

## Early revegetation of clear-cut and burned jack pine sites in northern lower Michigan<sup>1</sup>

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Received June 3, 1981

ABRAMS, M. D., and D. I. DICKMANN. 1982. Early revegetation of clear-cut and burned jack pine sites in northern lower Michigan. *Can. J. Bot.* **60**: 946–954.

Revegetation of clear-cut and (or) burned jack pine (*Pinus banksiana* Lamb.) sites in northern lower Michigan was characterized during the first 5 years following treatment. Burning promoted the establishment of a large variety of species not typical of unburned areas. A total of 89 species was recorded on burned sites, of which 40 were exclusive, compared with 51 species on unburned sites, of which only 2 species were exclusive. Burned sites consistently showed greater species richness compared with unburned sites of the same age. Low species diversity on the older unburned clear-cuts (years 3 to 6) and certain burned sites was directly influenced by the dominance of the sedge *Carex pensylvanica*. The total domination of *Carex* (up to 86% relative cover) on many of these sites appears to be unique to northern lower Michigan. It is hypothesized that *Carex*, acting as an opportunistic species, monopolizes the space and soil resources liberated following disturbances and suppresses or excludes other species.

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Des pinèdes à pin gris (*Pinus banksiana* Lamb.) ayant été soumises à une coupe à blanc et (ou) incendiées dans la région nord du Michigan inférieur, les auteurs caractérisent la reprise de la végétation pendant les 5 premières années après les traitements. Le feu provoque l'établissement d'un grand nombre d'espèces qui ne sont pas typiques des endroits non incendiés. Au total, 89 espèces ont été notées sur les sites incendiés, y compris 40 espèces exclusives, tandis que sur les sites non incendiés, 51 espèces ont été relevées dont seulement 2 étaient exclusives. Les sites incendiés présentent toujours une richesse spécifique plus élevée que les sites non incendiés de même âge. La faible diversité spécifique des sites coupés à blanc les plus âgés (depuis 3 à 6 ans) et de certains sites incendiés est directement attribuable à la dominance du *Carex pensylvanica*. La dominance de ce *Carex* (atteignant jusqu'à 86% de recouvrement relatif) dans plusieurs de ces sites semble être un phénomène unique à la région étudiée. Les auteurs émettent l'hypothèse que ce *Carex*, agissant comme une espèce opportuniste, monopolise l'espace et les ressources édaphiques libérées après les perturbations et qu'il élimine ou exclut les autres espèces.

[Traduit par le journal]

### Introduction

The role of fire as an ecological factor and a management tool in the Lake States is well documented (Ahlgren 1974; Cayford 1970; Eyre and LeBarron 1944; Heinselman 1973; Vogl 1970). A large portion of this 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 jack pine have utilized prescribed burning.

Studies of prescribed burning have mainly focused on slash reduction, seedbed preparation, and responses of seedlings to various environmental factors (Beaufait 1962; Eyre and LeBarron 1944). 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; Krefting and Ahlgren 1974;

Ohmann and Grigal 1979; Vogl 1970). Thus, a study was undertaken to characterize early revegetation of clear-cut and (or) burned jack pine sites in northern lower Michigan where this species is a predominant component of the tree vegetation on sandy soils.

### Description of study area

The work was conducted during the summers of 1979 and 1980 in Roscommon, Crawford, Oscoda, and Ogemaw counties in northeast lower Michigan. The elevation of these counties generally lies between 275 and 365 m above sea level, with little surface relief. The topography is a direct result of the Wisconsin glaciation, with level areas consisting of outwash and till plains or ground moraines (Veatch *et al.* 1923). Before the near-complete clearing by the lumber industry in the late 1800's, these areas were largely occupied by dense hardwood and coniferous forests. Small areas of bog, marsh, and grassland were also present. Today these counties are a patchwork of small woodlots, second- and third-growth hardwood and coniferous forests, farmlands, bracken grasslands, and swamp forests.

