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# Fire and Shade Effects on Ground Cover Structure in Kirtland's Warbler Habitat

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ABSTRACT.—Researchers and managers have suggested that a narrow range of ground-cover structure resulting from fire might be necessary for suitable Kirtland's warbler nesting conditions. Yet, Kirtland's warblers have bred successfully in numerous unburned stands and there is little direct evidence to indicate that ground cover structure is a limiting factor for nest sites or habitat suitability within appropriate landform-ecosystems. We documented the range of percent cover for dominant ground-cover structural components in burned and unburned habitat (stand ages 7–23 y) occupied by Kirtland's warblers. The mean percent cover for the dominant ground-cover structural components was lichen/moss (12.1%), blueberry (*Vaccinium angustifolium*) (9.5%), bare ground and litter (5.6%), sedge/grass (5.2%), deadwood (4.3%), sand cherry (*Prunus pumila*) (3.3%), sweet fern (*Comptonia peregrina*) (2.3%), coarse grass (1.8%) and bearberry (*Arctostaphylos uva-ursai*) (1.2%). Burned sites had significantly more deadwood, sweet fern and lichen/moss cover, while unburned sites had significantly more bare ground and sedge/grass.

We also investigated how fire, shade-history (*i.e.*, pre-fire tree crown cover approximated by tree height and density) and succession influenced the percent cover of the dominant ground-cover structural components from 1 to 5-y after wildfire disturbance. The magnitude of differences in percent cover among shade-histories changed through time for the ground-cover components sand cherry, deadwood, grass/sedge and coarse grass. The percent cover of sweet fern, bearberry and bare ground was significantly different between some shade-histories. All dominant ground-cover components showed significant difference between at least one shade-history when compared to an unburned harvested reference stand. This suggests that more similarities exist among the three burned sites than between the burned sites and the unburned reference site. Our results suggest that fire, shade-history and succession influence ground-cover, but that various ground-cover components are affected differently by these factors. Because of the complex role disturbance history plays in maintaining ground-cover in Kirtland's warbler habitat, optimal management prescriptions are difficult to specify, especially when aspects of Kirtland's warbler ecology other than nest location are also considered. Although suitable ground cover structure can result without fire, maintaining prescribed fire is still desirable because this is a historically fire-regulated system. However, the range of ground-cover structures accepted by the Kirtland's Warbler and its resilience to disturbance suggests that suitable ground-cover for Kirtland's warbler could be maintained in some stands without burning after every timber harvest.

## INTRODUCTION

The Kirtland's warbler (*Dendroica kirtlandii*) is a neotropical migrant bird with a restricted breeding range in northern Lower Michigan and several breeding locations in the central Upper Peninsula of Michigan (Probst, 1985). The warbler breeds exclusively in the young stages of jack pine (*Pinus banksiana*) forests found primarily on dry, excessively drained and nutrient poor Grayling and related sands found in glacial outwash ecosystems (Walkinshaw, 1983; Kashian and Barnes, 2000; Kashian *et al.*, *in press*). These poor quality soils maintain low shrubs important for nesting cover (Walkinshaw, 1983; Bocetti, 1994).

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The Kirtland's warbler's breeding habitat is characterized by dense, patchy jack pine forests >32 ha in size, 1.3 to 5.0 m high, and ranging from 5 to 23 years old (Walkinshaw, 1983; Probst, 1988; Probst and Weinrich, 1993). Optimum Kirtland's warbler breeding habitat has openings interspersed among dense thickets of jack pine (7500 stems per ha) with between 35% and 65% canopy cover of jack pine principally. However, warblers initially colonize stands having at least 20% to 25% tree cover and 2000 stems/ha (Probst, 1988).

An important factor in the decline of a stand's suitability may be the height of the lowest live branch (Walkinshaw, 1983; Probst, 1988; Probst and Weinrich, 1993) because the warblers construct nests on the ground usually near or at the edge of jack pine thickets (Walkinshaw, 1983; Bocetti, 1994) and Kirland's Warblers forage throughout the jack pine foliage (Probst and Weinrich, 1993; Fussman, 1997). As a stand matures, change in light regime may change the ground vegetation structure important for nesting and fledgling cover. Ground-cover vegetation in Kirtland's warbler breeding habitat is generally a mixture of low shrubs (*e.g.*, blueberry (*Vaccinium angustifolium*), sand cherry (*Prunus pumila*), bearberry (*Arctostaphylos uva-ursi*), sweetfern (*Comptonia peregrina*), grasses, sedges and forbs.

Periodic fire plays an important role in regenerating jack pine forests and creating the habitat characteristics required by the Kirtland's warbler. Jack pine is shade-intolerant, and fire or dry conditions with high temperatures facilitates opening of their serotinous cones (Rudolph and Laidly, 1990). During the 1960s, fire suppression and high precipitation reduced suitable habitat for the Kirtland's warbler and was partly responsible for a 60% population decline (Byelich *et al.*, 1976; Probst, 1986; Kepler *et al.*, 1996). Early habitat management efforts used prescribed burning following harvest to produce dense, unplanted jack pine stands and ground-cover vegetation similar to habitat produced by wildfire (Byelich *et al.*, 1976; Probst, 1988). However, prescribed burning proved to be unsuccessful in promoting dense natural regeneration and is costly and difficult to administer after every harvest (Probst, 1988; Kepler *et al.*, 1996), often leading to an unacceptable delay in creating new suitable habitat. Current habitat management focuses on plantations, using prescribed burns or mechanical site preparation to mimic habitat created by wildfires (Probst, 1988; Kepler *et al.*, 1996).

The floristic composition of jack pine plant communities has been described over a range of sites in Michigan (Abrams and Dickmann, 1982, 1984; Abrams *et al.*, 1985), and the broader ecosystem attributes of these landscapes are well described (Zou *et al.*, 1992; Kashian, 1998; Walker, 1999). A few studies have reported on the range in percent cover of the dominant ground-cover structural components (*e.g.*, low shrubs, bare ground and down woody material) acceptable to the Kirtland's warbler for foraging (Fussman, 1997) or nesting (Bocetti, 1994; Kashian, 1998), particularly over a broad range of regeneration types used as breeding stands. Less understood is how shade-history (*i.e.*, duration and amount of shade present before harvest or wildfire disturbance) and early successional trends interact with fire to regulate the ground-cover structure. For example, blueberry is favored in open or partial shade and may be disfavored in heavy shade (Hoefs and Shays, 1981).

