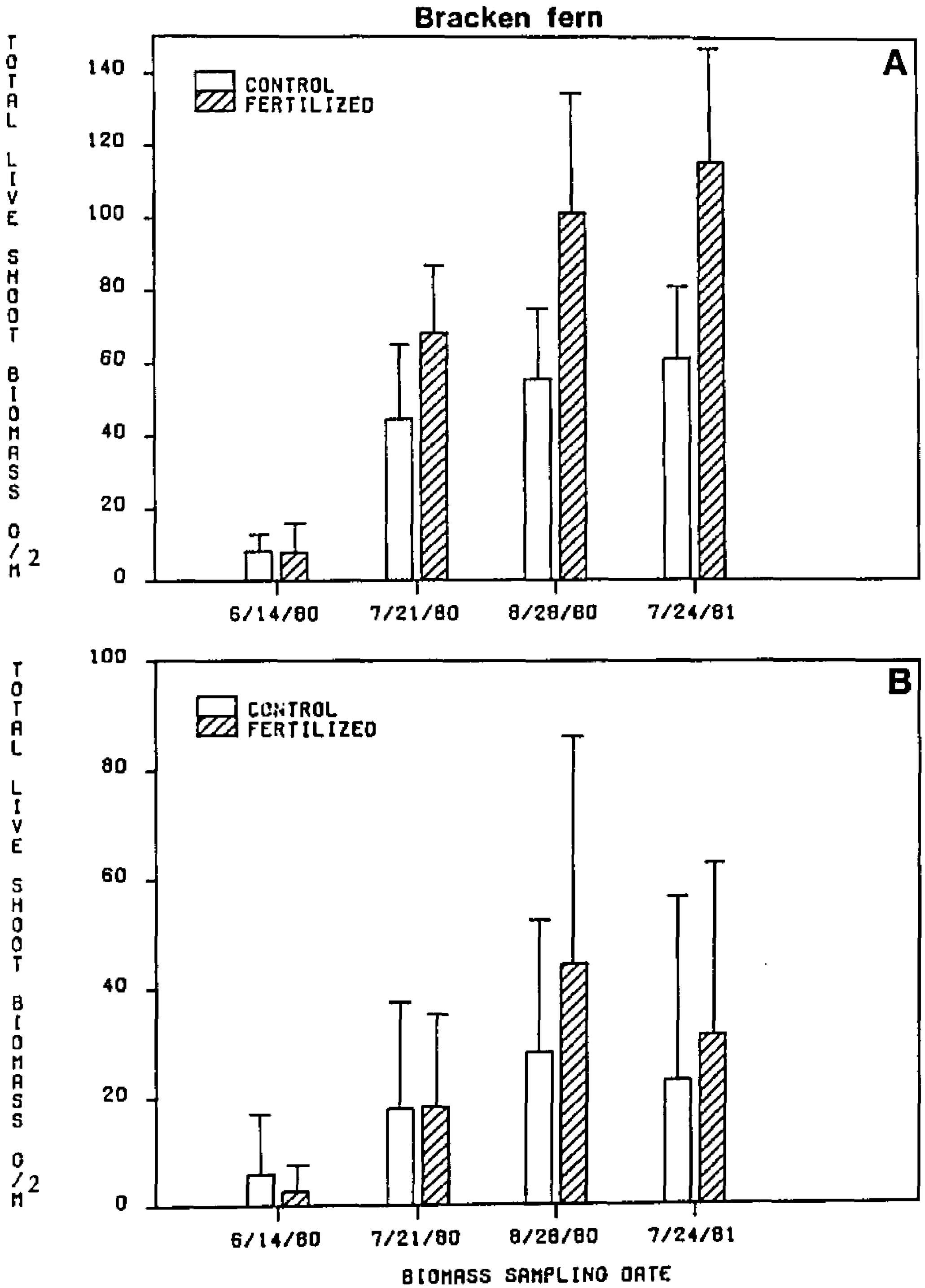

Fig. 6.4. Total live shoot biomass (g/m²) of bracken fern (*Pteridium aquilinum*) for the fertilized and control plots in A) mature jack pine and B) clear-cut jack pine. Vertical bars equal one SD.

plots in mature jack pine during sample periods 3 and 4, whereas no significant fertilizer effect was found in the clearcut area (Fig. 6.4A and 6.4B).

Fertilizer response, calculated as a ratio of live biomass on fertilized plots to that on control plots, was computed for sedge, blueberry, and bracken fern, as well as for total live shoot biomass (Fig. 6.5A and 6.5B). The biomass ratios of the three dominants indicate their treatment response and can be compared to the total live shoot biomass ratio, which is indicative of the average community response to fertilizer treatment. Only sedges consistently showed an above-average response to fertilization in mature jack pine (Fig. 6.5A). Biomass ratios for total annual production, sedge, blueberry, and bracken fern increased with time. This was most evident with sedges, which at sample period 1 had a fertilized to control ratio of 1.7; at sample period 4 this ratio had increased markedly to 4.9.

Biomass ratios for clearcut jack pine plots are shown in Fig. 6.5B. Sedges showed an above-average response to fertilization during all four sample periods, but this response was most impressive during periods 3 and 4. Trends in the biomass ratios with time as seen in the mature jack pine plots are not as apparent in the clearcut plots.

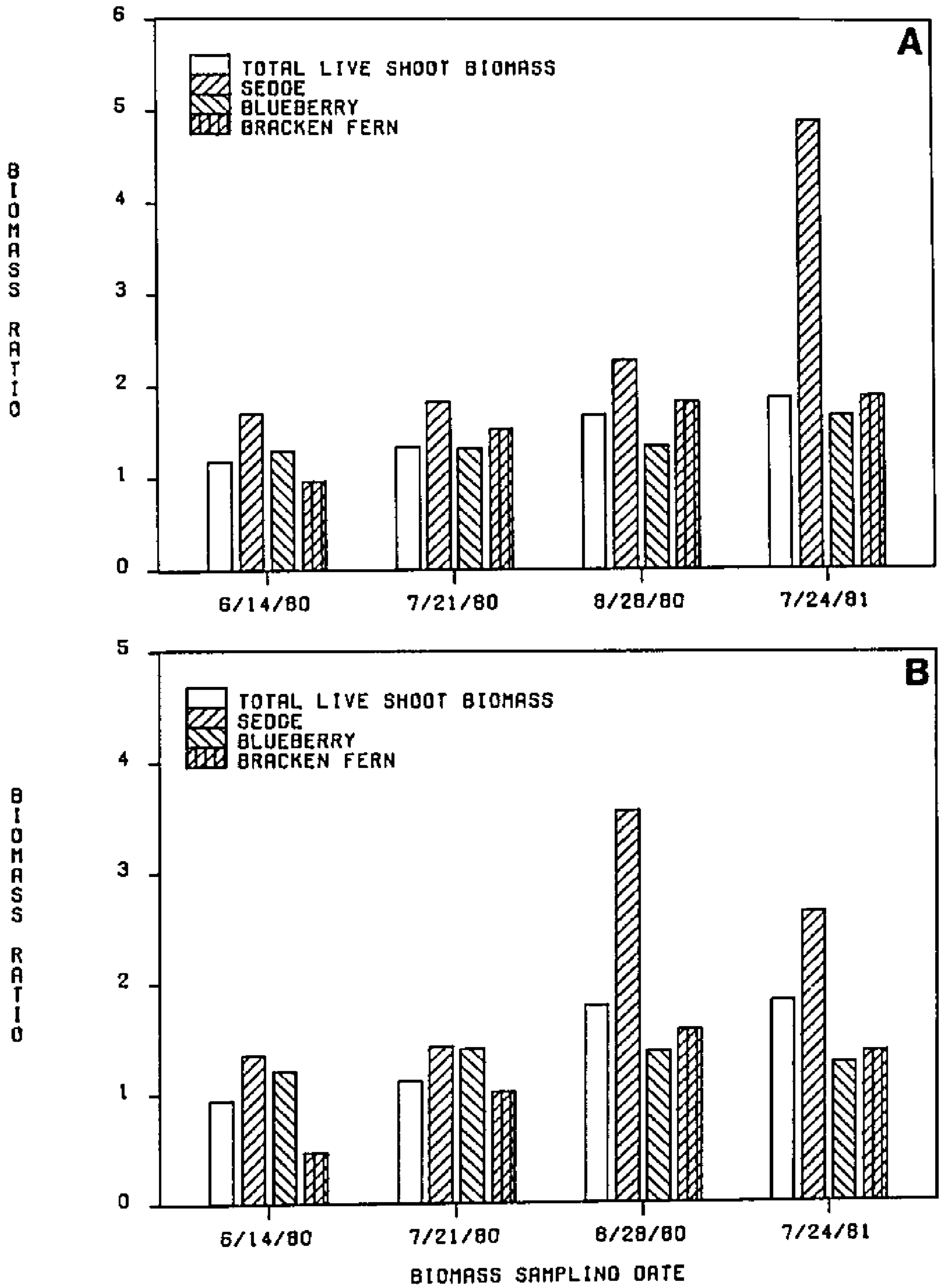

Fig. 6.5. Fertilized/control biomass ratios for total live shoot biomass, sedge, blueberry, and bracken fern in A) mature jack pine and B) clearcut jack pine.

Biomass data from the prescribed burn area are presented in Table 6.1. Monocots, particularly the sedges C. pensylvanica and C. rugosperma Mack., contributed greatly to the total live shoot biomass of the site. Grasses were also very productive, the dominant species including Danthonia spicata (L.) Beauv., Oryzopsis asperifolia Michx. and O. pungens Torr., Dichanthelium depauperatum Muhl., and Schizachne purpurascens Torr. Trees and shrubs were also an important group in terms of productivity on this burn, with Vaccinium spp., Prunus pumila L., and Comptonia peregrina L. dominating. Forbs, other than bracken fern, contributed little to the total biomass of the site, but greatly enriched species composition. Forb species commonly found throughout the burn were Aster laevis L., Hieracium aurantiacum L., Senecio tomentosus Michx., and Campanula rotundifolia L.