The Grayling sand soil series (a mixed, frigid, typic udipsamment) comprises large areas in these counties and is characterized by its loose consistence, incoherent structure, sandy or single-grained texture throughout, and perviousness

<sup>1</sup>Michigan Agricultural Experiment Station journal article No. 9983.

and nonretentiveness of 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.* 1923).

The climate of these areas is characterized by cold winters, short mild summers, a large number of cloudy days, low evaporation, and moderately high humidity (Veatch *et al.* 1923). Average yearly temperature generally falls within the range of 6 to 7°C, with mean monthly temperatures ranging from -8 to 19°C. Precipitation is fairly well distributed throughout the year, with a mean annual rainfall and snowfall of 77 and 180 cm, respectively (Anonymous 1971).

Jack pine forests dominate large areas of the above four counties. Because jack pine is an important pulpwood species and the nesting habitat for the endangered Kirtland's warbler, much attention has been paid to devising a workable silvicultural system for its perpetuation. For this reason large areas of jack pine forests are logged and burned each year. Wildfires are also a periodic occurrence in this region.

### Methods

All burned and unburned sites used in this study were located on the Grayling sand series and were chosen to encompass as little variation in topography and other environmental gradients as possible. However, no soil analyses were conducted on the study sites; therefore, the degree of soil uniformity among the sites is not known.

Only burns that occurred during the months of July, August, and September (summer burns) were included. One exception was site 10A (Table 2), which was prescribe-burned in October. Following treatment all areas were left unplanted. The range of site variation for burned areas is outlined under the treatment description (Table 2). Included in the burned areas for study were prescribed burns and wildfires in clear-cut mature jack pine, and prescribed burns and wildfires in 35-year-old standing jack pine. These variations represent concessions made by the authors because of a lack of available prescribe-burned clear-cut sites of mature jack pine.

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 1-m<sup>2</sup> circular plots 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. Generally, 30 frequency plots and three cover transects (60 m) were used to characterize each site. Deviation from this occurred because of high species richness (site 7B79-45 frequency plots and 90-m cover), low species richness (site 11-20 frequency plots and 40-m cover), and time constraints (site 1A-20 frequency plots and 40-m cover). 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 for all species follows Voss (1972) for gymnosperms and monocots and Fernald (1950) for other taxa.

### Results

The data presented are from certain sites sampled

once and other sites surveyed in both 1979 and 1980 (Tables 1 and 2). The age of these sites make up a sequence ranging from 0- (clear-cut the winter and spring previous to the summer sampling) to 5-year clear-cut sites (Table 1) and 1- (burned the summer previous to sampling) to 6-year burned sites (Table 2). We are cautious in suggesting that these sites are typical of those ages. Although sites were rigorously selected, the type, severity, and seasonal timing of the disturbance on each site varied. Also, differences most certainly existed in the predisturbance floristic composition of each site. Therefore, in many aspects each site is unique, making direct comparisons difficult. Nonetheless, we do feel that certain consistent differences in burned versus unburned sites can be discerned.

A comparison of three different measures of diversity (total species richness (number of species), average frequency per plot, and Shannon index<sup>2</sup>) of sites averaged within years for a 6-year progression is shown in Fig. 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 are shown in Tables 1 and 2 for unburned and burned areas, respectively. The burned areas consistently showed a higher diversity than the unburned areas of the same age during years 1 to 5. This trend is most evident in the species richness data, where rare and dominant species contribute equally. Average frequency and Shannon index, which reflect number of species and equitability, were only slightly greater on the burned versus the unburned areas for years 1 and 2. With all three indices, the unburned areas showed a general decline in diversity over the time sequence. Burned sites initially decreased in richness but nonetheless retained a high level when compared with their unburned counterparts.

It is important to note that, although the average frequency per plot and the Shannon index initially were nearly equal on burned and unburned sites, these sites differed qualitatively in species composition and richness. In other words, a greater number of species, mostly rare, contributed to these indices on burned sites, whereas fewer, but more common, species contributed on unburned clear-cuts.