Early investigators suggested that a narrow range of ground-cover composition and cover resulting from fire, especially abundant blueberry, were necessary for maintaining suitable nesting habitats for Kirtland's warblers (Mayfield, 1960; Walkinshaw, 1983). However, Kirtland's warblers have been observed nesting as successfully in unburned stands with little blueberry as in burned stands (Walkinshaw, 1983). Recent research has shown that, although some cover of blueberry and other low shrubs may be preferred around the nest (Bocetti, 1994), Kirtland's warblers will accept a variety of proportions of otherwise similar ground-cover composition in jack pine ecosystems (Zou *et al.*, 1992; Bocetti, 1994; Kashian, 1998; Houseman and Anderson, 2002). These findings suggest that blueberry may not be as limiting as adequate canopy cover (*i.e.*, tree stocking) in maintaining optimum breeding habitat.

Blueberry typically dominates the ground-cover in Kirtland's warbler breeding habitat (Walkinshaw, 1983; Bocetti, 1994; Kashian, 1998; Houseman and Anderson, 2002). However, sedge or "wiregrass" (*Carex pensylvanica*), which is usually present in low proportions in jack pine stands before harvest, can dominate in the early stages (<6 y) of naturally regenerating unburned sites after clear-cutting (Abrams and Dickmann, 1982, 1984; Abrams *et al.*, 1985). These *Carex* mats may prevent other species, including jack pine and blueberry, from re-establishing (Abrams and Dickmann 1982, 1984). On burned sites, the trends in early natural regeneration can be highly variable ranging from blueberry dominance to *Carex* dominance, but *Carex* became less dominant than on unburned sites over the time interval studied (Abrams and Dickmann, 1982, 1984). Therefore, managers have been advised to burn as many stands as possible in historically fire-regulated systems (Probst, 1988).

The Kirtland's warbler population is limited by the amount of suitable habitat available (Probst, 1986; Probst and Weinrich, 1993). Because wildfire cannot be predicted or relied upon to create suitable habitat, managers must plant enough acres with appropriate tree densities each year to sustain viable populations of this endangered species. The cost and logistical difficulties of applying prescribed burns after every stand rotation can easily prevent managers from creating enough suitable habitat. In this study, we quantify the range of ground-cover structure accepted by Kirtland's warblers. Our objectives were: (1) to document accepted lower and upper limits of percent cover for the dominant ground-cover structural components (including bare ground and deadwood) over a range of stand ages (7 to 23 y-old) and stand disturbance histories of habitat occupied by the Kirtland's warbler in the Lower Peninsula of Michigan, (2) to compare the differences in percent cover of the dominant ground-cover structures between previously burned and unburned habitat occupied by the Kirtland's warbler and (3) to investigate the influence that fire, shade-history, and time since the disturbance (*i.e.*, stage of succession) have on early regeneration of ground-cover structure (≤5 y; pre-occupation age for Kirtland's warblers) on similar sites.

## METHODS

*Ground-cover structure.*—We documented the range of dominant ground-cover structure in habitat used for nesting by the Kirtland's warbler in four burned (three wildfires and one prescribed burn) and five unburned (three plantations and two natural regeneration) sites. The sites were from 22–256 ha in size and 7–23 y old, and were located in Crawford and Oscoda counties, Michigan (Fig. 1). Stands were selected to represent a range of sites and disturbances used by Kirtland's warblers during the study period. Each site was sampled for dominant ground cover structural components once between 1977 and 1986 within the period 10 August and 25 August because all stand ages were not available at any one time. Nine years were required to adequately sample the range of stand ages and conditions because of stand availability and a 15 day sampling period imposed to prevent disturbance to an endangered species.

Kirtland's warblers may occupy small fractions of the total stand area during early and late occupancy, so sampling was conducted within the portions of stands actually used by warblers (>5 ha). Line transects were systematically placed on a grid in the occupied areas of each site and varied in number per site depending on site occupancy by warblers (Table 1). Each transect consisted of two 30.5 m segments perpendicular to each other, forming a single 61 m 'L-shaped' line transect. The 'L-shaped' transect design minimizes the chance of straight lines falling within recurring topography or other regular landscape patterns (*e.g.*, plantation furrows or ridges and swales) (Lindsay, 1955). Relative importance of each