Discussion

Both clearcutting and burning induce the release of nutrients stored in vegetation, and stimulate other nutrient cycling processes which "fertilize" the site. In the first growing season following clearcutting, Likens et al. (1978) described forest soils as both "irrigated" (increased soil moisture)

TABLE 6.1

BIOMASS DATA (g/m²) BY SPECIES GROUP
FOR THE 1978 PRESCRIBED BURN

	Sample Date			
	6/14/80	7/21/80	8/28/80	7/24/81
Forbs	2.3	9.4	13.3	8.2 ± 2.2
Monocots				
Grasses	23.1	41.6	42.6	88.3 ± 5.4
Sedges	77.6	92.5	134.1	165.9 ± 28.2
Trees and Shrubs				
Annual	45.6	101.8	123.7	86.4 ± 7.3
Residual	9.5	28.5	24.7	50.3 ± 5.2
Total Live Biomass	148.6	245.3	313.7	348.8 ± 10.6

and "fertilized" (elevated concentrations of dissolved substances in soil solution). Ahlgren (1960) attributes the rapid regrowth of vegetation and marked lushness during the first few post-fire growing seasons to the fertilizing action of nutrients from the ash. Bormann et al. (1968) have shown stimulated nitrification following clearcutting, which they attribute to warming of the soil and removal of vegetation which possibly inhibited the nitrification process. Increased nutrient availability and elevated levels of nitrogen fixation and nitrification have also been reported following fire (Jorgensen and Wells 1971, Christensen 1973, Debano and Conrad 1978).

Nutrient enrichment will increase primary productivity of biological communities. Morrison and Foster (1977), working in jack pine stands in northern Ontario, found a three-fold increase in dry matter increment following fertilization. In this study, a nearly two-fold increase in total live shoot biomass occurred by the middle of the second growing season due to fertilization in both mature and clearcut jack pine stands. The dominant species in these communities (sedge, blueberry, and bracken fern) consistently showed increased productivity in response to fertilization. Sedge (C. pensylvanica), however, was the only species that consistently showed a response above the community average.

Preferential uptake of fertilizers by certain species has profoundly altered the diversity and species dominance in widely varying communities. Working in an 8-year-old field in Georgia, Bakelaar and Odum (1978) found that fertilization increased the dominance of goldenrod (Solidago sp.), but reduced or eliminated other codominant species. In tropical forests in Costa Rica, Harcombe (1977) showed that fertilization retarded succession by enhancing the competitive ability of a single forb species (Phytolacca rivinoides). Stephenson (1973), working in old-field communities, observed a trend toward overall reduction in diversity and evenness following fertilization. On clearcut northern hardwood forests in New Hampshire, Stafford and Filip (1974) reported that fertilization greatly stimulated pin cherry to the detriment of commercial species such as yellow birch and paper birch. Specht et al. (1977), working on sand-heath vegetation in Australia, showed that eight years after fertilization heath species declined and the native grass, Themeda australis, expanded into vacated gaps.

Sedges are well-adapted to disturbances such as fire, radiation exposure and fertilizer application. Abrams and Dickmann (1982) reported extraordinary increases in sedge 3 to 6 years after clearcutting and/or burning in jack pine communities. The low diversity on many sites was a direct result of the domination of Carex pensylvanica. Disturbance, through a variety of avenues, apparently stimulates the active growth of the large "bank" of dormant buds accumulated by Carex (Noble et al. 1979).

Within the interval of this study, I did not see the expansion of Carex, or any other community member, to the point where it greatly suppressed or excluded neighboring species. In fact, no significant or even noticable differences existed in species richness between fertilized and control plots. What was shown was that the biomass of vegetation in clearcuts and under mature jack pine increased after fertilization, and that C. pensylvanica consistently showed an above average response. It is apparent, however, that the expansion of Carex following clearcutting and burning involves many more factors than simply its response to nutrient enrichment of the site. For example, in this study Carex biomass increased significantly in the clearcut control plots with later sampling date, but did not increase with time in the control plots under mature jack pine. Carex biomass was also greatly stimulated on the burned site compared to the mature jack pine site (Fig. 6.2A and

Table 6.1), although comparisons between these two sites must be made with caution. Other overt changes resulting from clearcutting and burning, besides nutrient enrichment, include the increased space made available from the destruction of vegetation, and increased light, soil temperatures, and moisture at the rooting zone. Most likely all these factors contribute to the response of *Carex* following disturbance.

CHAPTER VII

APPARENT HEAT STIMULATION OF BURIED SEEDS OF GERANIUM BICKNELLII BRITT. ON JACK PINE SITES IN NORTHERN LOWER MICHIGAN

Introduction

The germination of buried seeds is an important mechanism of species establishment during secondary plant succession in many ecosystems (Sweeney 1956, Major and Pyott 1966, Ahlgren 1979a, Hall and Swaine 1980, McGraw 1980). The appearance of a large variety of species, not seen on unburned areas, following fire has been attributed to stimulation of germination of buried seed (Went *et al*. 1952, Sweeney 1956, Floyd 1966, 1976, Christensen and Muller 1975, Shea *et al*. 1979). Various factors resulting from fire have been implicated in this phenomenon. Went *et al*. (1952) reported that removal of competition was a major factor in the abundant germination of chaparral species the first season after fire. McPherson and Muller (1969) concluded that heat from fire degrades some substance in the soil which otherwise suppresses germination of chaparral species. The abundance of the annual *Senecio sylvaticus* on one-year-old burned Douglas-fir *(Pseudotsuga* menziesii) clearcuts and its disappearance thereafter has been attributed to soil nutrient changes associated with burning (West and Chilcote 1968). Rupture or alteration of the water-impermeable seed coat of hard-seeded species allowing germination has been attributed to fire (Floyd 1966, Cushwa et al. 1968, Martin et al. 1975, Purdie and Slatyer 1976, McDonough 1977).

Germination of many species is restricted to the first year after fire (Horton and Kraebel 1955, Sweeney 1956, West and Chilcote 1968, Purdie and Slatyer 1976). On jack pine sites in northern lower Michigan, Abrams and Dickmann (1982) reported that many species on one-year-old burns were not present on the site the following year. The most striking example was Geranium bicknellii Britt., classified as an annual or biennial by Fernald (1950). This species represents as much as 22% of the vegetational cover on first-year burns, but by year two it was not present or was reduced to scattered individuals. It was hypothesized, therefore, that heat from fire was responsible for the appearance of this species on one-year-old burned sites.

To test this hypothesis, two series of experiments were initiated using freshly-matured geranium seeds and seeds buried in the soil of different-age jack pine sites. The primary objective of these experiments was to determine if heat was involved in the germination of geranium seed. However, it was also possible to discern how well the germinants from buried seed matched the existing flora of the site.

Experiments With Freshly-Matured Geranium Seed

Freshly-matured seeds collected from parent plants in mid to late August 1980 from sites 7A80 and 7B80 were used in this series of experiments. Geranium represented 13% of the plant cover on these one-year-old prescribed burns. The seeds from all plants were mixed together, air dried, then refrigerated at 1-2°C.

A series of small-scale germination tests were undertaken between March and May, 1981 to determine the factors important in geranium seed germination. All tests were conducted in petri dishes on Whatman #1 filter paper. Three or four replications, consisting of 10 to 20 seeds each, were used in each treatment. Petri dishes were placed under "cool white" florescent lights with a 14 hour photoperiod and a light intensity of approximately 20 microEinsteins m^{-2} sec^{-1}; temperatures fluctuated between 18 and 22°C. Moist heat was used in all treatments by placing seed on top of 3 or 4 layers of filter paper saturated with distilled water directly before heating in a laboratory drying oven. Seeds were scarified by nicking the radicle end of the seed with a razor blade. Stratification (strat) treatment consisted of refrigerating (1-2°C) seeds on moist filter paper for an 8 week period in darkness. The alternate wet-dry treatment, lasting 3 weeks, involved keeping seeds moist for 5 days, then withholding water for 5 days. During the tests seeds in all treatments, except the wet-dry regime, were kept continually moist with distilled water. Seeds were considered germinated when the radicle emerged from the seed coat.

The following treatments were applied to fresh scarified and unscarified geranium seed: no heat (control); 40°C-5 min; 70°C-5 min; 80°C-10 min; 60°C-60 min; 80°C-60 min; 70°C-10 min + strat; 70°C-20 min + strat; 70°C-60 min + strat; 70°C-10 min + freeze (1 week) + alternate wet-dry; 70°C-30 min + freeze (1 week) + alternate wet-dry.

Results

None of the unscarified seeds germinated. In contrast, 80-100% of the scarified seeds germinated in all treatments.

Experiments with Buried Seed

From the above results, it was apparent that if heat was involved in geranium seed germination, seeds require a period of dormancy in the soil before heat exposure. Therefore, surface soil samples were collected from three different-aged jack pine sites along a post-fire successional sequence. The areas used were site 7B81 (3-year-old prescribed burn), site 12A (35-year-old jack pine stand), and site 13C (55-year-old jack pine stand).

On May 19, 1981, 12 randomly located soil samples were collected from each site. The samples were 25 cm x 25 cm to a depth of 2.5 cm into mineral soil. Therefore, the volume of each sample varied with the depth of the overlying organic material. Samples were bagged separately and air-dried in the laboratory until May 30, 1981. After removing all green vegetation, each sample was sifted through 60 mm mesh screening to remove larger twigs, roots and rocks. From each sample a 1352 cm^3 subsample was taken. Four treatments (unheated control, heated 70°C-30 min., heated 90°C-30 min., and heated 70°C-30 min + strat), replicated 3 times, were randomly assigned to samples taken from each site. Heated samples were placed in metal trays, moistened slightly, and placed in a forced-air drying oven. To raise the samples to and maintain them at 70°C for 30 min, they were first exposed to 150°C for 20 min (preheating), followed by heating at 100°C for 30 min. During the preheating, samples were periodically stirred and moistened to allow even heating and moistening throughout. No additional stirring or moistening was done during the final heating period. A thermometer was inserted into the center of each sample to monitor temperature during heating. The heating regime used to raise and maintain samples to 90°C for 30 min. involved preheating samples at 180°C for 30 min. followed by heating at 120°C for 30 min. The samples were stirred and moistened during preheating, but not during the final heating. In both the 70°C and 90°C heating regimes the samples remained moist through the final heating period.

All samples were placed over a 3.5 cm layer of sterilized sand (autoclaved - 121°C for 60 min.) in 26 cm x 52 cm x 6.5 cm plastic flats. The samples were spread evenly over the sand to form a layer 1 cm deep. The flats designated for stratification were placed in refrigeration (1-2°C) for 8 weeks. All other flats were placed under "cool white" florescent lights in a completely randomized design. The flats were exposed to a 14 hour photoperiod with an approximate light intensity of 36 microEinsteins m^{-2} sec^{-1} and to temperatures that fluctuated between 20 and 25°C. Two flats containing only sterilized sand were used to detect possible contaminants to the experiment. The flats were systematically rotated once a week to reduce any possible position effects. Germination counts were made every two days for the first month of the experiment and once or twice a week thereafter. After stratification was completed, those flats were placed under the light trays with the other flats. Samples were kept moist throughout the experiment by adding tap water every 1 to 2 days. During stratification, samples were watered every 7 to 10 days. Germinants were recorded as they appeared. Individuals not readily identifiable were removed, potted, and grown until they could be identified. The experiment was concluded after 18 weeks.

