Effects of Jack Pine Plantation Management on Barrens Flora and Potential Kirtland's Warbler Nest Habitat

Gregory R. Houseman[1,2,3]
Roger C. Anderson[1]

Abstract

Jack pine barrens, once common in northern lower Michigan, mostly have been converted to managed jack pine plantations. Management of the disturbances associated with logging provides the opportunity to maintain the unique plant assemblages of jack pine barrens and nest habitat of the federally endangered Kirtland's warbler. Studies indicate that *Carex pensylvanica* can develop into dense mats and strongly compete with other barrens species such as *Vaccinium angustifolium*, which seem to be important species for Kirtland's warbler nest locations. According to forest managers, the most important factors facilitating high cover of *V. angustifolium* and reducing cover of *C. pensylvanica* are the amount of shade produced by tree crowns before harvest (pre-harvest shade), the length of time between harvest and planting (planting delay), and fire. We found that high or low levels of pre-harvest shade had no effect on cover of either V. *angustifolium* or *C. pensylvanica*. Planting delays of at least three years following prescribed burns generally increased cover of *V. angustifolium* in forest plots, which are important for warbler nesting. Analysis of community composition in openings indicated that burning enhanced the growth of barrens species. We found only weak evidence for a negative correlation between the cover of *V. angustifolium* and *C. pensylvanica* on our study sites. The openings created in the jack pine plantation are important refugia for barrens flora that would likely be lost under forests managed strictly for jack pine. Maintenance of jack pine barrens flora and Kirtland's warbler nest habitat is possible within the context of a heavily managed forest plantation system.

Key words: barrens restoration, Kirtland's warbler, endangered species, jack pine, plantations, *Vaccinium angustifolium*, *Carex pensylvanica*.

[1]Department of Biological Sciences, Illinois State University, Campus Box 4120, Normal, IL 61790, U.S.A.
[2]Current address: W. K. Kellogg Biological Station, Michigan State University, 3700 E. Gull Lake Dr., Hickory Corners, MI 49060, U.S.A.
[3]Address correspondence to G. R. Houseman, email housema3@pilot.msu.edu

Introduction

Historically, northern lower Michigan (U.S.A.) was dominated by jack pine barrens that occupied sandy outwash plains with coarse, sandy soils (Whitney 1986). Important tree species on historic barrens were *Pinus banksiana* (jack pine) and *Quercus ellipsoidalis* (Hill's oak), with an understory of sand prairie and northern forest forbs, graminoids, and shrubs. Jack pine barrens tended to be open with a mature tree density of fewer than 49 trees/ha (20 trees/acre) (Curtis 1959), although dense jack pine sites also occurred in the region (Voss & Crow 1976). Prior to European settlement, extreme temperatures and periodic fire maintained these barrens. Without fire, succession drove the barren to a closed forest community (Whitney 1986; Pregitzer & Saunders 1999).

Because of conversion of barrens to agriculture and forestry over the past two centuries, barrens are one of the most highly imperiled plant communities in North America (Heikens & Robertson 1994). Jack pine barrens or managed jack pine plantations that serve as barrens surrogates are the only known nesting habitat for the federally endangered Kirtland's warbler (Probst 1988). Thus, conservation and restoration of barrens habitats, and appropriate jack pine plantation management, are vital to species and communities.

Currently, most of the jack pine sites found in northern lower Michigan are located on state and national forests managed by the Michigan Department of Natural Resources or the United States Forest Service. Plantations are clear-cut on a 50-year rotation followed by the application of various management techniques to facilitate the 5–20-year-old jack pine sites used by the warbler. Typically, trees are planted at 1.2-m intervals in rows that are 1.8 m apart, resulting in 4,510 trees/ha. At the time of warbler occupancy, plantation densities range from 1,272—4,296 trees/ha (Probst & Weinrich 1993). Because openings are thought to be important for selection of nest sites (Walkinshaw 1983), generally large, elliptical openings are systematically integrated into the plantation. Approximately 25% of the site is unplanted (R. Marzolo, personal communication).