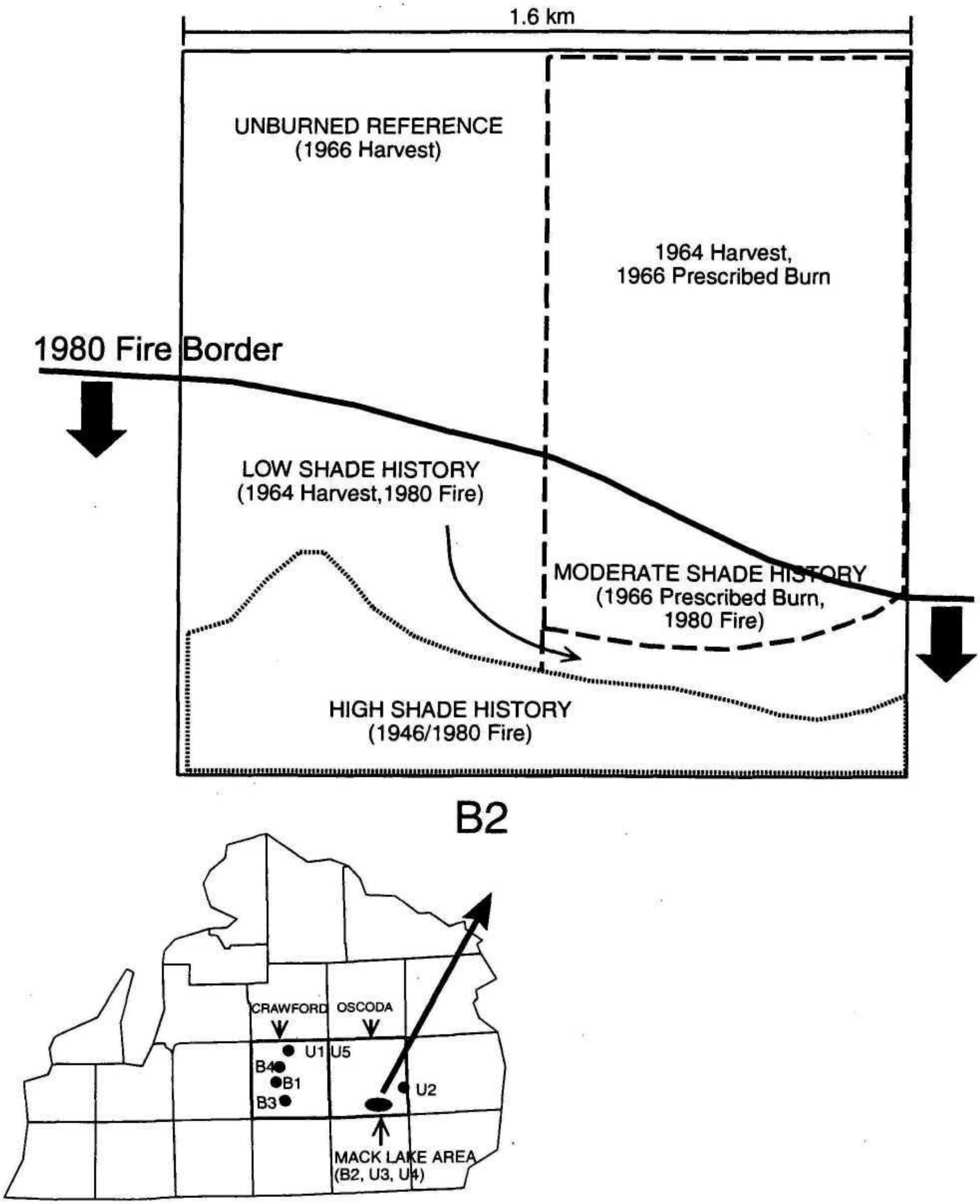



FIG. 1.—Location of burned and unburned stands in Crawford and Oscoda Counties, Lower Michigan, and a schematic map of the contrasting shade-histories within or adjacent to the 1980 Mack Lake Burn study area. See Table 2 for key to stand names

ground-cover structural component was measured by summing the distance intersected along the transect and calculating the percent. Only patches >3 cm long were included, so the summed percentages of all ground-cover components for a single transect did not total 100 percent.

TABLE 1.—Sites used by breeding Kirtland's warblers in the Lower Peninsula of Michigan sampled for percent cover of the dominant ground-cover structural components. Sites represent burned and unburned sites occupied by the Kirtland's warbler at various stand ages

| Site | Legal description | Type of disturbance | Year of disturbance | Year sampled | Stand age | Area (ha) | No. of transects |
|---|---|---|---|---|---|---|---|
| Rayburn | 26N 3W S. 3 | wildfire | 1972 | 1979 | 7 | 43 | 20 |
| Lovells North I | 28N 1W S. 6,7 | plantation | 1974 | 1983 | 9 | 120 | 10 |
| Mack Lake I | 25N 3E S. 2 | prescribed burn | 1966 | 1977 | 11 | 96 | 62[A] |
| McKinley | 26N 4E S. 2 | harvested, natural regeneration | 1970 | 1981 | 11 | 256 | 32[B] |
| Mack Lake II | 26N 3E S. 33 | harvested, planted | 1973 | 1984 | 11 | 22 | 60 |
| Mack Lake III | 25N 3E S. 2 | harvested, natural regeneration | 1966 | 1979, 1986 | 13, 20 | 96 | 20 |
| Lovells North II | 28N 1W S. 5 | plantation | 1963 | 1980 | 17 | 178 | 20 |
| Pere Cheney | 25N 3W S. 2,12 | wildfire | 1959 | 1979 | 20 | 118 | 34 |
| Artillery south | 27N 2W, 3W, S.19,24 | wildfire | 1955 | 1978 | 23 | 128 | 10 |

[A] Includes three stands of different stocking levels
[B] Includes 2 stands; disjunct harvest blocks

*Fire, succession and shade-history.*—We used a second set of study stands to examine the influence of fire, shade-history and time since disturbance on early regenerating ground-cover structure by documenting changes in percent cover of the dominant ground-cover components every 2 y in stands 1–5 y old, referred to as pre-occupation stands. The study was conducted within a 1 square-mile (2.59 $km^2$) Public Land survey section. We chose this section because it contained four contiguous, naturally regenerating jack pine stands with contrasting disturbance histories (1946 wildfire; 1964 harvest/1966 prescribed burn; 1964 harvest; and 1966 harvest, unburned by the 1980 Mack Lake Fire) that had different tree crown cover, and shade levels and duration before the 1980 fire (Fig. 1). We measured ground-cover structural components between 10 August and 25 August in 1981, 1983 and 1985 along 20–24 permanently marked transects in each stand using the L-shaped transects described above. We calculated changes in percent cover of dominant ground cover components.

Tree density and average height of trees killed by the wildfire were used to create relative levels of pre-fire shade intensity (*i.e.*, shade-history index) because the foliage had burned in the fire. The shade index was the sum of the tree heights per unit area, expressed as m/ha. Tree density and height are positively related to total tree crown cover (Buech, 1980) and tree crown cover generally increases with height (*see* Fig. 2 in Probst and Weinrich, 1993). We established two square sample plots (1860.5 $m^2$) perpendicular to the end of each transect segment. Within each plot, we counted all live and dead trees and measured their heights. The high shade-history stand was well-stocked from natural regeneration and plantings following a 1946 wildfire. The moderate shade-history stand was clearcut in 1964 and prescribed burned in 1966 with supplemental planting, so the tree stems were shorter and more numerous, although the index was closer to the high shade stand than the low shade stand. The low shade-history stand was sparsely stocked with natural regeneration following a 1964 clearcut. All stands had some history of plantation furrows before the 1980 wildfire; however, none were replanted after the 1980 wildfire.

Within the same surveyed section, an adjacent stand that was harvested in 1966, but not burned by the Mack Lake Fire, was used as an unburned unplanted reference stand. The

TABLE 2.—Mean percent cover of the dominant ground-cover structural components in sites occupied by nesting Kirtland's warblers in the Lower Peninsula of Michigan

| Site | Age | Burned vs. unburned[1] | Lichen/ moss | Blueberry | Bare ground | Sedge/ grass | Dead-wood | Sand cherry | Sweet fern | Coarse grass | Bear-berry |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Rayburn | 7 | B1 | 8.4 | 2.3 | 7.5 | 6.8 | 3.6 | 1.6 | 0.5 | 2.5 | 0.9 |
| Mack Lake I | 11 | B2 | 19.6 | 4.9 | 0.1 | 2.8 | 7.3 | 2.8 | 6.1 | 1.4 | 0.9 |
| Pere Cheney | 20 | B3 | 5.4 | 14.9 | 10.6 | 2.2 | 3.0 | 5.1 | 1.9 | 0.3 | 2.6 |
| Artillery South | 23 | B4 | 39.8 | 17.4 | 8.8 | 7.2 | 5.1 | 0.3 | 1.0 | 3.5 | 0.4 |
| Lovells North I | 9 | U1 | 4.3 | 0.5 | 5.5 | 11.6 | 0.0 | 6.8 | 1.1 | 1.5 | 0.6 |
| McKinley | 11 | U2 | 5.8 | 11.2 | 8.1 | 4.2 | 4.5 | 1.9 | 0.4 | 0.4 | 0.8 |
| Mack Lake II | 11 | U3 | 12.7 | 17.0 | 7.3 | 6.3 | 3.6 | 4.2 | 1.0 | 0.2 | 0.9 |
| Mack Lake III | 13 | U4 | 3.7 | 5.6 | 4.8 | 7.5 | 6.1 | 5.0 | 1.3 | 0.6 | 2.6 |
| Lovells North II | 17 | U5 | 10.5 | 0.3 | 2.8 | 7.3 | 0.0 | 0.8 | 1.9 | 12.5 | 0.7 |
| **Mean % cover** | | | 12.1 | 9.5 | 5.6 | 5.2 | 4.3 | 3.3 | 2.3 | 1.8 | 1.2 |
| **Standard error** | | | 1.5 | 1.2 | 0.8 | 0.7 | 0.6 | 0.5 | 0.5 | 0.5 | 0.3 |