At the conclusion of the buried seed experiment, the control flats from the 3-year and 35-year-old sites were heated to 70°C-30 min. (using the above procedure) to determine if geranium seeds in those flats would germinate when exposed to heat.

Results

No seeds germinated in the flats containing only sterilized sand. However, three seedlings of *Oxalis* sp. came up in other flats and were considered contaminants; this species has not been found on any of the jack pine sites studied in northern lower Michigan.

Most of the germinants appeared during the first 2 weeks of the experiment (Fig. 7.1). A moderate amount of germination occurred from weeks 3 to 8 and

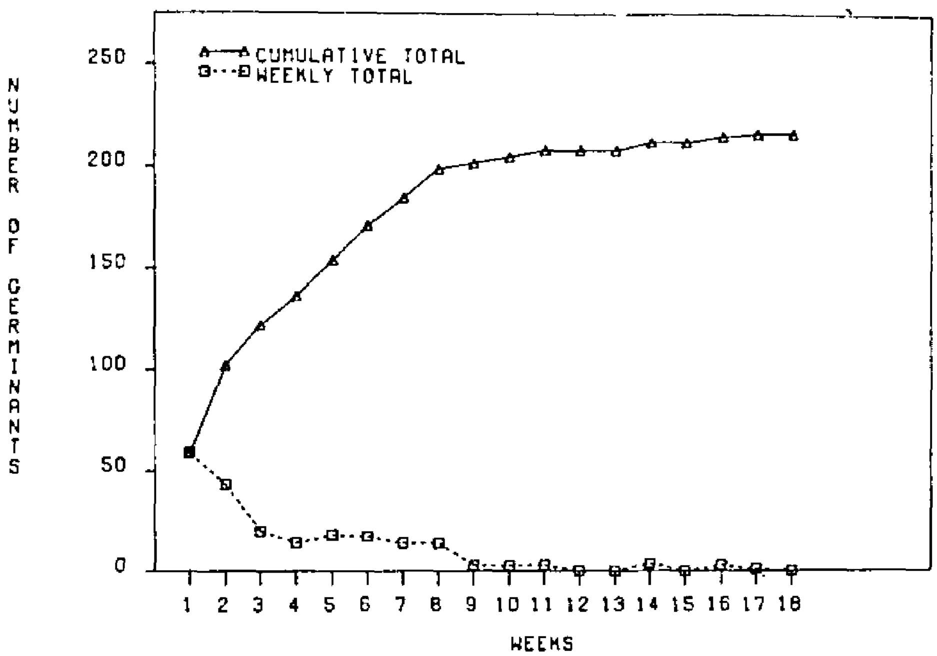

Fig. 7.1. Cumulative and weekly number of germinants from the control, 70°C-30 min, and 90°C-30 min treatments in the 3-year-old, 35-year-old, and 55-year-old sites (combined) during the buried seed experiment.

very little thereafter, but there were differences among species (Fig. 7.2.). Geranium germination peaked the first week, and by the fourth week no new geranium appeared. A substantial number of grass seeds germinated during the first week, but peak germination occurred during the second week. Peak germination of hawkweed (Hieracium spp.) occurred between weeks five and eight.

When heated treatments (70°C, 90°C, and 70°C + strat) are compared to the unheated controls at each site, some striking differences in species composition and number of germinants are evident (Table 7.1). Most importantly, geranium seedlings appeared only in the heated treatments from the 3- and 35-year-sites. The difference in the number of geranium germinants in the 90°C and 70°C + strat treatments compared to the unheated controls were significant ($P < .05$) using Wilcoxon's nonparametric two sample test (Steel and Torrie 1960). No seeds of geranium germinated in samples from the 55-year site. Only a few seeds of grasses and sedges germinated in the heated treatments from any site. In contrast, 58 and 22 grass and sedge germinants were recorded in the control flats from the 35-year and 55-year sites, respectively. The difference in the number of grass and sedge germinants between the heated and control treatments from all

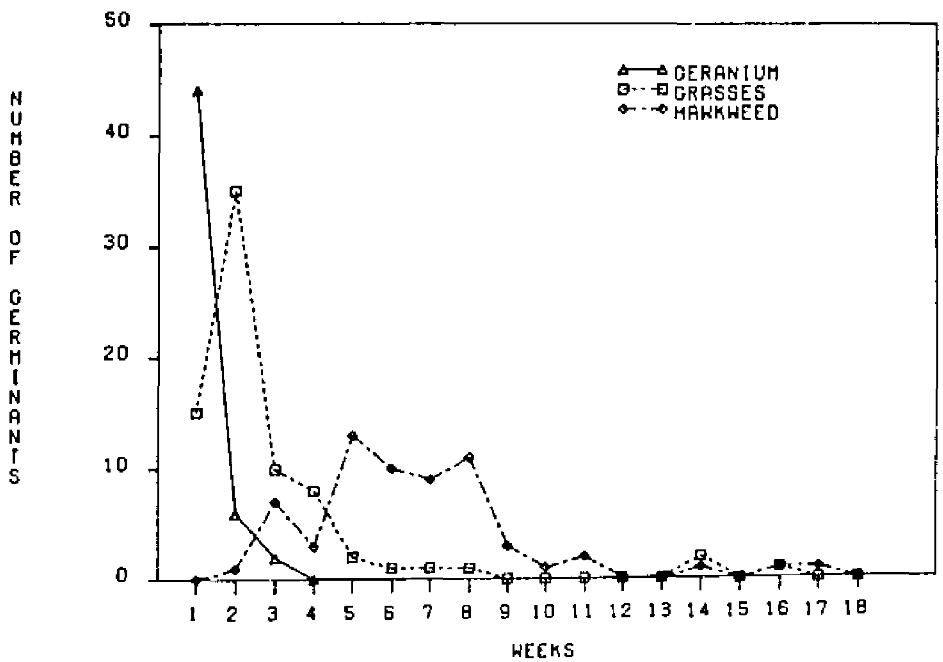

Fig. 7.2. Weekly total number of germinants of geranium, grasses (all species combined), and hawkweed (*Hieracium* spp.) from the control, 70°C-30 min, and 90°C-30 min treatments in the 3-year-old, 35-year-old, and 55-year-old sites (combined) during the buried seed experiment.

TABLE 7.1

TOTAL NUMBER OF GERMINANTS FOR SPECIES APPEARING IN SOIL SAMPLES FROM THE 3-YEAR, 35-YEAR-, AND 55-YEAR-OLD POST-FIRE SITES DURING THE BURIED SEED EXPERIMENT. TREATMENTS WERE AN UNHEATED CONTROL, 70°C-30 MIN, 90°C-30 MIN, AND 70°C-30 MIN + STRATIFICATION

	3-year				35-year				55-year			
Species	cont	70°C	90°C	70°C + strat	cont	70°C	90°C	70°C + strat	cont	70°C	90°C	70°C + strat
Annual herbs												
Geranium bicknellii		9	32	23		1	10	4				
Perennial herbs												
Antennaria neglecta			2		2							
Fragaria virginiana					1							
Hieracium spp.[1]	1	9	1		3		1		21	15		1
Viola adunca			2						3			
Woody perennials												
Chimaphila umbellata				1				1				
Gaultheria procumbens		2			1				10	3		
Grasses and sedges												
Carex spp.		1			2	1				2		
Danthonia spicata					23				2			
Dichanthelium depauperatum					4	1			1			
Oryzopsis pungens					7				17	1		
Panicum capillare					3				1			
Poa pratensis					17							
Unidentified grasses	1				2				1	1		
Treatment totals	2	21	37	24	65	3	11	5	56	22	0	1

[1] Hieracium aurantiacum and H. venosum

sites was significant ($P < .01$) using Wilcoxon's two sample test. The total number of germinants in treatments from each site ranged from 0 to 65, but the differences were not significant. However, the most frequently occurring species in each treatment from the sites differed. For example, 68% of the germinants on the 3-year site were geranium, and 71% of those on the 35-year site were grasses. Hawkweed, with 36 germinants, was the dominant species on the 55-year site. Grass species and wintergreen (*Gaultheria procumbens* L.) also were important members of the buried seed pool on this site.

Many important members of the plant community on the sites did not appear as emergents from buried seed (Appendix B.2.). Noteworthy is the scarcity of seedlings of *Carex* and absence of blueberry, both ubiquitous components of jack pine sites in northern lower Michigan. Also, many species that germinated from buried seed were not surveyed on the respective sites. Examples of this are wintergreen and *Chimaphila umbellata* (L.) Bart. (common pipsissewa) from the 3-year site, geranium, *Antennaria neglecta* Greene (field pussytoes), wintergreen, *Panicum capillare* L., and common pipsissewa from the 35-year site, and hawkweed, *Viola adunca* Sm., (hooked-spur violet), *Danthonia spicata* (L.) Beauv., *Dichanthelium depauperatum* Muhl., and *P. capillare* from the 55-year site.

When the control flats from the 3-year and 35-year-old sites were heated, one flat from the 3-year site produced 7 geranium germinants and two flats from the 35-year site produced 2 and 3 geranium germinants.

Discussion

Many chaparral species common to recently burned areas produce seeds which remain dormant in the soil between fires (Sweeney 1956, Christensen and Muller 1975b). Heat treatment has been shown to release seeds of several chaparral species from endogenously enforced dormancy (Stone and Juhren 1951, Sweeney 1956, Christensen and Muller 1975a, 1975b). Consistent with geranium germination in this study, germination of buried seed of certain chaparral species occur after heating soil samples, whereas freshly matured seed did not germinate after heat treatment (McPherson and Muller 1969, Christensen and Muller 1975a). Christensen and Muller (1975a) speculate that germination of these species may be dependent on the gradual deterioration of seed tissue imposing mechanical restriction on the embryo; dormancy of seeds stored in the soil for long periods may result from chemical inhibition by neighboring vegetation. Researchers suggest fire removes the source of toxins (e.g. shrub foliage) and denatures residual chemicals in the soil, thereby allowing increased germination of many species (Muller *et al*. 1968, McPherson and Muller 1969, Christensen and Muller 1975a, 1975b). However, abundant germination of many hard-seeded species following fire has been attributed directly to alteration of the seed coat by heat (Cushwa *et al*. 1968, Purdie and Slatyer 1976, Gill 1977).