The quality of the ground cover associated with jack pine plantations also affects the nesting potential of Kirtland's warblers. Zou et al. (1992) noted that the height and patchiness of the jack pine and the character of the ground cover vegetation were critical in the initial occupancy of a site. Smith (1979) and Buech (1980) suggested that tree and ground cover components were factors in habitat selection, and that management techniques encouraging the herbaceous component should be evaluated. Moreover the breeding success is influenced by the quality of available habitat (Probst & Hayes 1987; Bocetti 1994). Locations with high cover of *Vaccinium angustifolium* (lowbush blueberry) and other low shrubs are preferred as nesting sites by Kirtland's warblers (Smith 1979; Bocetti 1994). Thus, management practices facilitating the growth of *V. angustifolium* should foster jack pine plantations that are high-quality warbler habitat.

Vaccinium angustifolium grows best under full sunlight to partial shading; dense shade may reduce its cover (Hoefs & Shay 1981). *V. angustifolium* may also be affected by competition from *Carex pensylvanica* (sedge). Abrams and Dickmann (1982) found that aerial cover of *C. pensylvanica* and *V. angustifolium* was inversely related, although on burned sites *C. pensylvanica* stabilized at much lower levels than on unburned sites. Following tree harvest, the release of inorganic nutrients and increases in space, light, soil temperature, and moisture resulted in *C. pensylvanica* forming dense mats that excluded other species (Abrams & Dickmann 1982, 1984). Forest managers consider prescribed burning (or wildfire), pre-harvest shade, and the length of time between harvest and planting to have the greatest effect on ground cover (J. Probst, personal communication). Variation in pre-harvest shade associated with 50-year stand rotation can profoundly affect the ground layer. Long periods of time under dense tree cover are likely to reduce or eliminate *V. angustifolium* and other sand prairie species and affect regeneration potential following harvest.

Some harvested sites lie dormant for several seasons resulting in a "planting delay," with the disturbances of tree harvest and mechanical planting occurring during different growing seasons rather than a single growing season. *Carex pensylvanica* may increase in response to the multi-year disturbance seasons (Abrams & Dickmann 1982, 1984) that are associated with a 3–5 year "planting delay." Increases in *C. pensylvanica* may lead to decreased cover *of V. angustifolium.*

Additionally, several studies have indicated that *V. angustifolium* responds positively to burning (Hall 1955; Barker & Collins 1963*a*; Smith & Hilton 1971). Periodic fire was historically an important disturbance factor that strongly affected the species composition of jack pine barrens (Pregitzer & Saunders 1999). Thus, prescribed burning may increase *V. angustifolium* and other barrens species on these sites.

We examined the effects of pre-harvest shade, prescribed burning, and planting delays on the cover of *V. angustifolium* and *C. pensylvanica* and other ground cover species in plantations. These effects were quantified as "forest habitats" and "openings." Forest habitat includes areas within the site that were planted with jack pine seedlings and are critical to Kirtland's warbler nesting. Open habitats are areas that were not planted but are most important to the maintenance of jack pine barrens ground flora. These results were compared with those from a naturally regenerated jack pine area following the Mack Lake wildfire in the spring of 1980.

The Mack Lake fire burned over 9,717 ha including 4,356 ha of jack pine (Simard et al. 1983). Most of the burned area regenerated to even-age jack pine that became one of the most productive Kirtland's warbler breeding areas in recent times (Bocetti 1994). Mack Lake provided reference sites for comparison with plantations to determine treatments that lead to vegetation most similar to natural regeneration following wildfire and associated with successful Kirtland's warbler breeding.