As shown in Table 3, 89 different species were recorded on burned sites compared with 51 species on unburned sites. Forty species were exclusive to burned sites, whereas only two species were exclusive to unburned areas (Table 3). Three of the 11 annuals and biennials, 12 of the 21 grasses and sedges, 16 of the 34

<sup>2</sup>Shannon index of diversity ( $H$ ) =  $-\sum P_i \log P_i$ , where  $P_i$  is relative cover (Odum 1971).

TABLE 1. Relative cover (C), relative frequency (F), and species richness (R) for various vegetational groups on unburned clear-cut sites

Site number	Years since treatment	Area, ha	Annuals and biennials			Grasses and sedges			Perennial herbs			Trees and shrubs				Total cover per 60 m
			C	F	R	C	F	R	C	F	R	C	F	R	R	
1A	0	16	—	0.7	1	32.5	26.1	6	15.0	31.2	9	52.5	42.0	10	26	36.0
1B	0	16	0.49	—	2	12.9	20.4	7	29.9	33.3	9	56.9	46.3	13	31	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	29.7	34.6	9	27	50.7
3B79	2	16	—	1.9	1	36.5	24.8	5	13.6	31.2	10	49.6	40.7	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	0.1	—	1	83.4	52.7	7	5.1	16.4	6	11.4	30.9	6	20	37.7
4A80	4	32	—	—	—	66.0	50.0	6	0.3	10.6	5	32.9	39.7	8	19	64.5
5A79	4	4	—	—	—	76.7	34.5	2	2.2	14.3	1	20.9	50.0	7	10	41.7
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	0.2	2.9	3	22.5	51.5	10	16	30.1

\*Site numbers starting with the same combination of number and letter represent the same site surveyed twice; the numbers 79 and 80 indicate the year surveyed (1979 and 1980).

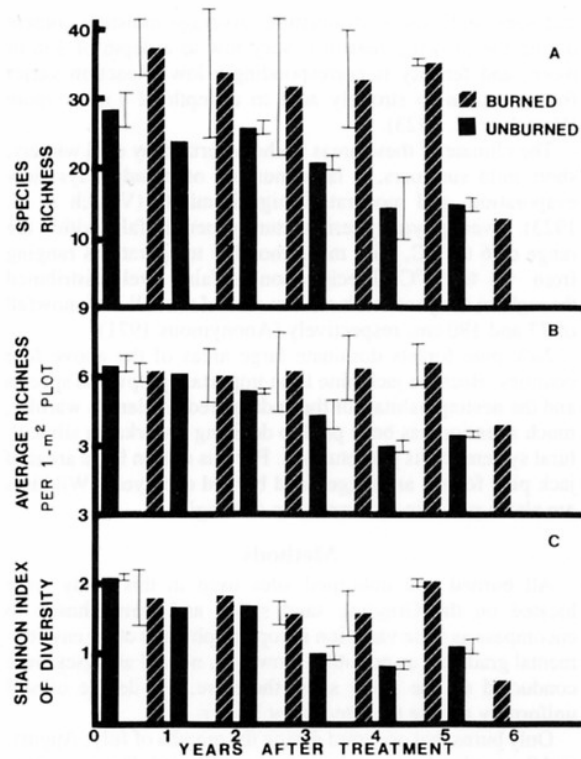


FIG. 1. (A) Species richness, (B) average richness per 1-m<sup>2</sup> plot, and (C) Shannon index of diversity versus years after treatment on burned and unburned sites. Vertical bars are  $\pm$  standard deviation. Only one observation at year 2 unburned and year 6 burned.

perennial herbs, and 19 of the 24 trees and shrubs recorded on all sites were present on unburned areas. In contrast, burned sites contained all 11 annuals and biennials, all 21 grasses and sedges, 33 of the 34 perennial herbs, and 21 of the 24 trees and shrubs.

Figure 2 shows only slightly higher cover values on burned areas than comparable unburned areas. Over the temporal sequence, burned areas showed a steady increase in cover through year 5, whereas no definite trend was evident on unburned sites. However, every site surveyed in 1979 and again in 1980 (Tables 1 and 2) showed an increase in total cover over that of the previous growing season.