[1] *See* Figure 1 for site locations

percent cover of the ground components was previously measured in 1979 when the stand was 13 y old (Table 1; Mack Lake II site). The stand was resampled in 1986 at age 20 to investigate the change in percent cover of the dominant ground-cover components over time without fire disturbance. Change in jack pine cover in this unburned site used previously published data (Probst and Weinrich, 1993). Thus, some stands used in the comparisons in occupied stands for objective one and two were used as reference to these pre-occupation, burned stand comparisons for objective three.

Because most songbirds are known to respond to vegetation structure rather than species composition (MacArthur and MacArthur, 1961; Probst *et al.*, 1992; Herkert, 1996), we emphasized major ground cover structural components relevant to the Kirtland's warbler life history (nesting, foraging) to show differences in relative importance of components rather than in species composition. Four individual plant species, three vegetative categories and two nonvegetative categories, were used to describe the dominant ground-cover structure. The plant species were blueberry, sand cherry, sweet fern (*Comptonia peregrina*) and bearberry. Grasses were separated into "coarse grass" and "sedge/grass" categories. The coarse grass category primarily consisted of bluegrass (*Andropogon gerardii* and *Schizachyrium scoparium*), and brome grass (*Bromus* sp.). The sedge/grass category included sedges (*Carex pensylvanica*), poverty grass (*Danthonia* sp.), hairgrass (*Deschampsia flexuosa*), junegrass (*Koeleria maecrantha*) and ricegrass (*Oryzopsis* sp.). The third plant category was lichen/moss. Two nonvegetative elements, bare ground/herbaceous litter and deadwood, were also included as dominant ground-cover structural components.

Percent cover of each component was compared between burned and unburned sites using a Mann-Whitney U test (objective two). For the pre-occupation sites (1–5 y), each component was rank-transformed and repeated-measures analysis of variance on those ranks was used to investigate the response of percent cover of each component to time since disturbance (*i.e.*, wildfire), and shade-history (objective three). To further examine whether fire effects were transitory, these stands were compared to the adjacent 13-y old, unburned reference stand using Mann-Whitney U tests. The significance level was adjusted by a Bonferroni procedure for multiple comparisons.

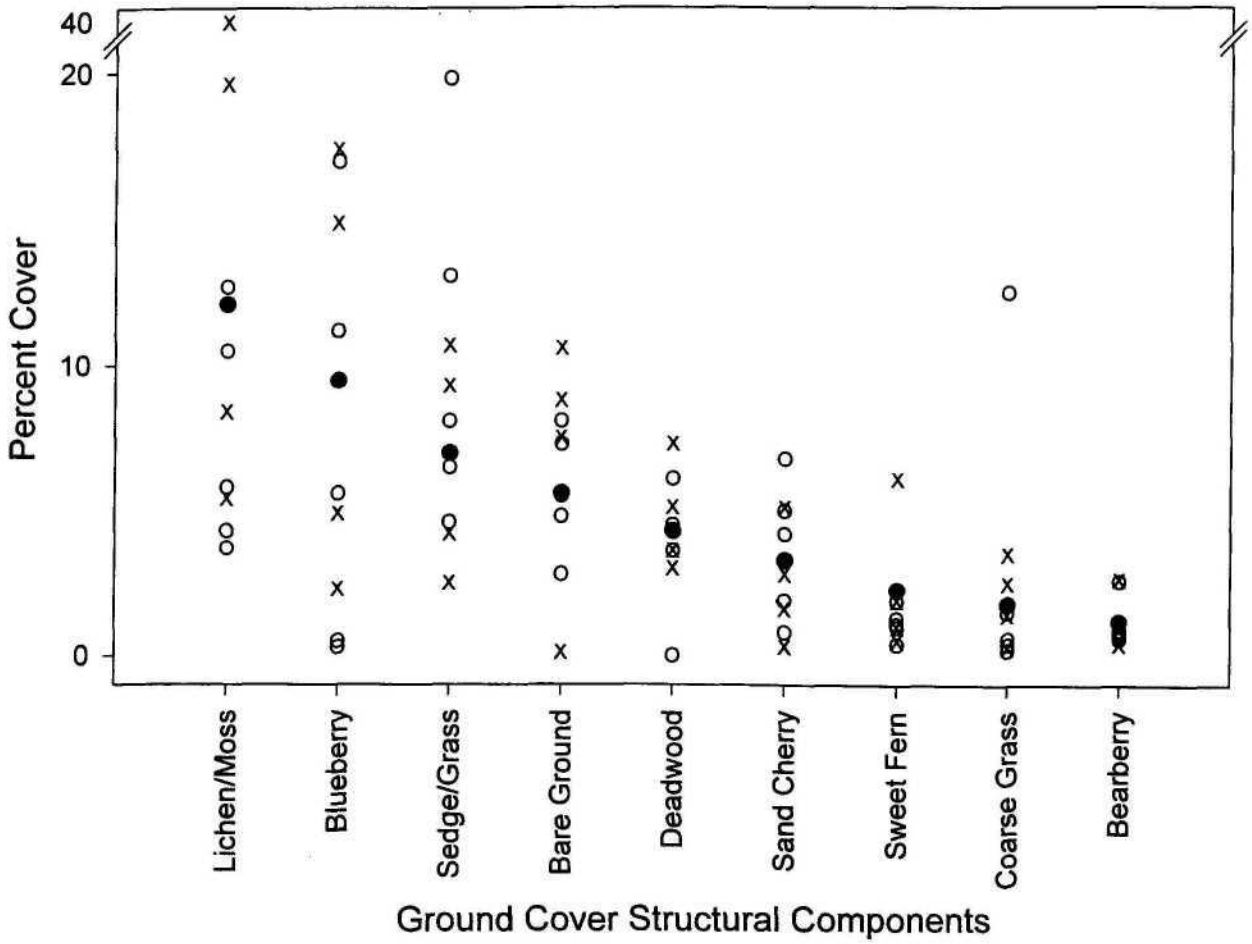



FIG. 2.—Range and mean percent cover for the dominant ground-cover components in burned (X) and unburned (O) habitat occupied by Kirtland's warbler in the Lower Peninsula of Michigan. Black circles represent the mean percent cover of the ground-cover component