Methods

Sample Design and Site Selection

The study design was a three-factor complete block design with two levels of each factor: site preparation (prescribed burn or no prescribed burn), planting delay (1 year or 3 or more years after either harvest or prescribed burning), and high or low pre-harvest shade. Tree basal area of the site prior to harvest, which was obtained from forestry site maps and timber sales, provided an indirect measure of canopy cover (Barbour et al. 1999) and consequently, pre-harvest shading. High pre-harvest shade sites had basal areas (BA) greater than 16.26 m^2/ha, whereas low pre-harvest shade sites had BA less than 9.10 m^2/ha. Planting delay was defined as the length of time between harvest and mechanical planting on unburned sites or between prescribed burning and planting for burned sites. Sites with a planting delay of more than three years are referred to as three-year planting delay because only two sites had a planting delay greater than three years. Prescribed burned sites were locations where the slash was burned following tree harvest. Study sites were located using forestry site maps and were within 60 km of Mio, Michigan, U.S.A. (lat 44°40′ N, long 84°07′30′′ W, elevation 311.5 m and ranged from 21–278 acres). We selected 28 jack pine plantations that were 8–18 years old, corresponding to the age at which plantations are occupied by the warbler, and five 17-year-old Mack Lake reference sites. All sites were relatively level and occurred on sandy soils.

Sampling Procedures

The boundary of each site was identified, and the sampling area within each site was determined using randomly selected coordinates. A 300-m transect was oriented through the longest axis of the site. Using a stratified random procedure (Greig-Smith 1964), five sampling transects were located at right angles to the 300-m transect. Because of the probable importance of openings for nest sites and barrens flora, we sampled the first opening within 50 m of the sampling transects and the forest habitat adjacent to the opening. An opening had a diameter equal to or greater than the maximum height of the surrounding trees. Most openings resulted from the planting pattern used by forestry personnel to create openings for the warbler. This sampling design ensured that we sampled each site at the same scale (100 × 300–m area) regardless of the size of the site.

Preliminary work (B. Barnes, personal communication) indicated that a randomly located 5 × 10–m plot was the appropriate scale to sample ground cover on these sites. Thus we established a 5 × 10–m plot in the opening with the maximum dimension parallel to the longest axis of the opening. A second 5 × 10–m paired plot was located in the forest adjacent to the opening. This plot was oriented in the same fashion as the plot in the opening and was at least 10 m from the nearest edge of the open plot.

Within these two plots, we estimated cover by species for all vegetation below 1 m. The plot was systematically traversed and the number of 0.25-m quadrat frames of cover that each species would fill within the entire plot was estimated (Lapin & Barnes 1995). The number of frames of each species was then converted to total percent cover for the entire plot. Species identification and nomenclature followed Voss (1996). Woody vegetation above breast height (1.4 m) in each plot was tallied by species in the following diameter at breast height (dbh) size classes: 0–3 cm, greater than 3–6 cm, greater than 6–9 cm, greater than 9 cm. Total stem count by species was multiplied by the midpoint basal area of the respective size class. These values were summed across size classes to yield basal area by species for each plot. Three 15-cm soil cores were extracted from each plot, and the soils from plots were combined by site. We measured the A1 horizon depth in centimeters for each soil core. Soils were analyzed for texture, pH and selected inorganic nutrients (available P [Bray 1] and K, and exchangeable Ca and Mg, total N) by the Wisconsin State Plant and Soil Analysis Laboratory, Madison, Wisconsin.

Data Analysis

We used a three-way fixed effects MANOVA (Scheiner 1993) with cover data of *V. angustifolium* and *C. pensylvanica* as response variables and pre-harvest shade, planting delay, and prescribed burning as main effects on forest plots. A one-way MANOVA with contrasts was used to compare Mack Lake reference sites with burned sites with either 1- or 3-year planting delay. We tested for the assumptions of MANOVA by examining the residuals for univariate normality and heteroscedacity (Scheiner 1993). Data were transformed when necessary to meet these assumptions. When MANOVA was significant, we used protected ANOVAs as follow-up tests. Statistical significance was accepted when p is less than 0.05.

We performed Detrended Correspondence Analysis (DCA) using PC-ORD (McCune & Mefford 1999) to examine community patterns of the ground cover vegetation (Hill & Gauch 1980). Ground cover species occurring in less than 5% of all plots were removed from the analysis, and rare species were downweighted. Separate species ordinations were conducted for open and forest plots. We used an after-the-fact relative Euclidean distance to determine the variance explained by each axis (McCune & Mefford 1999).