The trend in relative cover and frequency of annuals and biennials over the temporal sequence is shown in Tables 1 and 2. On unburned sites, species in this group were virtually absent, except for *Melampyrum lineare* Lam. (cow wheat), which is present in the understorey of mature jack pine stands. On burned sites, species in this group, mainly *Geranium bicknellii* Britt. (geranium) and *Corydalis sempervirens* L. (rock-harlequin), pre-

TABLE 2. Relative cover (C), relative frequency (F), and species richness (R) for various vegetational groups on burned areas

Site number <sup>a</sup>	Treatment description <sup>b</sup>	Years since treatment	Area, ha	Annuals and biennials			Grasses and sedges			Perennial herbs			Trees and shrubs			Total cover per 60 m	
				C	F	R	C	F	R	C	F	R	C	F	R		Total R
7A	PB-ST	1	11	14.2	13.3	4	30.5	34.4	10	2.5	13.3	12	52.8	39.0	10	36	35.8
7B79	PB-ST	1	26	25.6	12.0	5	27.0	34.6	13	8.1	18.0	13	38.7	34.6	14	45	28.7
7C	PB-CC	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	PB-CC	1	24	0.1	2.8	3	73.5	44.6	9	8.5	24.3	12	17.0	27.1	10	34	30.6
7B80	PB-ST	2	26	—	1.1	2	60.8	44.0	10	12.9	14.7	10	26.3	40.1	8	30	43.7
7D80	PB-CC	2	24	—	—	—	71.6	56.3	9	12.4	21.1	8	15.4	22.5	8	25	48.5
8A79	WF-ST	2	32	0.1	1.8	4	44.0	39.2	14	2.8	17.6	16	53.0	40.5	13	47	47.4
8A80	WF-ST	3	32	0.1	2.2	2	39.4	33.2	12	6.6	23.1	15	54.2	41.5	11	40	52.8
9A79	PB-ST	3	31	0.6	—	2	63.7	41.0	12	1.2	14.9	12	34.4	44.2	12	38	54.9
9B79	WF-ST	3	30	—	—	—	60.2	49.6	7	1.1	3.5	5	38.5	47.0	6	18	42.9
9A80	PB-ST	4	31	—	0.5	1	62.7	40.7	11	1.2	18.0	13	36.0	40.7	11	36	56.7
9B80	WF-ST	4	30	—	—	—	71.8	50.0	7	0.7	9.9	8	27.1	40.1	6	21	54.7
10A79	PB-CC	4	26	—	1.6	1	71.8	35.7	13	15.2	39.3	13	13.0	23.3	9	36	58.2
10B79	PB-CC	4	23	0.2	3.9	1	53.5	40.0	14	22.9	23.3	10	23.4	32.3	14	39	45.4
10A80	PB-CC	5	26	0.1	1.7	2	57.3	38.2	11	18.5	32.9	16	24.1	27.2	7	36	75.7
10B80	PB-CC	5	23	0.8	5.4	3	57.3	37.3	10	8.0	23.5	8	33.5	33.9	14	35	61.6
11	WF-CC	6	6	—	—	—	91.4	59.0	6	0.5	10.3	1	7.8	30.8	6	13	31.2

<sup>a</sup>See Table 1.  
<sup>b</sup>PB, prescribed burn; WF, wildfire; ST, standing timber (35-year-old jack pine); CC, clear-cut mature jack pine (50-65 years old).

TABLE 3. Plant species encountered on burned and unburned sites in northern lower Michigan

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Species exclusive to burned areas (40 species total)

Annuals and biennials (eight species)

*Brassica nigra* L.  
*Cirsium* sp.  
*Corydalis sempervirens* L.  
*Erigeron canadensis* L.  
*Geranium bicknellii* Britt.  
*Krigia virginica* L.  
*Lithospermum arvense* L.  
*Silene antirrhina* L.