The appearance of *Geranium bicknellii* following fire (Ahlgren 1960, Ohmann and Grigal 1979, Outcalt and White 1981, Abrams and Dickmann 1982) and other disturbances such as cultivation, building removal, and road construction (Ahlgren, personal communication) has been documented in the Lake States. On jack pine sites in northern Lower Michigan, peak occurrence of geranium is restricted to the first year after fire; either no or very rare individuals of this species are present on older burned sites. This pattern of geranium behavior, however, does not occur on all Lake States sites where this species grows. For example, Ahlgren (1979c) reported that *G. bicknellii* occurred in 90% of his sample plots three years (equivalent to 2 years using my criteria of disturbance age) after an old-growth red pine stand in northeastern Minnesota was burned. Krefting and Ahlgren (1974), also working in northeastern Minnesota, found geranium in 27% of the plots surveyed on a 5-year-old burn (4-years using my criteria).

Ahlgren (1979a, 1979b, 1979c) extracted buried seeds in soil samples from many sites of different forest types and burning histories, and consistently found geranium to be an important component. Interestingly, when Ahlgren (1979c) monitored seedling emergence from intact soil blocks collected from a 270 year-old red pine stand burned 3 years previously and from an adjacent unburned area, geranium appeared only from the burned soil. Ahlgren (1979a) planted soil-extracted geranium seed in sterile greenhouse soil and obtained 30% germination.

These data are in contrast to the findings in my experiments. In Ahlgren's experiments, no heat treatment was given to the soil samples or soil extracted seed, yet the geranium seed germinated. In my experiments with buried seed, geranium seeds germinated only in flats exposed to heat treatment. This was further substantiated when in 3 of 6 control flats from the 3-year and 35-year sites, which showed no geranium germination for 18 weeks, geranium germinated after the soil was heated. Also, seeds extracted from bulk soil samples from the 3-year site when heated to 90°C-30 min. showed 20% germination (37 seeds total), whereas unheated seeds showed 0% germination (30 seeds total) (Abrams and Dickmann, unpubl.).

Geranium in Minnesota, in the field at least, does not require heat from fire for germination (Ahlgren, personal communication). The apparent heat requirement for geranium germination in northern lower Michigan suggests that ecotypic differences exist for this species.

CHAPTER VIII

SUMMARY AND CONCLUSION

1. Burning promoted the establishment of a large variety of species not found on unburned clearcuts. The longevity of most of these species was short (temporary fire-followers), resulting in large drops in species richness between one and two years after fire.
2. Through year six after fire, most burned sites remained more diverse than unburned clearcut sites of analogous ages. Site diversity, however, on both burned and unburned sites was directly affected by the domination of the sedge, *Carex pensylvanica*.
3. The proliferation of *C. pensylvanica* (up to 86% relative cover) following disturbance indicates that it is an opportunistic species capable of monopolizing resources liberated following disturbance and suppressing or excluding other species.
4. Unburned clearcut sites consistently converted rapidly to *Carex* meadows. Burned sites, however, showed multiple successional patterns, including domination by shrub and early successional hardwood

species, conversion to *Carex* meadows, and the establishment of jack pine reproduction.

5. Comparisons made by the index of similarity (S) showed that succession on each site is highly unique. Therefore, the individualistic nature of each site, rather than age following disturbance, becomes the dominant aspect in discerning successional relationships in these communities.
6. Through the use of permanent plots established prior to burning in a jack pine clearcut area, it was shown that the intensity of the same fire going through two adjacent blocks with similar floristic composition and edaphic features was markedly different. Fire intensity, measured by organic matter reduction, proved to affect the addition and loss of species, species dominance, diversity, and plant cover on the blocks.
7. Fertilization experiments on mature and clearcut jack pine sites showed that biomass of understory vegetation increased after fertilization. *Carex pensylvanica* consistently showed an above average response to fertilizer, supporting its reputation as an opportunistic species.
8. Experiments conducted with surface soil samples from different-aged jack pine sites indicated that the overwhelming dominance of *Geranium biknellii*

on many one-year-old burned sites was due to the heat-stimulated germination of buried seed.

APPENDIX A

RELATIVE COVER AND RELATIVE FREQUENCY DATA
FOR SPECIES SURVEYED ON UNBURNED
CLEARCUT SITES

TABLE A 1

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES ON SITE 1B80-81 SURVEYED AS A 0-YEAR AND 1-YEAR-OLD CLEARCUT.[1]

Species	1980 Cover	1980 Freq	1981 Cover	1981 Freq
Annuals and biennials				
Lactuca canadensis	.3			.5
Melampyrum lineare	.1			
Grasses and sedges				
Bromus kalmii	.8	.6		
Carex pensylvanica	9.8	9.7	9.2	13.9
Danthonia spicata	.1	.5		
Dichanthelium depauperatum		.5		.5
Oryzopsis asperifolia	1.9	6.4	1.5	3.0
Oryzopsis pungens		1.6		.5
Schizachne purpurascens	.2	1.1	16.6	4.9
Perennial herbs				
Apocynum androsaemifolium	.9	7.5	.4	4.5
Asclepias syriaca	.1			
Aster laevis	.1	.5		1.0
Fragaria virginiana	.1			
Gaultheria procumbens	1.4	5.4	.1	2.5
Hieracium aurantiacum				.5
Maianthemum canadense	1.1	4.3	.1	4.9
Physalis virginiana		.5		
Pteridium aquilinum	26.0	14.5	33.7	12.4
Solidago spp.	.2	.5		.5
Viola adunca				.5
Trees and shrubs				
Amelanchier sp.	13.5	5.9	3.6	6.9
Arctostaphylos uva-ursi	.4	1.1		1.5
Comptonia peregrina	.3	2.7	.6	3.0
Crataegus sp.	2.9	.5	.1	3.4
Epigea repens	2.2	3.8	.4	.5
Prunus pumila	1.8	5.9	3.5	7.9
Prunus serotina	2.7	2.7	2.8	5.0
Prunus virginiana	.6	.5		
Quercus spp. (red oak)		2.1		
Rubus pensilvanicus	1.3	4.3	2.8	7.4
Rosa blanda		.5		
Salix glaucophylloides		.5		
Vaccinium spp.	31.0	15.6	24.8	14.8

[1] *Indicates a value less than .05.

TABLE A 2

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES ON SITE 2 SURVEYED AS A 1-YEAR-OLD CLEARCUT

Species	1979 Cover	1979 Freq
Grasses and sedges		
Andropogon gerardii	4.4	9.7
Carex pensylvanica	19.2	14.6
Deschampsia flexuosa		1.6
Oryzopsis asperifolia	1.1	
Oryzopsis pungens		1.6
Perennial herbs		
Anemone quinquefolia	.2	3.2
Antennaria neglecta		.5
Aster laevis	.7	5.4
Epigea repens		1.1
Gaultheria procumbens	6.2	6.0
Helianthus occidentalis		1.6
Hieracium venosum		1.6
Liatris novae-angliae		.5
Maianthemum canadense		1.1
Pteridium aquilinum		.5
Solidago spp.		1.1
Spiranthes gracilis		.5
Trees and shrubs		
Arctostaphylos uva-ursi	11.2	13.5
Comptonia peregrina	2.5	10.3
Pinus banksiana	1.1	1.6
Prunus pumila	6.2	9.2
Prunus serotina	.4	
Quercus spp. (red oak)		.5
Vaccinium spp.	46.8	14.1

TABLE A 3

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES ON SITE 3A SURVEYED AS A 2-YEAR-OLD CLEARCUT

Species	1980 Cover	1980 Freq
Grasses and sedges		
Agrostis hyemalis		.6
Bromus kalmii	.6	4.9
Carex pensylvanica	44.3	17.9
Danthonia spicata	.4	4.9
Dichanthelium depauperatum	2.5	6.2
Koeleria macrantha	.1	.6
Oryzopsis asperifolia		1.2
Oryzopsis pungens	1.7	5.6
Panicum columbianum		1.8
Perennial herbs		
Apocynum androsaemifolium	.1	1.2
Aster laevis	.5	2.5
Campanula rotundifolia	*	1.2
Hieracium aurantiacum	.6	1.8
Hieracium venosum		1.8
Liatris novae-angliae		.6
Pteridium aquilinum	19.6	10.5
Solidago spp.		.6
Trees and shrubs		
Amelanchier sp.	1.3	3.1
Arctostaphylos uva-ursi	1.1	1.8
Comptonia peregrina	1.7	4.9
Crataegus sp.	.2	.6
Pinus banksiana		.6
Prunus pumila	.6	6.8
Prunus serotina	1.6	
Quercus spp.	2.5	1.2
Rubus pensilvanicus		1.2
Vaccinium spp.	20.6	15.4

TABLE A 4

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES ON SITE 3B79-80-81 SURVEYED AS A 2-YEAR-, 3-YEAR-, AND 4-YEAR-OLD CLEARCUT

Species	1979 Cover	1979 Freq	1980 Cover	1980 Freq	1981 Cover	1981 Freq
Annuals and biennials						
Melampyrum lineare		1.9				1.4
Grasses and sedges						
Andropogon gerardii	5.7	3.8			.2	2.9
Bromus kalmii				3.3		
Carex pensylvanica	28.8	15.3	51.4	17.3	44.8	21.7
Danthonia spicata		.6		2.0		
Deschampsia flexuosa		1.9				
Dichanthelium depauperatum				1.3		.7
Oryzopsis asperifolia	1.5	1.3	1.5	1.3	.6	2.9
Oryzopsis pungens	.5	1.9	.3	6.0		1.4
Schizachne purpurascens				.7		.7
Perennial herbs						
Apocynum androsaemifolium	.5	.6				
Aster laevis		3.2			.2	2.2
Fragaria virginiana	.1					
Gaultheria procumbens	2.7	13.4	2.0	9.3	1.0	13.0
Hieracium aurantiacum	.1					
Hieracium venosum		.6		1.3		
Liatris novae-angliae				.7		
Pteridium aquilinum	9.7	12.7	2.3	10.0	.4	3.6
Solidago spp.	.3	.6		2.7		.7
Viola adunca						1.5
Viola pedatifida				.7		
Trees and shrubs						
Amelanchier sp.	.4		.1	1.3	.4	.7
Arctostaphylos uva-ursi		1.2	.1	3.3		2.2
Comptonia peregrina	6.7	11.5	.3	6.0	.7	7.2
Diervilla lonicera						.7
Epigaea repens	.1			1.3		2.9
Pinus banksiana	1.4	1.3			1.6	
Prunus pumila	4.3	5.7	1.3	9.3	4.2	8.0
Prunus virginiana		.6				
Quercus spp. (red oak)		1.9	.3	.7		1.5
Rosa blanda				.7		
Rubus pensilvanicus	.1	.6		1.3	.1	2.2
Vaccinium spp.	36.9	19.1	40.4	19.3	45.8	21.7