## RESULTS

*Ground-cover structure.*—Lichen/moss was the most abundant ground-cover component (12.1%) in all 7–23 y old sites occupied by the Kirtland's warbler (Table 2). Blueberry was the second-ranked component with a mean percent cover of 9.5%, bare ground/litter was third (5.6%), and sedge/grass was fourth (5.2%). Lichen/moss had the greatest variation in mean percent cover ranging from 3.7 to 39.8% (Table 2). Mean percent cover of blueberry on the sites ranged from 0.3 to 17.4%, whereas mean percent cover for sedge/grass ranged from 2.2 to 11.6%. The range of importance of ground cover structural components found in sites occupied by Kirtland's warbler in this study helps define the limits of acceptable Kirtland's warbler habitat (Fig. 2).

*Comparison of burned vs. unburned sites.*—There was considerable overlap in the percent cover of ground-cover components among burned and unburned stands (Fig. 2). In burned sites, lichen/moss, blueberry and deadwood were the three most dominant ground-cover components. In the unburned sites, blueberry, lichen/moss and sedge/grass were the top three ranked dominant ground-cover components. The percent cover of lichen/moss, deadwood, and sweet fern were significantly more abundant in the burned areas (Table 3). There was moderate evidence that blueberry percent cover was more abundant in the unburned sites (Table 3), but results were not significant at the 95% confidence level

TABLE 3.—Comparison of percent cover of the dominant ground-cover structural components between burned and unburned sites used by Kirtland's warblers for nesting in Lower Peninsula of Michigan

| Ground cover component | Burned (n = 126 transects) | | | Unburned (n = 142 transects) | | | |
|---|---|---|---|---|---|---|---|
| | Mean | SE | Range | Mean | SE | Range | P |
| Lichen/moss | 15.6 | 1.4 | 0–81 | 9.0 | 0.7 | 0–43 | <0.001* |
| Blueberry | 8.2 | 0.8 | 0–48 | 10.5 | 0.9 | 0–41 | 0.082 |
| Bare ground | 4.8 | 0.7 | 0–40 | 6.3 | 0.5 | 0–30 | <0.001* |
| Sedge/grass | 3.6 | 0.4 | 0–26 | 6.5 | 0.6 | 0–54 | <0.001* |
| Deadwood | 5.4 | 0.6 | 0–50 | 3.4 | 0.3 | 0–20 | <0.001* |
| Sand cherry | 3.0 | 0.3 | 0–16 | 3.5 | 0.4 | 0–19 | 0.912 |
| Sweet fern | 3.7 | 0.5 | 0–24 | 1.0 | 0.2 | 0–13 | <0.001* |
| Coarse grass | 1.4 | 0.2 | 0–10 | 2.1 | 0.4 | 0–23 | <0.005* |
| Bearberry | 1.3 | 0.2 | 0–16 | 1.1 | 0.2 | 0–14 | 0.471 |

* Rank-sum differences were significantly different among burned and unburned sites using Mann-Whitney U Tests (significance level was set at $\alpha < 0.05$)

($P < 0.082$). Bare ground/litter, sedge/grass and coarse grass percent cover was significantly less in the burned sites (Table 3).

During the years Kirtland's warblers occupy jack pine sites (ages 7–23), blueberry percent cover increased with site age in the burned sites, increasing from 2.3% at age 7 to 17.4% at age 23 (Table 2). The remaining ground-cover components did not show stand-age trends.

*Early revegetation (≤5 y old stands).*—Three ground components differed significantly in percent cover among shade-histories (Table 4). Bare ground was more abundant in the high shade-history stand, but the difference was only significant when compared to the moderate shade-history stand ($P < 0.01$). Bearberry was as much as three times more abundant in the high shade-history stand than in the low and moderate shade-history stands ($P = 0.01$). The percent cover of sweet fern was significantly greater in the moderate and high shade-history stands than in the low shade-history stand ($P < 0.01$). Percent cover of blueberry increased as level of shade-history increased, but differences were not significantly different at the 95% confidence level ($P = 0.12$). All three shade-history stands had negligible amounts of lichen/moss develop during the short recovery from disturbance (Table 4). Coarse grass cover was not significantly different among shade-history stands or time intervals.

Most ground-cover components in the moderate shade-history stand (prescribed burned in 1966) differed in percent cover 11 y before and one year after the 1980 fire (Table 4). Percent cover of deadwood, sweet fern, and lichen/moss was significantly less after the fire (1981) in all stand-histories ($P < 0.01$), whereas percent cover of bare ground, sand cherry, blueberry and sedge/grass was greater one y after the fire ($P < 0.01$).

In the unburned reference stand (no known fire disturbance in recent decade), several components changed in percent cover since harvest, from age 13 to age 20 (Table 4). Jack pine percent cover increased from 18 to 30% (data from Probst and Weinrich, 1993), thereby increasing shade. Blueberry increased in percent cover from 5.6% to 13.6% ($P = 0.002$) (Fig. 3), whereas bearberry (2.6% to 0.5%; $P = 0.08$) and deadwood (6.1% to 3.6%; $P = 0.03$) decreased in percent cover (Table 4).