Results

Soil Inorganic Nutrients

Jack pine plantations in northern lower Michigan occur on nutrient-poor, acidic sites. Mean soil pH for the study sites was 4.8, and levels of all measured soil parameters were low (Table 1). However, the availability of inorganic nutrients is quite varied in jack pine barrens and pine plantations in the Great Lakes region. For example, exchangeable Ca for our study sites was similar to that reported for jack pine stands in northeastern Minnesota (Green & Grigal 1980). However, our study sites had substantially lower exchangeable Ca than pine barrens in Wisconsin (Curtis 1959) and a harvested jack pine stand in Wisconsin, which was prescribed burned following harvest (Boyle 1973). Available K and exchangeable Ca were lower in Wisconsin sand barrens (Curtis 1959) than in our study sites. Soil pH, available P, and exchangeable Mg were lower on the sites we investigated than those reported for the comparison communities (Table 1). Total N was low in all jack pine stands, including our study sites.

Dominant Ground Layer Species

The herbaceous vegetation on the site is a mixture of sand prairie species and dry northern and boreal forests as defined by Curtis (1959). The two dominant species in open and forest plots based on cover or frequency

Table 1. Soil nutrient values for all plantations and Mack Lake sites compared with similar jack pine studies. Values for total N and extractable P (Bray 1), and exchangeable Ca, K and Mg are means in μg/g.

	Depth (cm)	*Total N*	*Extractable P*	*Ca*	*K*	*Mg*	*pH*
Houseman (1998) 33 jack pine stands in northern lower Michigan	1–15	1,000	14.6 ± 1.1	143 ± 15	28.8 ± 1.3	17.9 ± 1.2	4.8
Curtis (1959) 26 stands in Wisconsin pine barrens	—	—	22	4,025	70	—	5.2
Curtis (1959) 20 stands in Wisconsin sand barrens	—	—	30	50	17	—	6.2
Green and Grigal (1980) 15 jack pine stands in northeastern Minnesota*	0–100	463	41	144	42	24	—
Boyle (1973) 1 harvested jack pine stand in Wisconsin 15 months after a prescribed burn*	0–20	1126 ± 67.9	104 ± 3.8	524 ± 30.4	70 ± 2.1	—	5.1

*Values for Green and Gringal (1980), and Boyle (1973) were obtained by converting from kg/ha to μg/g using an estimated bulk density of 1.2 g/cc.

were *Carex pensylvanica* and *Vaccinium angustifolium.* Both species occurred with frequencies greater than 95% in open and forest plots (Table 2). Sand prairie species common to open and forest plots included: *Viola pedata* (bird's-foot violet), *Schizachyrium scoparium* (little bluestem), *Aster laevis* (smooth aster), *Solidago speciosa* (showy goldenrod), *S. nemoralis* (gray goldenrod), *Campanula rotundifolia* (harebell), *Danthonia spicata* (poverty grass), *Panicum linearifolium* (panic grass), *Antennaria neglecta* (pussy-toes), *Fragaria virginiana* (strawberry), and *Rosa* spp. In addition to the shared species, forest plots included *Calystegia spithamaea* (low bindweed), *Crataegus* spp. (hawthorn), *Helianthemum canadense* (rockrose), *Maianthemum canadense* (lily-of-the-valley), *Panicum depauperatum* (panic grass), and *Solidago hispida* (hairy goldenrod); open plots included *Koeleria macrantha* (June grass), *Liatris cylindracea* (blazing star), and *Polygala polygama* (milkwort).

Response of *V. angustifolium* and *C. pensylvanica*

For the three-way MANOVA of forest plots, we found a significant two-way interaction (Fig. 1) between prescribed burning and planting delay for *V. angustifolium* ($df = 2, 19$, Wilks' $\lambda = 0.541$, F value $= 8.04$, $p = 0.0029$). The ANOVA indicated that *V. angustifolium* responded to the interaction between the effect of burning and delay ($df = 1, 20$, F value $= 15.45$, $p = 0.0008$), whereas *C. pensylvanica* was not significantly affected by the burn–delay interaction ($df = 1, 20$, F value $= 0.00$, $p = 0.9657$). Percent cover of *V. angustifolium* was higher on burned sites with a 3-year planting delay (mean = 15.00, SE = 1.98) than on burned sites with a 1-year planting delay (mean = 6.48, SE = 1.01) or on unburned sites with planting delays of either 1 (mean = 8.01, SE = 1.14) or 3 years (mean = 5.44, SE = 1.32). However, burned sites with a 1-year delay did not significantly differ from unburned sites with either level of planting delay. No other significant effects were detected on forest plots.