TABLE A 5

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES
ON SITE 4A79-80-81 SURVEYED AS A 3-YEAR-,
4-YEAR-, AND 5-YEAR-OLD CLEARCUT

	1979		1980		1981	
Species	Cover	Freq	Cover	Freq	Cover	Freq
Annuals and biennials						
Arabis glabra	.1					
Grasses and sedges						
Bromus kalmii	.8	6.4				
Carex pensylvanica	77.5	27.3	64.1	30.9	78.1	31.6
Danthonia spicata	.4	1.8		2.1	.8	2.1
Deschampsia flexuosa	3.4	15.5	.7	6.4	.5	8.4
Dichanthelium depauperatum	1.1			1.1		1.1
Oryzopsis asperifolia		.9	.6	2.1	1.1	1.1
Oryzopsis pungens	.3	.9	.7	7.4	.7	7.4
Perennial herbs						
Aster laevis	.3		.1	1.1		3.2
Campanula rotundifolia		.9				2.1
Hieracium aurantiacum		.9				
Hieracium venosum	.3		*	1.1	.1	1.0
Lycopodium obscurum				1.1		
Pteridium aquilinum	4.5	14.5		7.4		1.1
Solidago spp.			.2			
Viola adunca		.9				2.1
Trees and shrubs						
Amelanchier sp.				2.1		1.1
Arctostaphylos uva-ursi	1.1	1.8	.2	1.1	.1	2.1
Comptonia peregrina		3.6		1.1		2.1
Pinus banksiana		2.7	1.0	4.3	1.9	3.2
Populus tremuloides				2.1	.7	1.1
Prunus serotina		.9		.4		1.1
Quercus spp. (red oak)		.9		1.1		
Vaccinium spp.	10.3	20.0	31.6	27.6	15.4	28.4

TABLE A 6

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES ON SITE 5A79-80-81 SURVEYED AS A 4-YEAR-, 5-YEAR-, AND 6-YEAR-OLD CLEARCUT

	1979		1980		1981	
Species	Cover	Freq	Cover	Freq	Cover	Freq
Grasses and sedges						
Bromus kalmii	.2	1.2		1.8		2.0
Carex pensylvanica	76.7	34.5	66.8	26.9	64.6	30.0
Danthonia spicata				1.8		
Dichanthelium depauperatum				3.7	.3	1.0
Oryzopsis pungens			.4	2.8	.7	2.0
Perennial herbs						
Aster laevis			.6	1.8		3.0
Gaultheria procumbens			*	2.8	.1	4.0
Pteridium aquilinum	2.2	14.3	2.2	13.9	9.0	5.6
Solidago spp.			.1	.9		
Viola adunca						2.0
Trees and shrubs						
Arctostaphylos uva-ursi	7.0	3.6	1.9	3.7	.3	8.0
Amelanchier sp.	.2	2.4	.2	3.7		2.0
Epigaea repens					.2	
Pinus banksiana	1.4	3.6	5.4	2.9	3.2	2.0
Prunus pumila	.2	5.9	.1	8.3		5.0
Prunus serotina		1.2				
Quercus spp. (red oak)		1.2			.8	2.0
Vaccinium spp.	12.0	32.1	22.3	25.0	24.3	28.0

TABLE A 7

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES ON SITE 6 SURVEYED AS A 5-YEAR-OLD CLEARCUT

	1979	
Species	Cover	Freq
Grasses and sedges		
Carex pensylvanica	66.0	26.2
Deschampsia flexuosa	6.0	9.7
Oryzopsis asperifolia	5.3	9.7
Perennial herbs		
Gaultheria procumbens		1.9
Pteridium aquilinum	.1	
Solidago spp.		1.0
Trees and shrubs		
Arctostaphylos uva-ursi		1.0
Comptonia peregrina		1.0
Diervilla lonicera		1.0
Pinus banksiana	1.5	4.8
Populus tremuloides		1.9
Prunus pumila	.3	2.9
Prunus serotina	6.6	5.8
Rubus pensilvanicus	1.5	8.7
Salix glaucophylloides		1.0
Vaccinium spp.	12.6	23.3

APPENDIX B

RELATIVE COVER AND RELATIVE FREQUENCY DATA
FOR SPECIES SURVEYED ON SITES BURNED BY
PRESCRIPTION OR WILDFIRE

TABLE B 1

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES ON SITE 7A80-81 SURVEYED AS A 1-YEAR- AND 2-YEAR-OLD PRESCRIBED BURN

Species	1980 Cover	1980 Freq	1981 Cover	1981 Freq
Annuals and biennials				
Cirsium sp.	.1	.5		
Corydalis sempervirens	1.2	4.1		
Erigeron canadensis		2.1		
Geranium bicknellii	13.0	6.7		.6
Krigia virginica				.6
Lactuca canadensis				.6
Melampyrum lineare				1.2
Grasses and sedges				
Agropyron trachycaulum				.6
Andropogon gerardii	1.1	3.6	.1	2.9
Andropogon scoparius	.1	2.1	.2	1.2
Carex pensylvanica	27.8	14.4	44.7	17.0
Danthonia spicata		3.6	.3	3.5
Deschampsia flexuosa				1.2
Dichanthelium depauperatum	.6	3.6	.2	2.9
Koeleria macrantha		.5	.1	2.3
Muhlenbergia mexicana	.5	1.0		
Oryzopsis pungens	.1	3.6	2.0	5.9
Panicum capillare	.2	1.5		
Sorghastrum nutans		.5		
Perennial herbs				
Anemone riparia	.3			
Antennaria neglecta		.5		.6
Aster junciformis		.5		.6
Aster laevis	.1	2.5	.1	2.9
Campanula rotundifolia	.2	.5	.1	1.2
Fragaria virginiana		1.0	.1	1.2
Helianthemum canadense				1.2
Hieracium venosum		1.5		1.2
Liatris novae-angliae	.1	1.5		
Maianthemum canadense				1.2
Pteridium aquilinum		1.0		
Senecio tomentosus	1.8	2.1		.6
Solidago spp.		.5	.4	1.7
Viola adunca			.1	
Viola pedatifida				.6
Trees and shrubs				
Amelanchier sp.	4.6	5.6	2.1	8.2
Arctostaphylos uva-ursi	1.4	2.1	1.0	1.2
Ceanothus ovatus	.1	.5		1.2
Comptonia peregrina	.5	5.1	.5	4.1
Crataegus sp.				.6
Prunus pumila	5.0	10.3	17.4	12.9
Prunus virginiana		1.0	2.7	.6
Rosa blanda		.5		1.2
Rubus pensilvanicus		.5		
Symphoricarpos albus	.2	1.0		.6
Vaccinium spp.	40.9	12.3	27.7	17.5

TABLE B 2

SPECIES COVER AND FREQUENCY DATA FROM SITE 7B(1-, 2-, AND 3-YEAR-OLD BURN), SITE 12A(35-YEAR-OLD JACK PINE STAND), AND SITE 13C(55-YEAR-OLD JACK PINE STAND) USED IN THE BURIED SEED EXPERIMENT

	site 7B						site 12A		site 13C	
	1-year		2-year		3-year		35-year		55-year	
Species	Cover	Freq	Cover	Freq	Cover	Freq	Cover	Freq	Cover	Freq
Annuals and biennials										
Cirsium sp.		1.4		.6						
Corydalis sempervirens	2.8	1.4								
Erigeron canadensis						.5				
Geranium bicknellii	22.4	8.8		.6		.5				
Krigia virginica	.5									
Melampyrum lineare							*	.9	.8	9.8
Silene antirrhina		.4								
Grasses and sedges										
Agropyron trachycaulum		.7								
Andropogon gerardii		1.1		.6	.8	1.2	2.1	3.1		
Andropogon scoparius	.5					.5	1.0	2.7		
Bromus kalmii	1.2	1.4						.4		.5
Carex spp.	17.2	14.5	39.8	17.0	41.7	16.1	6.1	12.4	13.7	15.5
Danthonia spicata			.1	2.8	1.5	3.2	5.1	5.3		
Deschampsia flexuosa	.9	.7					3.4	2.6		
Dichanthelium depauperatum	1.6	4.9	3.6	7.9	5.4	10.7		.9		
Koeleria macrantha		1.8	.5	2.8	.3	1.1				
Oryzopsis asperifolia			4.7	1.7	1.6	1.1	.1			.5
Oryzopsis pungens	3.7	3.5	5.1	6.8	2.5	6.4	2.7	4.4		1.0
Panicum columbianum	.6	3.2		1.1	.8	3.8		.4		
Muhlenbergia mexicana	.9	1.1				.5				
Schizachne purpurascens	.5	1.8	6.8	3.4	4.1	3.2				
Sorghastrum nutans			.1							
Perennial herbs										
Anemone quinquefolia										1.5
Apocynum androsaemifolium		.3					*	.9	.7	2.6
Aster junciformis								.4		
Aster laevis		2.1	.2	2.3	.3	1.6	.3	2.6		
Campanula rotundifolia	.9	3.2		.5	*	.5				
Cypripedium acaule								.4		
Equisetum hyemale	*	1.1								

TABLE B 2 (continued)