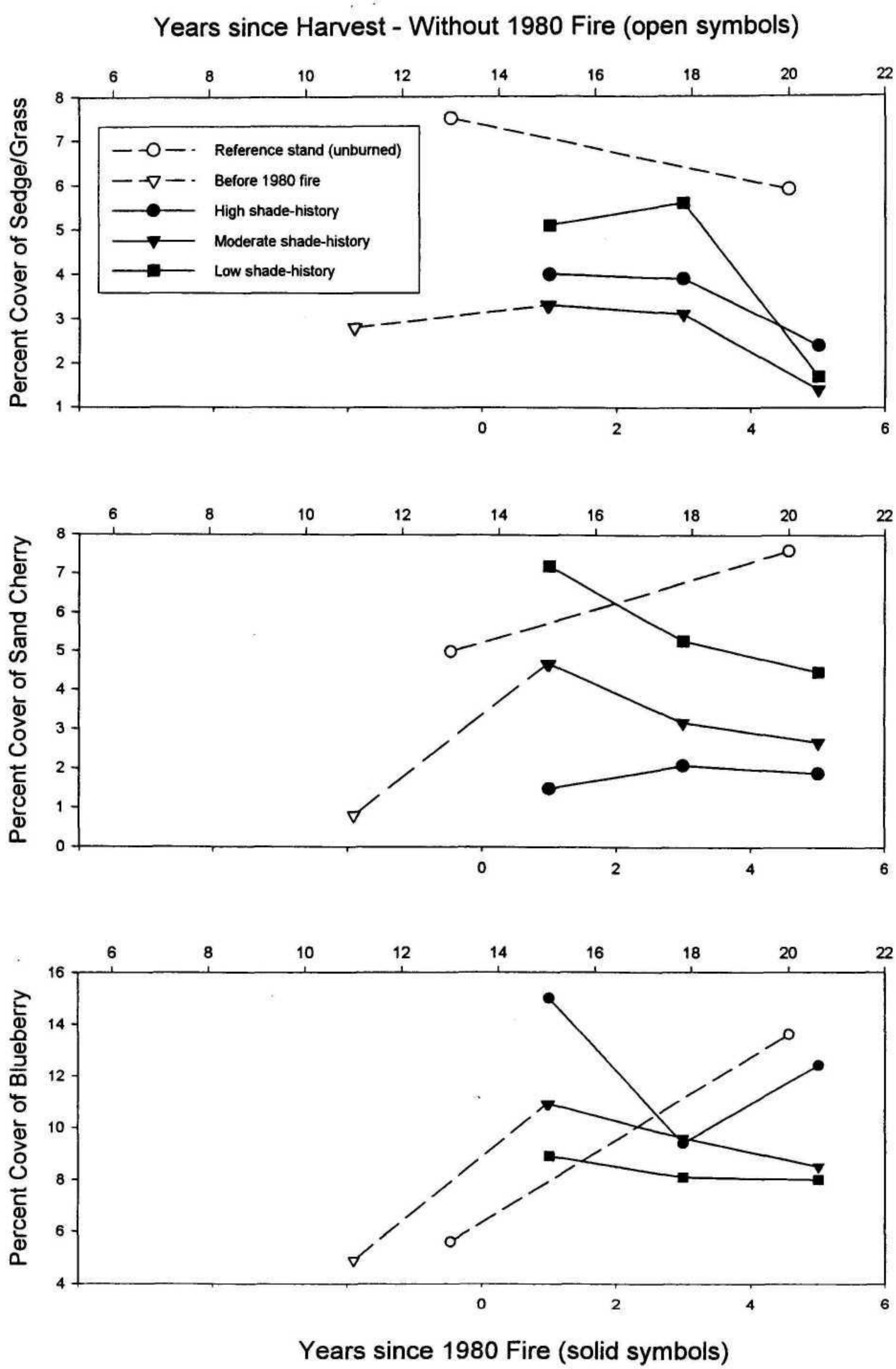
Percent cover at age 5 after the 1980 fire was compared to the 13-y old unburned reference stand, five components suggested convergence or some lasting effects of fire. Blueberry cover was greater in the high and moderate shade-history stands with recent fire and denser shade ($P < 0.01$) than in the 13-y old unburned reference stand (Fig. 3); 2 shade-histories suggest convergence in time. The percent cover of bare ground was also

TABLE 4.—Mean percent cover of early regeneration ground-cover structure components (≤5 y); on 4 stands with different shade histories (SI = Shade Index) before burning in the 1980 Mack Lake Fire. Shade-history categories (before 1980) of the natural regeneration before burning are (1) high shade following 1946 wildfire (SI = 776 m/ha), (2) moderate shade following 1964 harvest/1966 prescribed burn (SI = 645 m/ha), (3) low shade following 1964 harvest (SI = 295 m/ha) and (4) 13 y old reference stand unburned in 1980 and harvested in 1966 (SI = 408 m/ha)

| Ground-cover component | Shade-history category | Year sampled | | | | | Mean |
|---|---|---|---|---|---|---|---|
| | | 1979 | 1981 | 1983 | 1985 | 1986 | |
| Blueberry | 1 | — | 15.0 | 9.4 | 12.4 | — | 12.3 |
| | 2 | — | 10.9 | 9.6 | 8.5 | — | 9.7 |
| | 3 | — | 8.9 | 8.1 | 8.0 | — | 8.4 |
| | 4 | 5.6 | | | | 13.6 | — |
| Sand Cherry | 1 | — | 1.5 | 2.1 | 1.9 | — | 1.8 |
| | 2 | — | 4.7 | 3.2 | 2.7 | — | 3.5 |
| | 3 | — | 7.2 | 5.3 | 4.5 | — | 3.7 |
| | 4 | 5.0 | — | — | — | 7.6 | — |
| Sedge/grass | 1 | — | 4.0 | 3.9 | 2.4 | — | 3.4 |
| | 2 | — | 3.3 | 3.1 | 1.4 | — | 2.9 |
| | 3 | — | 5.1 | 5.6 | 1.7 | — | 4.1 |
| | 4 | 7.5 | — | — | — | 5.9 | — |
| Sweet fern | 1 | — | 2.1 | 1.7 | 2.7 | — | 2.2 |
| | 2 | — | 5.1 | 1.7 | 1.9 | — | 2.9 |
| | 3 | — | 0.6 | 0.5 | 0.6 | — | 0.6 |
| | 4 | 1.3 | — | — | — | 1.5 | — |
| Bearberry | 1 | — | 1.5 | 2.5 | 1.4 | — | 1.8 |
| | 2 | — | 0.6 | 1.0 | 0.3 | — | 0.6 |
| | 3 | — | 0.5 | 1.2 | 0.5 | — | 0.7 |
| | 4 | 2.6 | — | — | — | 0.5 | — |
| Coarse grass | 1 | — | 0.8 | 0.8 | 0.7 | — | 0.8 |
| | 2 | — | 0.8 | 1.7 | 0.6 | — | 1.0 |
| | 3 | — | 0.6 | 0.7 | 0.9 | — | 0.7 |
| | 4 | 0.6 | — | — | — | 0.4 | — |
| Bare ground | 1 | — | 9.1 | 9.7 | 9.6 | — | 9.4 |
| | 2 | — | 5.6 | 7.1 | 4.8 | — | 5.8 |
| | 3 | — | 9.1 | 7.2 | 6.0 | — | 7.4 |
| | 4 | 4.8 | — | — | — | 5.1 | — |
| Deadwood | 1 | — | 0.2 | 1.0 | 3.5 | — | 1.5 |
| | 2 | — | 1.8 | 3.3 | 1.7 | — | 2.2 |
| | 3 | — | 1.7 | 2.9 | 1.7 | — | 1.5 |
| | 4 | 6.1 | — | — | — | 3.6 | — |
| Lichen/moss | 1 | — | 0.0 | 0.0 | 0.0 | — | −0.0 |
| | 2 | — | 0.0 | 0.0 | 2.5 | — | 0.01 |
| | 3 | — | 0.2 | 0.0 | 2.8 | — | 0.01 |
| | 4 | 3.7 | — | — | — | 5.0 | — |