Grasses and sedges (nine species)

*Agropyron trachycaulum* Link  
*Andropogon scoparius* Michx.  
*Carex rugosperma* Mack.  
*Festuca* sp.  
*Muhlenbergia mexicana* L.  
*Panicum capillare* L.  
*Panicum xanthophysum* Gray.  
*Poa pratensis* L.  
*Sorghastrum nutans* L.

Perennial herbs (18 species)

*Anemone riparia* Fern.  
*Aster junciformis* Rydb.  
*Aster sagittifolius* Wedemeyer  
*Convolvulus spithameus* L.  
*Equisetum hyemale* L.  
*Hieracium canadense* Michx.  
*Hieracium gronovii* L.  
*Lechea minor* L.  
*Physalis virginiana* Mill  
*Polygala polygama* Walt.  
*Polygonum cilinode* Michx.  
*Potentilla arguta* Pursh.  
*Potentilla simplex* Michx.  
*Potentilla tridentata* Ait.  
*Rumex acetosella* L.  
*Senecio tomentosus* Michx.  
*Scrophulariaceae* (unidentified)  
*Viola adunca* Sm.

Trees and shrubs (five species)

*Acer rubrum* L.  
*Ceanothus ovatus* Desf.  
*Quercus alba* L.  
*Rubus hispidus* L.  
*Symphoricarpos albus* L.

Species exclusive to unburned areas (two species total)

*Spiranthes gracilis* Bigel. (perennial herb)  
*Corylus americana* Walt. (shrub)

Species common to both burned and unburned areas (49 species total)

Annuals and biennials (three species)

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

Grasses and sedges (12 species)

*Agrostis hyemalis* Walt.

TABLE 3. (concluded)

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

Perennial herbs (15 species)

*Anemone quinquefolia* L.  
*Antennaria neglecta* Greene  
*Aster laevis* L.  
*Campanula rotundifolia* L.  
*Epigaea repens* L.  
*Fragaria virginiana* Duchesne  
*Gaultheria procumbens* L.  
*Helianthus occidentalis* Ridd.  
*Hieracium aurantiacum* L.  
*Hieracium venosum* L.  
*Liatris novae-angliae* Lunell  
*Maianthemum canadense* Desf.  
*Pteridium aquilinum* Desf.  
*Solidago* spp.  
*Viola pedatifida* G. Don.

Trees and shrubs (18 species)

*Amelanchier* sp.  
*Apocynum androsaemifolium* L.  
*Arctostaphylos uva-ursi* L.  
*Comptonia peregrina* L.  
*Crataegus* sp.  
*Diervilla lonicera* Mill.  
*Pinus banksiana* Lamb.  
*Populus tremuloides* Michx.  
*Prunus serotina* Ehrh.  
*Prunus virginiana* L.  
*Quercus* spp. (red oak group)  
*Rosa blanda* Ait.  
*Rubus pensilvanicus* Poir.  
*Salix glaucophylloides* Fern.  
*Salix pellita* Arderss.  
*Vaccinium angustifolium* Ait.  
*Vaccinium myrtilloides* Michx.  
*Vaccinium vacillans* Torr.

dominated in the 1st year after burning and averaged 15% relative cover on all sites, with a maximum level (26%) on site 7B79. A possible heat stimulation of germination of these species is indicated by the drastic reduction and subsequent low levels in years 2 to 6 following fire.

Perennial grasses and sedges were dominant on both burned and unburned sites (Tables 1 and 2), but burned sites showed a greater richness of these species for each