Species	site 7B 1-year Cover	Freq	2-year Cover	Freq	3-year Cover	Freq	site 12A 35-year Cover	Freq	site 13C 55-year Cover	Freq
Convolvulus spithamaeus	1.2	.4		3.4	.2	1.1				
Fragaria virginiana				.5		.5		.9		1.0
Gaultheria procumbens									27.5	12.4
Helianthus occidentalis		.4			.1	.5		2.1		
Hieracium aurantiacum						.5				
Hieracium gronovii		.4								
Hieracium venosum		.7					.6	4.9		
Liatris novae-angliae				.6				3.1		
Maianthemum canadense						1.1			.6	6.7
Polygala polygama				.6				.9		
Polygonum cilinode		1.1								
Potentilla tridentata						.5				1.5
Pteridium aquilinum	6.9	4.6	12.1	5.6	4.3	4.8	.8	2.6		1.0
Senecio tomentosus	.2	1.4	.1	.6		1.1		1.8		
Solidago spp.		1.4	.5					2.1	*	.5
Spiranthes gracilis								.4		
Viola adunca		1.4	*	.6			*	.4		
Trees and shrubs										
Acer rubrum							.4			1.6
Arctostaphylos uva-ursi		.4		.6	.5	1.1		.9		
Amelanchier sp.	.6	1.4		2.8	.9	4.3	2.2	4.4	2.2	8.2
Ceanothus ovatus		.7		.6		1.3			.3	1.6
Comptonia peregrina	1.4	6.4	.8	4.5	1.4	5.4	12.3	9.3		
Crataegus sp.									.3	
Epigea repens									3.2	4.1
Pinus banksiana		.3				.5		.9		
Prunus pumila	4.4	6.7	2.1	10.2	5.0	6.4	12.9	9.3	1.2	5.7
Prunus serotina	3.0	.4			.8			.9	1.9	1.0
Prunus virginiana	.7							.4		
Quercus spp. (red oak)	.7	.7			2.9	.5	1.0			4.6
Rosa blanda	.2	1.1	.2	2.3						
Rubus hispidus									.3	3.1
Rubus pensilvanicus	9.0	3.9	2.2	3.4	.9	3.8	.2	2.7		
Salix glaucophylloides		.7								
Vaccinium spp.	18.6	11.7	21.0	15.8	23.9	14.5	48.4	11.9	47.3	15.5

TABLE B 3

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES, BY SPECIES GROUP, SURVEYED IN 1979 (SITE 1A, 0-YEAR CLEARCUT), AND 1980 AND 1981 (SITE 7C80-81, 1-AND 2-YEAR PRESCRIBED BURN)

	Year of Survey					
	1979		1980		1981	
Species	Cover(%)	Freq(%)	Cover(%)	Freq(%)	Cover(%)	Freq(%)
Annuals and biennials						
Melampyrum lineare	-	.7	-	-	-	.7
Geranium carolinianum	-	-	13.5	3.8	-	-
Corydalis sempervirens	-	-	4.8	2.2	-	-
Cirsium sp.	-	-	-	.5	-	-
Lactuca canadensis	-	-	-	.5	-	-
Grasses and sedges						
Carex pensylvanica	21.7	14.5	28.7	14.1	36.8	19.9
Danthonia spicata	-	-	-	2.2	-	2.0
Oryzopsis pungens	-	-	1.8	5.4	8.1	11.9
Koeleria macrantha	-	.7	2.2	3.8	-	1.3
Panicum columbianum	-	-	-	1.6	.2	-
Bromus kalmii	5.0	2.2	.2	2.7	-	-
Festuca sp.	-	-	.8	.5	.3	.7
Poa pratensis	-	-	2.1	1.1	-	-
Schizachne purpurascens	4.6	2.2	-	.5	-	-
Oryzopsis asperifolia	.8	5.1	-	-	-	.7
Deschampsia flexuosa	.4	1.5	-	-	.2	2.0
Perennial herbs						
Anemone quinquefolia	.4	2.9	.6	7.1	.1	2.7
Aster laevis	1.2	3.6	1.2	4.4	.2	2.0
Solidago sp.	.2	2.9	-	.5	.7	.7
Viola adunca	-	-	.3	3.3	-	-
Pteridium aquilinum	7.1	7.2	-	.5	-	1.3
Liatris novae-angliae	-	-	.4	1.6	-	-
Maianthemun canadense	1.3	5.8	-	.5	-	2.0
Helianthus occidentalis	-	-	-	3.3	-	-
Apocynum androsaemifolium	.4	-	-	-	-	-
Convolvulus spithamaeus	-	-	-	1.1	-	-
Hieracium aurantiacum	-	1.5	.1	1.6	-	1.3
Hieracium venosum	-	-	-	.5	-	-
Hieracium canadense	-	-	.1	-	-	-
Campanula rotundifolia	-	-	.2	.5	.1	.7
Polygala polygama	-	-	-	.5	-	-
Fragaria virginiana	1.3	1.4	-	.5	-	.7
Gaultheria procumbens	3.1	5.8	-	-	-	1.3
Trees and Shrubs						
Vaccinium spp.	29.6	13.8	33.1	15.2	40.2	19.9
Amelanchier sp.	13.8	8.0	3.5	4.9	2.2	6.0
Prunus pumila	4.2	8.0	4.2	7.1	6.9	11.9
Arctostaphylos uva-ursi	1.2	5.1	-	1.1	1.8	6.0
Comptonia peregrina	3.5	2.9	2.1	4.4	1.7	3.3
Prunus virginiana	-	1.4	-	-	-	-
Prunus serotina	-	.7	-	-	-	-
Rosa blanda	-	1.4	-	-	.5	.7
Rubus pensilvanicus	-	.7	-	-	-	.7
Pinus banksiana	.2	-	-	.5	-	-
Symphoricarpos albus	-	-	.1	1.6	-	-

TABLE B 4

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES ON SITE 7D79-80-81 SURVEYED AS A 1-YEAR-, 2-YEAR-, AND 3-YEAR-OLD PRESCRIBED BURN

	1979		1980		1981	
Species	Cover	Freq	Cover	Freq	Cover	Freq
Annuals and biennials						
Geranium carolinianum	.6	.6				
Lactuca canadensis		.6				
Melampyrum lineare	.3	1.7				
Grasses and sedges						
Agropyron trachycaulum		.6				
Agrostis hyemalis	.3	1.1		1.4		
Andropogon gerardii	4.6	7.9	2.7	4.2	.3	3.3
Carex pensylvanica	66.5	19.8	50.0	20.4	50.7	23.8
Danthonia spicata	.8	7.9	3.4	5.6	4.0	3.3
Deschampsia flexuosa	.3	.6	.4	.7		
Dichanthelium depauperatum	.2		11.2	12.7	8.6	9.8
Koeleria macrantha			1.5	1.4		2.5
Oryzopsis pungens			.3	1.4	.1	3.3
Panicum columbianum	.3	6.2	2.1	8.4	2.5	6.6
Poa pratensis	.5	.6				.4
Perennial herbs						
Apocynum androsaemifolium		1.1				
Aster laevis	1.0	3.4	.7	3.5	.1	4.9
Campanula rotundifolia		1.7				
Fragaria virginiana		.6		.7		
Hieracium aurantiacum	1.0	.6				
Hieracium canadense		.6				
Hieracium venosum	.6	4.5				3.3
Helianthemum canadense						2.5
Helianthus occidentalis		1.1			.3	
Lechea minor				4.2		1.6
Liatris novae-angliae		.6				
Physalis virginiana				2.1		
Pteridium aquilinum	1.6	8.5	11.3	7.8	12.3	9.8
Rumex acetosella	3.6	.6	.3	2.1		1.6
Solidago sp.	.6	1.7	.1		.2	1.6
Viola adunca				.7		
Trees and shrubs						
Arctostaphylos uva-ursi		.6			.4	
Comptonia peregrina	17.0	13.0	14.7	14.1	13.2	14.7
Gaylussacia baccata		.6				
Pinus banksiana				.7	.3	
Prunus pumila		1.7		.7	.5	
Prunus serotina		.6	.1			.8
Prunus virginiana		.6				
Quercus spp. (red oak)		3.4	.6	1.4	2.9	1.6
Rosa blanda		.6		.7		
Rubus pensilvanicus		1.3		2.8	2.8	2.5
Vaccinium spp.		5.1		2.1		2.5

TABLE B 5

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES
ON SITE 8A79-80-81 SURVEYED AS A
2-YEAR-, 3-YEAR-, AND 4-YEAR-OLD WILDFIRE

Species	1979		1980		1981	
	Cover	Freq	Cover	Freq	Cover	Freq
Annuals and biennials						
Corydalis sempervirens		.4				.5
Erigeron canadensis		.4	*	1.7	.2	.4
Lithospermum arvense	.1	.9		.4		
Melampyrum lineare						.9
Grasses and sedges						
Agropyron trachycaulum		.4				.5
Andropogon gerardii	4.3	4.0	1.3	1.3	1.5	3.1
Andropogon scoparius	4.0	3.1		.4		.9
Bromus kalmii					.7	1.8
Carex pensylvanica	29.3	12.3	27.4	11.8	34.4	13.5
Danthonia spicata	.3	1.7		1.3		1.8
Deschampsia flexuosa		.4		.4		1.8
Dichanthelium depauperatum	1.1	3.1		2.6	.5	2.2
Festuca sp.	1.5	.4		.9	.7	.9
Koeleria macrantha	1.7	4.9	1.6	3.5	.4	2.2
Muhlenbergia mexicana		.9		2.2		1.4
Oryzopsis pungens	1.1	7.0	6.5	7.0	5.0	6.7
Panicum columbianum	.2	.4	.1			.9
Poa pratensis		.4				
Sorghastrum nutans	.4	.4	2.5	1.7	.4	.9
Perennial herbs						
Anemone riparia		.4				
Antennaria neglecta				.4		.5
Apocynum androsaemifolium		.8		3.5	.3	1.3
Aster laevis	.6	4.8	.1	4.8	.6	5.4
Brassica sp.	*					
Campanula rotundifolia	*	.4	.1			
Convolvulus spithamaeus		1.3		1.3	.4	.9
Equisetum hyemale	*	*				
Fragaria virginiana		.4		.9	.2	.5
Gaultheria procumbens						.5
Helianthus occidentalis	.3	.4				1.4
Hieracium aurantiacum						.9
Hieracium venosum	.2	.4		1.3	.1	1.8
Houstonia longifolia		.4				.4
Liatris novae-angliae		.9			.1	.4
Maianthemum canadense		.4				
Physalis virginiana				.4		
Polygala polygama				.9		
Pteridium aquilinum		3.5	6.0	2.6	5.4	2.7
Senecio tomentosus	1.4	.9	.1	2.6	.3	1.4
Solidago spp.	.2			.4		1.3
Unidentified monocot		.4				
Viola adunca	.1	2.2		2.6		
Viola pedatifida				.4		
Trees and shrubs						
Amelanchier sp.	.2	5.7	1.6	5.7	.7	2.2
Arctostaphylos uva-ursi	.3	.4	.2	1.8	1.0	2.7
Ceanothus ovatus		.9	1.1		.8	.4
Comptonia peregrina	13.6	4.8		3.9	10.4	4.5
Crataegus sp.		.9				
Pinus banksiana	.2	3.5	2.4	5.7	1.4	4.5
Prunus pumila	9.8	10.6	4.4	9.6	4.8	9.0
Prunus virginiana	.4		2.6	1.3		
Quercus spp. (red oak)		.4	.8	.9	2.0	.4
Rosa blanda		.9				
Rubus pensilvanicus	.2			.9		1.8
Salix glaucophylloides						.5
Symphoricarpos albus		.9	.3	.4		.9
Vaccinium spp.	28.2	11.5	40.6	11.3	27.2	13.0