→

FIG. 3.—Successional trends of sedge/grass, sand cherry, and blueberry at Mack Lake Burn study areas in two overlapping disturbance recoveries. Study plots outside or before the 1980 fire are represented by open symbols and are connected by dotted lines (upper label) and permanent plots within the 1980 Mack Lake Burn are solid symbols and are connected by solid lines (lower label)


Years since Harvest - Without 1980 Fire (open symbols)
Reference stand (unburned)
Before 1980 fire
High shade-history
Moderate shade-history
Low shade-history
Percent Cover of Sedge/Grass
Percent Cover of Sand Cherry
Percent Cover of Blueberry
Years since 1980 Fire (solid symbols)

significantly greater in the high shade-history stand than in the unburned reference stand ($P < 0.01$), suggesting some lasting effects of fire. The amount of sedge/grass was significantly less in all three shade-history stands than in the reference stand ($P < 0.01$), but results suggest convergence (Fig. 3). Lichen/moss cover was greater in the unburned reference stand, but only significantly greater than the high shade-history stand ($P < 0.01$). Deadwood was significantly less in the low and moderate shade-history stands ($P < 0.01$), the stands with a recent harvest history with or without fire. In summary, results suggest that fire and shade effects may be transitory for only some components.

Three ground-cover structural components had significant shade-history by time interactions where the magnitude of differences among shade-histories changed through time (Table 4). The amount of deadwood was significantly less ($P < 0.01$) in the high shade-history stand than in the moderate and low shade-history stands during 1981 and 1983. Additionally, the amount of deadwood increased between 1981 and 1983 among all three shade-histories; however, by 1985, the amounts of deadwood (coarse litterfall) increased in the high shade-history stand, but declined (decomposition) in the low and moderate shade-history stands. Sand cherry was most prevalent in the stands having low and moderate shade-histories before the 1980 fire and remained significantly greater in the low shade-history stands for all 3 time comparisons (Fig. 3). However, sand cherry cover increased with time in the high shade-history stand and decreased with time in the low and moderate shade-history stands. Sedge/grass was more abundant in the low shade-history stand in 1981 and 1983, but only significantly more than in the moderate shade-history stand (Fig. 3). From 1983 to 1985 the percent cover of sedge/grass fell significantly in all shade-history stands and became more abundant in the high shade-history stand.

## DISCUSSION

This study investigated the dominant ground-cover structural components in sites occupied by the Kirtland's warbler. These areas are typically 7–23 y-old, resulting from a variety of site disturbances (*e.g.*, wildfire, plantations, prescribed burns, natural regeneration). Secondly, we investigated how early natural regeneration (≤5 y) following a wildfire is influenced by the stand's shade-history before disturbance. The range in percent cover of the ground-cover structural components accepted by the Kirtland's warbler in this study supports the general findings of other studies (Zou *et al.*, 1992; Bocetti, 1994; Kashian, 1998; Houseman and Anderson, 2002). The lower limits of blueberry percent cover and wide range of component covers accepted by the Kirtland's warbler suggests that the amount of blueberry cover is not limiting for nesting Kirtland's warblers within their required landform ecosystems.

It is difficult to compare studies investigating the difference in ground-cover structure between burned and unburned sites because of the confounding effects of regeneration type and site disturbance by harvesting and tree planting (*i.e.*, furrows). This study compared ground-cover structure between naturally regenerating burned sites (3 wildfire and 1 prescribed burn) and unburned sites with natural regeneration (2 sites) and tree plantings (3 sites). We found little difference in percent cover for the dominant shrubby species between burned and unburned sites, suggesting that shrubby species may be fairly resilient to furrowing; however, not all unburned sites had been furrowed. The greater sweet fern cover in burned sites may be highly influenced by the prescribed burn site, which had greater sweet fern cover than all other sites.

Among 8–18 y old plantations, Houseman and Anderson (2002) noted that blueberry cover was greater on prescribed burn sites with a 3-y planting delay than on burned sites with a 1-y planting delay or on unburned sites. Additionally, they found blueberry cover was less in a wildfire reference stand than in prescribed burn sites; however, the greater canopy cover in the wildfire stand resulted in lower levels of cover for all ground layer species. Bocetti (1994) found bearberry cover to be significantly less in plantations than in wildfire sites, but site preparation for some of the plantations involved prescribed burning, making comparisons difficult.

Our results indicated that both grass categories were more abundant in the unburned sites, of which 3 sites were plantations. A possible explanation is that some grasses and sedges, especially *Carex*, are aggressive colonizers after disturbances (Abrams and Dickmann, 1982), such as furrowing before planting. However, Abrams and Dickmann (1982) found *C. pensylvanica* was greater on burned sites than unburned sites, but they examined stands <5 y old, whereas this study examined stands over intermediate stand ages (7–23 y old). Housemann and Anderson (2002) also examined intermediate-aged stands and concluded that burning and planting delay in forested plots of plantations did not significantly affect *C. pensylvanica* cover ultimately, but that sedge was less on sites with a 3 y planting delay versus a 2 y planting delay. Clearly, there may be temporal effects occurring between the stand ages studies by Abrams and Dickmann (1982, 1984) vs. the later stand ages studied by Houseman and Anderson (2002) and this study.

Harvesting may explain the lower amounts of deadwood in the unburned sites. Site preparation may have either broken up or moved deadwood off the site. Alternatively, burning could result in greater deadwood in the intermediate stages of a stand due to snags falling with time. Bocetti (1994) also found more woody debris in wildfires than plantations, and some of her plantations had prescribed burning history. Bare ground was probably higher in the unburned sites due to more soil exposed from plowing when planting trees. Lichen/moss may be less abundant in unburned sites because furrowing breaks up the topsoil crust where lichens usually thrive, but 2 of our unburned plantations had more lichen/moss than the unburned natural regeneration stands.