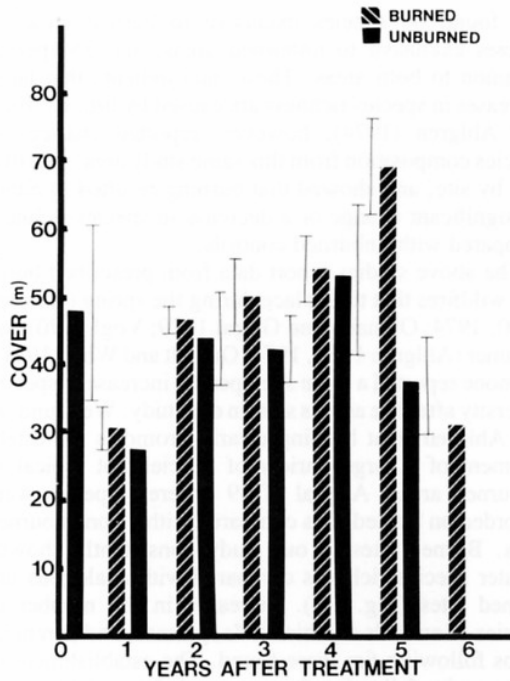


FIG. 2. Total vegetational cover (metres) versus years after treatment on burned and unburned sites. Vertical bars are  $\pm$  standard deviation. Only one observation at year 2 unburned and year 6 burned.

year in the sequence. During years 2 and 3 the highest number of species was recorded on unburned sites, with lower levels during years 4 and 5. The number of species appears remarkably consistent on the burned sites for years 1 through 5, but a drastic decrease, approaching that of the unburned sites, was observed at year 6 (site 11). Site 9B (years 3 and 4) also showed an atypically low number of grasses. Frequently occurring grasses and sedges found exclusively on burned sites included *Andropogon scoparius* Michx. (little bluestem), *Muhlenbergia mexicana* L., and *Carex rugosperma* Mack. (sedge).

Number of species, relative cover, and relative frequency of perennial herbs are tallied in Tables 1 and 2 for unburned and burned sites, respectively. The number of herbs on both the burned and unburned sites was similar for year 1, but thereafter a steady decline occurred on the unburned sequence, whereas the burned sequence retained a relatively high number of herbs through year 5. Again, atypically low levels of herbs were recorded at year 6 (site 11) and on site 9B. Bracken fern (*Pteridium aquilinum* L.) and wintergreen (*Gaultheria procumbens* L.) were the dominant contributors to relative cover in this species group. All other perennial herbs contributed little to the relative cover, but added greatly to the species richness on all sites, especially those that had been burned. Some frequently

occurring perennial herbs exclusive to burned sites included *Hieracium canadense* Michx. (Canadian hawkweed), *Rumex acetosella* L. (sheep sorrel), and *Senecio tomentosus* Michx. (groundsel).

The number of species of trees and shrubs was higher on burned than on unburned areas of the same age, but little change in either sequence occurred during years 1 to 5 (Tables 1 and 2). Of the four major species groups, trees and shrubs showed the least increase in species richness after fire. Relative cover of these species showed a decrease with time in both sequences. However, sites 4A, 5A, 10A, and 10B showed substantial increases in the cover of this species group over the 1979 and 1980 growing seasons (Tables 1 and 2). Initially, unburned sites had a much higher cover of trees and shrubs, but by year 4 and 5 nearly equal cover occurred in both sequences. The species dominating this group on both burned and unburned sites include *Vaccinium* spp. (blueberry), *Populus tremuloides* Michx. (aspen), *Quercus* spp. (oak), *Prunus serotina* Ehrh. (black cherry), and *Rubus pensilvanicus* Poir. (dewberry).

*Carex* and *Vaccinium* comprised the majority of cover on nearly all sites (Fig. 3). The cover of *Carex pensylvanica* Lam., a strong competitor on jack pine sites, steadily increased on unburned clear-cut sites to a