TABLE B 6

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES ON SITE 9A79-80-81 SURVEYED AS A 3-YEAR-, 4-YEAR-, AND 5-YEAR-OLD PRESCRIBED BURN

Species	1979 Cover	1979 Freq	1980 Cover	1980 Freq	1981 Cover	1981 Freq
Annuals and biennials						
Cirsium sp.	.4					
Erigeron canadensis	.3					
Krigia virginica					.1	
Lactuca canadensis				.5	.2	
Melampyrum lineare						.5
Grasses and sedges						
Agropyron trachycaulum	*	.9				
Andropogon gerardii	2.7	5.1	2.1	4.1	3.2	3.6
Andropogon scoparius	.6	3.3		1.8		
Bromus kalmii		.5	.7	2.3	1.0	2.0
Carex pensylvanica	57.6	13.5	54.1	13.9	39.3	15.3
Danthonia spicata		.9	1.8	1.8	1.4	3.1
Deschampsia flexuosa	1.8	5.1	1.4	5.1	.2	4.6
Dichanthelium depauperatum	.2	1.9	.9	1.8	.3	1.0
Festuca sp.					.2	
Koeleria macrantha	.4	2.3		2.3	1.6	
Oryzopsis pungens	*	4.6	1.7	6.0	2.5	6.6
Panicum columbianum	.1	.9		.5		
Schizachne purpurascens	.2	1.9		.9		.5
Perennial herbs						
Anemone quinquefolia				1.5		
Antennaria neglecta		.5				
Apocynum androsaemifolium			*	.9		1.5
Aster junciformis	*					
Aster laevis	.6	5.6	.7	6.5	1.4	8.2
Campanula rotundifolia			*	.5		
Convolvulus spithamaeus		.9		.5		1.5
Fragaria virginiana	.1	1.4				1.5
Helianthus occidentalis	.2	.5		.5		.5
Hieracium aurantiacum	.3	1.4	.1	1.8		
Hieracium venosum			.2	2.3	.1	1.5
Lechea minor		.5				1.0
Liatris novae-angliae			.1	.9		1.0
Maianthemum canadense				.5		
Potentilla tridentata				.5		
Pteridium aquilinum		.5			1.5	.5
Senecio tomentosus		.9		.9		
Solidago spp.		.9		.5		1.0
Viola adunca	*	1.9		1.8	.2	1.5
Trees and shrubs						
Amelanchier sp.	.9	3.3	.6	5.1	.2	4.1
Arctostaphyles uva-ursi	.2	1.9	.4	2.3	.6	1.5
Ceanothus ovatus	2.5	2.8	.5	1.8	1.9	1.5
Comptonia peregrina	2.6	6.5	.8	6.0	1.3	5.1
Pinus banksiana	.3				1.7	
Prunus pumila	4.2	10.7	9.1	9.3	11.7	6.6
Prunus serotina		.5		.5		
Prunus virginiana		1.9		.5	3.1	.5
Quercus spp. (red oak)		.5	1.6	.5	.4	
Rosa blanda					.2	.5
Rubus pensilvanicus	3.5	3.3	1.4	2.3	7.2	4.6
Salix glaucophylloides	3.6	.5			1.8	1.0
Symphoricarpos albus						1.5
Vaccinium spp.	16.7	12.6	21.7	12.0	18.2	14.3

TABLE B 7

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES ON SITE 9B79-80-81 SURVEYED AS A 3-YEAR-, 4-YEAR-, AND 5-YEAR-OLD WILDFIRE

Species	1979		1980		1981	
	Cover	Freq	Cover	Freq	Cover	Freq
Grasses and sedges						
Andropogon gerardii	3.3	2.6	.3	2.8	.7	3.3
Carex pensylvanica	51.3	25.2	67.3	21.1	60.6	24.8
Danthonia spicata	.4	2.6	.3	.7		.8
Dichanthelium depauperatum	4.4	11.3	2.1	12.0	.8	9.9
Koeleria macrantha	.1	.8		2.1		
Oryzopsis pungens	.7	3.5	1.8	8.4	.7	2.5
Panicum columbianum		3.5		2.8		1.7
Perennial herbs						
Antennaria neglecta		.9				
Apocynum androsaemifolium				1.4		
Aster laevis	.1	.9	.2	2.1		
Campanula rotundifolia			*			
Hieracium venosum						.8
Maianthemum canadense				.7		
Potentilla tridentata		.9	.2	3.5		1.6
Solidago spp.			.3			
Unidentified dicot	1.1					
Viola adunca		.9		.7		
Viola pedatifida				1.4		
Trees and shrubs						
Amelanchier sp.		2.6	1.3	2.8	1.4	4.1
Arctostaphylos uva-ursi	1.3	6.1	.6	4.9	.4	4.1
Comptonia peregrina			.7	1.4	.1	1.7
Pinus banksiana		2.6	.2	1.4	.3	2.5
Prunus pumila	3.5	10.4	2.7	10.6	7.5	18.2
Quercus spp. (red oak)	.2	.9				
Vaccinium spp.	33.5	24.4	22.2	19.0	27.6	24.0

TABLE B 8

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES ON SITE 10A79-80-81 SURVEYED AS A 4-YEAR-, 5-YEAR-, AND 6-YEAR-OLD PRESCRIBED BURN

Species	1979 Cover	1979 Freq	1980 Cover	1980 Freq	1981 Cover	1981 Freq
Annuals and biennials						
Arabis glabra				.4		
Cirsium sp.						.2
Lactuca canadensis		1.6	.1	1.3		.6
Grasses and sedges						
Agropyron trachycaulum					.5	
Agrostis hyemalis	.1	.8		.9		
Bromus kalmii	.3					
Carex pensylvanica	17.4	9.6	21.8	10.9	30.9	13.7
Danthonia spicata	9.6	4.0	3.0	5.3		.5
Deschampsia flexuosa		.8				
Dichanthelium depauperatum	.2	2.8		1.3		1.6
Festuca sp.			.4			
Muhlenbergia mexicana	.2	.4				
Oryzopsis asperifolia	32.5	10.8	25.5	10.5	25.6	14.7
Oryzopsis pungens		.8	.5	2.2	.2	1.1
Panicum columbianum		.8		.9		
Panicum xanthophysum	.5	.4		1.3	.1	1.1
Poa pratensis	.2					
Schizachne purpurascens	10.8	4.4	6.0	4.0	9.3	6.6
Sorghastrum nutans				.9		
Perennial herbs						
Anemone quinquefolia				.4	.4	2.2
Apocynum androsaemifolium			.2	3.5		
Aster laevis	1.8	6.4	.2	3.5	.6	4.9
Aster sagittifolius			1.0	1.8	.4	2.2
Campanula rotundifolia	.1	1.6	*	2.6	.1	1.6
Convolvulus spithamaeus		2.8	.1		.5	1.1
Epigea repens				.4		
Fragaria virginiana	1.0	6.4	.7	5.3	1.3	2.7
Gaultheria procumbens	.1	.4			.1	1.1
Helianthus occidentalis						1.1
Hieracium venosum		.4		.4	.4	
Liatris novae-angliae			*	.9		
Maianthemum canadense	.2	4.0	.2	1.8	.5	4.9
Polygonum cilinode						.6
Potentilla simplex		.4				
Pteridium aquilinum	11.5	10.8	15.9	10.1	4.5	9.8
Rumex acetosella				.4		
Senecio tomentosus		.4		.4		
Solidago spp.	.2	.4		.4	.1	1.1
Viola adunca	.3	5.2	.2	.9	.1	1.1
Trees and shrubs						
Acer rubrum		.4				
Amelanchier sp.	.5	.8	.2			1.1
Crataegus sp.		.8	1.7	1.3		
Diervilla lonicera		.4			.1	1.6
Pinus banksiana		.4				.6
Populus tremuloides					1.9	2.5
Prunus pumila				.4		
Prunus serotina	1.9	2.0	2.9	1.3	10.3	2.2
Quercus spp.	.3		.8	1.3		.6
Rubus pensilvanicus	9.6	9.6	11.0	12.7	.7	9.3
Vaccinium spp.	.6	8.8	7.5	10.1	10.8	9.8

TABLE B 9

RELATIVE COVER AND RELATIVE FREQUENCY OF EACH SPECIES ON SITE 10B79-80-81 SURVEYED AS A 4-YEAR-, 5-YEAR-, AND 6-YEAR-OLD PRESCRIBED BURN

Species	1979 Cover	1979 Freq	1980 Cover	1980 Freq	1981 Cover	1981 Freq
Annuals and biennials						
Erigeron canadensis	.2	3.8	.3	3.6	.8	2.3
Lactuca canadensis				1.2		
Lithospermum arvense			.5	.6		
Grasses and sedges						
Agropyron trachycaulum		.7				
Agrostis hyemalis		1.3				
Bromus kalmii			.3	.6		1.2
Carex pensylvanica	43.5	19.4	44.9	18.1	38.8	17.4
Danthonia spicata	.1	1.3				
Deschampsia flexuosa		.6				.6
Dichanthelium depauperatum	1.3	5.8	2.5	4.2	.9	2.9
Koeleria macrantha		.7	.3	.6	.3	1.2
Muhlenbergia mexicana		.6				
Oryzopsis pungens	.9	3.2	4.8	8.4	3.0	8.1
Oryzopsis asperifolia			4.1	1.8	4.8	4.1
Panicum columbianum		1.3	.4	1.2		1.2
Poa pratensis		1.3		1.2		
Schizachne purpurascens	7.7	3.2		.6	2.5	1.7
Panicum xanthophysum		.6				.6
Perennial herbs						
Apocynum androsaemifolium		1.3				
Aster laevis		.6	1.6	.6	.1	2.3
Convolvulus spithamaeus		.7			.9	1.7
Fragaria virginiana					.3	1.2
Gaultheria procumbens		.6	.1	1.2	.1	2.3
Hieracium aurantiacum		.7				.6
Maianthemum canadense		.6	*	1.8	.2	.6
Potentilla arguta		.6	.1	.6		
Potentilla tridentata				.6		.6
Pteridium aquilinum	22.4	14.8	8.3	13.2	9.8	7.0
Senecio tomentosus				2.4	.9	1.7
Solidago spp.		1.3				
Viola adunca	.4	1.9	.1	3.0	.3	3.5
Trees and shrubs						
Amelanchier sp.						1.2
Arctostaphylos uva-ursi	.2	.6		.6		.6
Ceanothus ovatus		1.3	.7			
Comptonia peregrina	.4	3.2	1.5	2.4		4.7
Crataegus sp.	.2	.7	.2	1.2		1.7
Diervilla lonicera			.6	1.2	2.5	1.7
Pinus banksiana	.4			.6		.6
Populus tremuloides	14.9	3.9	10.1	3.6	14.2	1.7
Prunus pumila	.7	2.6	2.3	3.6	1.2	4.6
Prunus serotina	.1	.6	2.8	.6	2.2	1.7
Quercus spp.	.4	1.3	1.8	2.4	2.0	
Rosa blanda	.2	.7				
Rubus pensilvanicus	.6	3.9	.8	4.8		1.7
Salix glaucophylloides		.6	.2		2.4	1.7
Symphoricarpos albus		1.3	.5	.6	.4	1.7
Vaccinium spp.	5.2	11.6	12.1	12.1	12.1	14.5