We demonstrated patterns of early plant succession by following stands having different shade and fire histories through a 5-year period after wildfire. Prior successional trends or stand conditions may alter the initial post-disturbance community. Low shrubs responded to fire with vigorous growth and then may die back (Fig. 3), but sedge/grass increased in unburned areas initially after harvest (Fig. 3). Ground-cover percentages for some components such as blueberry and sand cherry (Table 4; Fig. 3) in these early revegetation stands were similar to those found in the unburned reference stand and in Kirtland's warbler occupied habitats (Table 3). Within the 5-year period before Kirtland's warblers occupy a stand, most plant species decreased in percent cover. However, some species (*e.g.*, blueberry) may increase later (*see* 1979–1986 reference stand comparison in Results, Table 4). This suggests that several components became similar to each other through time in the three stands burned in 1980 by the Mack Lake Fire rather than becoming similar to the unburned sites (Fig. 3, Table 4). Thus, temporal change could mimic or contradict some disturbance effects in studies where comparisons in space are substituted for time. The effects of site attributes on ground cover vegetation are comparable to disturbance effects such as fire.

Other studies suggested convergence of ground-cover composition through time in a synchronous comparison of different-aged burned and unburned stands (Abrams and Dickmann, 1982). The importance of site and stand-history probably explains why Abrams *et al.* (1985) found that ground-cover vegetation in dry jack pine communities is more similar within stands over time than between stands of the same age. The relative influence of disturbances such as fire would be best evaluated by paired treatments in adjacent stands up sites for diverse plant colonists (Probst, 1988; Bocetti, 1994). We conclude that the need for fire to maintain "optimal" ground-cover for Kirtland's Warbler habitat, at least in the short term, has still not been demonstrated by carefully controlled research. However, fire is still desirable for plant diversity, Kirtland's warbler habitat, and other wildlife management objectives.

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## LITERATURE CITED

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

——— AND ———. 1984. Floristic composition before and after prescribed fire on a jack pine clear-cut site in northern lower Michigan. *Can. J. For. Res.*, **14**:746–749.

———, D. G. SPRUGEL AND D. I. DICKMANN. 1985. Multiple successional pathways on recently disturbed jack pine sites in Michigan. *Forest Ecol. and Manage.*, **10**:31–48.

BOCETTI, C. I. 1994. Density, demography, and mating success of Kirtland's Warbler in managed and natural habitats. Ph.D. Dissertation, Ohio State University, Columbus, Ohio. 140 p.

BUECH, R. R. 1980. Vegetation of a Kirtland's Warbler breeding area and 10 nest sites. *Jack-Pine Warbler*, **58**:59–72.

BYELICH, J., M. E. DECAPITA, G. W. IRVINE, R. E. RADTKE, N. I. JOHNSON, W. R. JONES, H. MAYFIELD AND W. J. MAHALAK. 1976, revised 1985. Kirtland's Warbler recovery plan. U.S. Fish and Wildlife Service, Minneapolis, Minnesota. 100 p.

FUSSMAN, J. L. 1997. Foraging ecology of Kirtland's warblers in managed and natural breeding habitat. M.Sc. Thesis, The Ohio State University, Columbus. 73 p.

HERKERT, J. R. 1991. Prairie birds of Illinois: population response to two centuries of habitat change. *Illinois Natural History Survey Bulletin*, **34**:393–399.

HOEFS, M. E. G. AND J. M. SHAY. 1981. The effects of shade on shoot growth of *Vaccinium angustifolium* Ait. after fire pruning in southeastern Manitoba. *Can. J. Bot.* **59**:166–174.

HOUSEMAN, G. R. AND R. C. ANDERSON. 2002. Effects of jack pine plantation management on barrens flora and potential Kirtland's warbler nest habitat. *Restoration Ecol.*, **10**:27–36.

KASHIAN, D. M. 1998. Landscape ecosystems of northern Lower Michigan and the occurrence and management of the Kirtland's warbler. Master's Thesis, University of Michigan, Ann Arbor. 266 p.

——— AND B. V. BARNES. 2000. Landscape influence on the spatial and temporal distribution of the Kirtland's warbler at the Bald Hill burn, northern Lower Michigan, U.S.A. *Can. J. of Forest Research*, **30**:1895–1904.

———, ——— AND W. S. WALKER. Landscape ecosystems of northern Lower Michigan and the occurrence and management of the Kirtland's warbler. *Forest Sci.*, in press.

KEPLER, C. B., G. W. IRVINE, M. E. DECAPITA AND J. WEINRICH. 1996. The conservation management of Kirtland's warbler, *Dendroica kirtlandii*. *Bird Conservation International*, **6**:11–22.

LINDSAY, A. 1955. Testing the line strip method against full tallies in diverse forest types. *Ecology*, **36**:485–495.

MACARTHUR, R. H. AND J. W. MACARTHUR. 1961. On bird species diversity. *Ecology*, **42**:594–598.

MAYFIELD, H. F. 1960. The Kirtland's warbler. Cranbrook Institute of Science, Bloomfield Hills, Michigan. 242 p.

PROBST, J. R. 1985. Summer records and management implications of Kirtland's warbler in Michigan's Upper Peninsula. *Jack-pine Warbler*, **63**:9–16.

———. 1986. Factors limiting the Kirtland's warbler on the breeding grounds. *Am. Midl. Nat.*, **116**:87–100.

———. 1988. Kirtland's Warbler breeding biology and habitat management, p. 28–35. *In:* Integrated Forest Management for Wildlife and Fish. USDA Forest Service, General Technical Report, NC-122.

———, D. S. RAKSTAD AND D. J. RUGG. 1992. Breeding bird communities in regenerating and mature broadleaf forests in the USA Lake States. *Forest Ecology and Management,* **49**:43–60.

——— AND J. WEINRICH. 1993. Relating Kirtland's warbler population to changing landscape composition and structure. *Landscape Ecology,* **8**:257–271.

RUDOLPH, T. D. AND P. R. LAIDLY. 1990. Jack pine, p. 280–293. *In:* R. M. Burns and B. H. Honkala (tech. coords.). Silvics of North America: 1. Conifers. Agriculture Handbook 654. U.S. Department of Agriculture Forest Service, Washington, DC.

WALKER, W. S. 1999. Landscape ecosystems of the Mack Lake burn, northern Lower Michigan, and the occurrence of the Kirtland's warbler. Master's Thesis, University of Michigan, Ann Arbor. 148 p.

———, B. V. BARNES AND D. M. KASHIAN. Landscape ecosystems of the Mack Lake burn, northern Lower Michigan, and the occurrence of the Kirtland's warbler. *Forest Sci.,* in press.

WALKINSHAW, L. H. 1983. Kirtland's Warbler, the natural history of an endangered species. Cranbrook Inst. Sci., Bloomfield Hills, Michigan. 210 p.

ZOU, X., C. THEISS AND B. V. BARNES. 1992. Pattern of Kirtland's warbler occurrence in relation to the landscape structure of its summer habitat in northern Lower Michigan. *Landscape Ecology,* **6**:221–231.

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