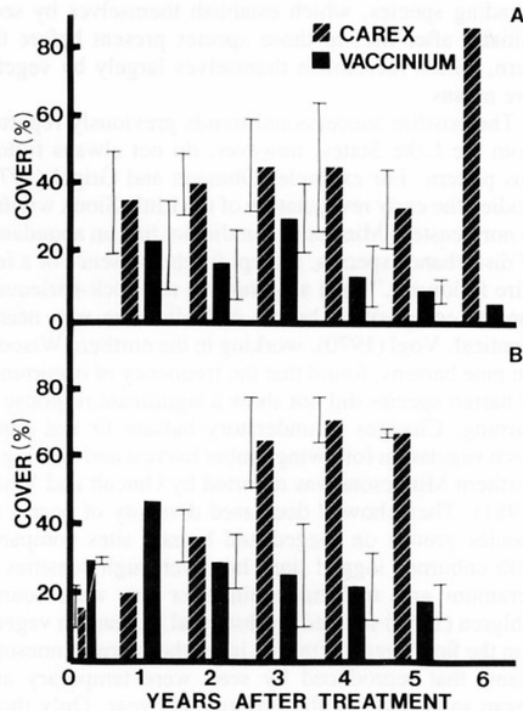


FIG. 3. (A) Percent cover of *Carex* and *Vaccinium* versus years after treatment on burned sites and (B) percent cover of *Carex* and *Vaccinium* versus years after treatment on unburned sites. Vertical bars are  $\pm$  standard deviation. Only one observation at year 2 unburned and year 6 burned.

maximum of 70% at year 4. On burned sites, *Carex* generally stabilized at a much lower level than comparable unburned sites; however, at year 6 after burning, site 11 had the highest cover value for *Carex* of any site surveyed in this study (86%). *Vaccinium* spp. showed a trend opposite that of *Carex* over time, with decreases in dominance that seemed to mirror the corresponding increases in *Carex* dominance. To facilitate data gathering in the field, the frequency and cover of blueberry was quantified simply as *Vaccinium* spp. The dominant species encountered on the study sites were *V. angustifolium* Ait. (late low blueberry), *V. myrtilloides* Michx. (velvetleaf blueberry), and *V. vacillans* Torr. (early low blueberry).

### Discussion

The increase in species diversity and dominance of certain plant groups occurring after fire seen in this study is a phenomenon well documented in a variety of ecosystems (Ahlgren and Ahlgren 1960; Christensen and Muller 1975; Dyrness 1973; Little and Moore 1949; Purdie and Slatyer 1976; Shafi and Yarranton 1973). This increased diversity after fire is temporary, however, usually 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 burn, 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 the 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 was 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 and burning in northern Minnesota was reported by Outcalt and White (1981). They showed decreased diversity of nearly all species groups on logged and burned sites compared with unburned logged sites; however, high densities of geranium and rock-harlequin after fire were found. Ahlgren (1960) showed a substantial increase in vegetation the first 2 years after fire in northeastern Minnesota. Plants that reproduced by seed were temporary and began to decline by the 3rd and 4th year. Only those species that were of vegetative origin maintained an important position during a 5-year period after fire. 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 are caused by 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 a decrease in species richness compared with unburned controls.

The above studies report data from prescribed burns and wildfires that took place during the spring (Ahlgren 1960, 1974; Ohmann and Grigal 1979; Vogl 1970) and summer (Ahlgren 1960, 1974; Outcalt and White 1981), but none reported a large site-specific increase in species diversity after fire as was seen in our study. We found, as did Ahlgren, that burning clearly promotes the establishment of a large variety of species not typical to unburned areas. A total of 89 different species were recorded on burned sites compared with 51 on unburned sites. Burned sites in our study consistently showed greater species richness compared with analogous unburned sites (Fig. 1A). Increases in the number of species of annuals and biennials, grasses, and perennial herbs following fire were found. The establishment of new species following fire can result from viable seeds stored in the forest floor (Ahlgren 1979; Livingston and Alessio 1968; Tredici 1977) or from seed transported by wind and animal vectors.

The longevity of many of the fire followers is short; 2 years after fire many are gone. In the later years following fire, species that perpetuate themselves mainly by vegetative means and that were probably members of the preexisting vegetation dominate. Four- and 5-year-old burned sites (sites 10A and 10B) in the present study retained a high level of diversity supported by a mixture of fire-stimulated grasses and herbs, whose presence appears to be waning, and trees and shrubs (probably present before burning), whose dominance is increasing (Table 2).