TABLE B 10

RELATIVE COVER AND RELATIVE FREQUENCY FOR EACH SPECIES ON SITE 11 SURVEYED AS A 6-YEAR-OLD WILDFIRE

Species	1979 Cover	Freq
Grasses and sedges		
Carex pensylvanica	86.0	28.2
Danthonia spicata	3.5	10.3
Deschampsia flexuosa		2.6
Dichanthelium depauperatum	2.0	14.1
Oryzopsis pungens	.3	2.6
Panicum columbianum		1.3
Perennial herbs		
Pteridium aquilinum	.5	10.3
Trees and shrubs		
Arctostaphylos uva-ursi		1.3
Comptonia peregrina		2.6
Pinus banksiana	2.8	
Quercus alba		1.3
Quercus spp. (red oak)		2.6
Vaccinium spp.	5.0	23.1

APPENDIX C

RELATIVE COVER AND RELATIVE FREQUENCY DATA FOR UNDERSTORY SPECIES SURVEYED ON INTERMEDIATE-AGE AND MATURE JACK PINE STANDS

TABLE C 1

RELATIVE COVER AND RELATIVE FREQUENCY FOR EACH SPECIES ON SITE 12 B SURVEYED AS AN INTERMEDIATE-AGE (35-YEAR-OLD) JACK PINE STAND

Species	1981 Cover	Freq
Annuals and biennials		
Melampyrum lineare	*	2.6
Grasses and sedges		
Andropogon gerardii	.2	3.1
Bromus kalmii	1.7	3.7
Carex pensylvanica	17.5	15.1
Danthonia spicata	.5	1.6
Deschampsia flexuosa	4.7	6.8
Dichanthelium depauperatum		1.0
Muhlenbergia mexicana	.3	
Oryzopsis pungens	.4	5.2
Schizachne purpurascens	.4	.8
Perennial herbs		
Apocynum androsaemifolium		.5
Aster laevis	2.3	4.2
Fragaria virginiana	*	1.0
Gaultheria procumbens		.5
Helianthemum canadense		1.0
Helianthus occidentalis	.1	2.6
Hieracium venosum	.3	6.3
Liatris novae-angliae	.5	1.0
Potentilla tridentata	.1	2.6
Solidago sp.		.5
Viola adunca		1.6
Trees and shrubs		
Amelanchier sp.	.5	3.1
Arctostaphylos uva-ursi	1.9	3.1
Comptonia peregrina	5.3	7.8
Pinus banksiana	.8	1.6
Prunus pumila	9.3	9.9
Prunus serotina	1.5	
Quercus spp. (red oak)	.2	
Vaccinium spp.	50.7	13.5

TABLE C 2

RELATIVE COVER AND RELATIVE FREQUENCY FOR EACH SPECIES ON SITE 13B SURVEYED AS A MATURE JACK PINE STAND

Species	1981 Cover	1981 Freq
Annuals and biennials		
Melampyrum lineare	1.2	14.9
Grasses and sedges		
Andropogon gerardii	2.2	5.4
Andropogon scoparius	.7	.7
Carex pensylvanica	12.9	20.3
Muhlenbergia mexicana		.7
Oryzopsis pungens		.7
Perennial herbs		
Aster laevis		.7
Gaultheria procumbens	.3	2.0
Helianthus occidentalis		.7
Hieracium venosum		.7
Potentilla tridentata		.7
Pteridium aquilinum	7.8	9.5
Solidago sp.	.1	
Viola adunca		1.4
Trees and shrubs		
Amelanchier sp.	1.0	2.0
Arctostaphylos uva-ursi	.6	6.8
Comptonia peregrina	3.7	3.4
Pinus banksiana	1.7	.7
Prunus pumila	.8	5.4
Quercus spp. (red oak)	3.7	4.0
Vaccinium spp.	63.4	19.6

TABLE C 3

RELATIVE COVER AND RELATIVE FREQUENCY FOR EACH SPECIES ON SITE 13D SURVEYED AS A MATURE JACK PINE STAND

Species	1981 Cover	1981 Freq
Annuals and biennials		
Melampyrum lineare	.6	7.4
Grasses and sedges		
Carex pensylvanica	8.6	15.3
Danthonia spicata	.1	
Oryzopsis pungens	*	1.6
Schizachne purpurascens	1.0	1.6
Perennial herbs		
Apocynum androsaemifolium	.2	1.1
Aster laevis	.3	2.6
Chimaphila umbellata	.2	
Fragaria virginiana		.5
Gaultheria procumbens	2.7	9.5
Helianthus occidentalis		.5
Maianthemum canadense		2.6
Pteridium aquilinum	38.1	13.6
Solidago spp.	*	.5
Trees and shrubs		
Amelanchier sp.		3.7
Arctostaphylos uva-ursi	.9	2.1
Comptonia peregrina	.5	4.2
Crataegus sp.	.8	1.1
Epigea repens	3.0	5.8
Pinus banksiana	.4	
Pinus strobus		.5
Populus tremuloides		.5
Prunus pumila	1.9	5.3
Prunus serotina	.9	2.1
Quercus spp. (red oak)	.6	.5
Rubus pensilvanicus		2.1
Vaccinium spp.	39.0	15.8

Appendix D

National Cooperative Soil Survey

for the Grayling Series

National Cooperative Soil Survey for the Grayling Series.

GRAYLING SERIES

The Grayling series is a mixed, frigid Typic Udipsamments. These soils are sand throughout. Typically, they have black and grayish brown A horizons, dark brown and strong brown B horizons, and light brown C horizons.

Typical Pedon: Grayling sand - forested. (Colors are for moist soil unless otherwise stated.)

A1 & A2—0 to 3 inches; black (N 2/) (A1), and grayish brown (10YR 5/2) sand, (A2); coated and uncoated sand grains mixed throughout the horizon, giving a salt and pepper appearance; moderate organic matter content in upper part; weak medium granular structure; very friable; very strongly acid; abrupt smooth boundary. (2 to 4 inches thick)

B21ir—3 to 9 inches; dark brown (7.5YR 4/4) sand; weak coarse granular structure; very friable; strongly acid; clear smooth boundary. (4 to 8 inches thick)

B22ir—9 to 15 inches; strong brown (7.5YR 5/6) sand; very weak coarse granular structure; very friable; medium acid; clear irregular boundary. (4 to 14 inches thick)

B3—15 to 23 inches; brown (7.5YR 5/4) sand; single grained; loose; medium acid; gradual smooth boundary. (3 to 10 inches thick)

C—23 to 60 inches; light brown (7.5YR 6/4) sand; single grained; loose; medium acid.

Type Location: Delta County, Michigan; SW¼, SW¼, SE¼, SW¼, Sec. 34, T. 41 N., R. 23 W.; 0.2 mile south of U. S. 2 on I-21 then east 100 feet.

Range in Characteristics: Thickness of the solum ranges from about 15 to 30 inches. The upper eight inches of the solum is sand or loamy sand and the rest of the solum is sand; medium sand is dominant. The upper part of the soil is very strongly acid or strongly acid and the lower part is medium acid or slightly acid. Mean annual soil temperature is estimated to range from about 38 to 43° F. Some pedons have an O1 horizon, ½ to 1½ inches thick. It is dark grayish brown (10YR 4/2) to black (10YR 2/1) and is composed of oak leaves or jack pine needles, and some twigs and roots in various stages of decomposition. The A1 and A2 horizons are normally intermixed in a single layer, but some pedons have a separate A2 horizon. In the latter pedons the A1 horizon ranges from 1 to 3 inches in thickness and the A2 horizon from 1 to 3 inches in thickness, but the A2 horizon is intermittent within the pedon. The A1 horizon has hue of 7.5YR or 10YR, value of 2 through 4 and chroma of 1 or 2. The A2 horizon has hue of 7.5YR or 10YR, value of 5 or 6, and chroma of 2. The B21ir horizon has hue of 5YR, 7.5YR or 10YR, value of 4 or 5, and chroma of 4; the B22ir horizon has similar hue but value ranges from 4 through 6, and chroma from 6 through 8. The B3 horizon has hue of 5YR, 7.5YR or 10YR, value of 5 or 6, and chroma of 6 through 8. The C horizon has hue of 2.5YR, 5YR, 7.5YR or 10YR, value of 6 or 7, and chroma of 2 through 4. Some pedons have coarse sand in the C horizon. Dark minerals are more common in the northwestern part of the soils range.

Competing Series and Their Differentiae: These are the Claire, Friendship, Menahga, Nymore, Plainbo, Sartell, Serden and Shawano series in the same family and the Croswell, Deer Park, Hiwood, Oakville, Omega, Plainfield, Rubicon, Vilas and Windsor soils. Claire and Serden soils are less acid. Friendship soils have mottles in the control section. Menahga soils (see Remarks). Nymore soils have coarser sands. Plainbo soils have bedrock at depths of 20 to 40 inches. Sartell and Shawano soils have finer sands. Croswell, Rubicon, Vilas and Windsor soils have spodic horizons. Deer Park soils have albic horizons overlying darker colored B horizons and have less acid sola. Hiwood soils have dominantly fine sand throughout the control section. Oakville, Plainfield and Windsor soils have mean annual soil temperature greater than 47° F. Omega soils have loamy sand B horizons.

Setting: Grayling soils are on outwash plains and lake plains of Wisconsin age. Slope gradients are dominantly less than 8 percent but range from 0 to about 15 percent. These soils formed in sandy glaciofluvial sediments. The climate is continental. Average annual precipitation ranges from 26 to 33 inches; mean annual temperature from about 41 to 45° F.; and mean summer temperature from 60 to 68° F.

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