There are many interacting factors that affect the vegetational cover on these study sites. Time following disturbance and species number and equitability are certainly important. Initially following disturbance, such as clear-cutting or burning, the gaps created are recolonized and cover increases with time. On site 11, however, *Carex pensylvanica* formed a monolayer cover and prevented the establishment of a stratified canopy. This explains the anomalous large decrease in cover seen between years 5 and 6 on the burned sequence in Fig. 2.

The decrease in diversity on the unburned sequence and the low diversity of certain burned sites is linked to the dominance of *Carex pensylvanica*. The loss in diversity on unburned sites is closely matched by the increased cover of *Carex*. Further evidence exists from

the least diverse burned sites (9B and 11), which have relative cover values for *Carex* of 67 and 86% during years 4 and 6, respectively. Burning appears to stimulate *Carex* production in the 1st year after treatment, although this response depends on the intensity of the burn. From personal observation *Carex* appears more susceptible to injury from very "hot" burns compared with certain trees and shrubs whose rootstocks penetrate deep into the mineral soil. From years 3 to 5 after burning the dominance of *Carex* stabilized at a much lower level than on equivalent unburned sites. Other dominants competing with *Carex* on older burns and preventing its spread include *Oryzopsis asperifolia* Michx. and *Schizachne purpurascens* Torr. (tussock grasses), *Pteridium aquilinum* (bracken fern), and *Populus tremuloides* (aspen).

The decrease in blueberry in the later years of each sequence appears to be, at least in part, related to a reduced ability of these species to compete in full sunlight. A consistent pattern observed on these sites was the vigorous growth of blueberry in and around the shade of slash piles, while *Carex* dominated the larger open areas. It is apparent from other observations in mature, uncut jack pine stands, clear-cut sites, and burned sites that *Carex* is outcompeted by blueberry in the shade of an uncut stand, but the reverse is true in full sunlight. The inability of blueberry to compete in exposed areas is consistent with Hoefs and Shay (1980), who found that *V. angustifolium* grew faster under intermediate shade than in full sun in southeastern Manitoba.

An increase in sedges following fire has previously been documented (Ahlgren 1960; Outcalt and White 1981; Vogl 1970). However, the overwhelming dominance of *Carex* observed in our study seems to be unique to jack pine sites in northern lower Michigan. There are indications that a *Carex* meadow, once established, is capable of excluding tree and shrub seedling reproduction for many years (Niering and Goodwin 1974; Noble 1980). In fact, on all sites surveyed during 1979 and 1980, jack pine reproduction was conspicuously absent; none of the areas in this study showed adequate jack pine stocking. We feel that the competitiveness of *Carex* greatly contributed to the failure of jack pine regeneration.

There are several possible mechanisms that explain the dominance of *Carex pensylvanica*. One possibility may be the ability of *Carex* to exploit nutrients and space made available following a perturbation such as clear-cutting and (or) burning. Recent studies involving disturbances have shown that certain exploitative species, due to their life-history characteristics, can monopolize resources liberated by disturbances and suppress or exclude other species. Marks (1974) showed pin cherry (*Prunus pensylvanica*) to be such an exploitative

species on New Hampshire clear-cut sites. 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 preempting certain subordinates, thus reducing overall diversity. Ahlgren (1960) also showed that nutrients released following fire have a fertilizing effect that stimulates the growth of certain species. Though results of a study initiated in May 1980 to test this hypothesis are not yet available, it is conceivable that the release of *Carex* may be via a similar mechanism.

#### Acknowledgements

This research was supported by the United States Department of Agriculture Forest Service under Cooperative Research Agreement 13-635. Cooperation by the Michigan Department of Natural Resources, on whose land these studies were performed, is also acknowledged. We would like to thank C. E. Ahlgren, D. G. Sprugel, P. G. Murphy, and E. S. Menges for their reviews of early drafts of this manuscript. S. N. Stephenson and R. Gereau provided invaluable assistance in identifying many of the plant taxa collected during this study.

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