Table 2. Species frequency and percent cover for 165 open and forest plots across all sites.

	Open		*Forest*	
Species	*Percent Occurrence*	*Percent Cover*	*Percent Occurrence*	*Percent Cover*
Carex pensylvanica	97.1	2.72	97.9	1.40
Vaccinium angustifolium	95.7	7.25	99.3	7.53
Prunus pumila	90.7	1.10	87.9	0.61
Cladonia spp.	87.1	2.16	90.7	0.66
Andropogon gerardii	68.6	0.34	66.4	0.24
Arctostaphylos Uva-ursi	62.1	0.42	60.0	0.22
Oryzopsis pungens	58.6	0.07	65.7	0.07
Moss	55.7	0.21	81.4	0.28
Comptonia peregrina	49.3	0.86	76.4	0.72
Quercus ellipsoidalis	48.6	0.25	76.4	0.72
Melampyrum lineare	12.86	0.01	52.9	0.04

Comparison of Prescribed Burns and Wildfire Sites

We also used a one-way MANOVA with follow-up contrasts to compare cover of *V. angustifolium* and *C.*

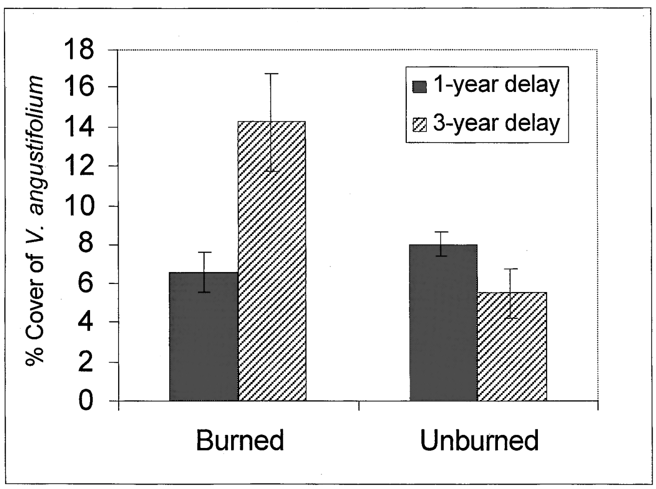

Figure 1. Two-way interaction between planting delay and burning for mean percent cover of *V. angustifolium* on burned and unburned sites.

pensylvanica on Mack Lake sites to burned sites with a 1-year planting delay or a 3-year planting delay in forest plots (Table 3). MANOVA indicated significant differences in cover of *V. angustifolium* and *C. pensylvanica* between Mack Lake sites and burned sites with a 1-year delay in planting ($df = 2, 15$, Wilks' $\lambda = 0.5096$, F value $= 7.22$, $p = 0.0064$) or a 3-year delay in planting ($df = 2, 15$, Wilks' $\lambda = 0.402$, F value $= 11.18$, $p = 0.0011$). Mack Lake sites had lower cover of *C. pensylvanica* ($df = 1, 16$, F value $= 12.53$, $p = 0.0027$) than sites with a 1-year planting delay (Table 3). Mack Lake sites also had lower (Table 3) *V. angustifolium* cover ($df = 1, 16$, F value $= 23.79$, $p = 0.0002$) than burned sites with a 3-year planting delay, but had similar cover of *C. pensylvanica* ($df = 1, 16$, F value $= 0.39$, $p = 0.5409$).

At Mack Lake the distribution of openings and forest habitat was more heterogeneous with a more strongly aggregated distribution of trees than on the plantation sites. Consequently forest plots at Mack Lake sites had higher tree densities (mean = 8,950 trees/ha, SE = 1,340) and BA (mean = 13.6 m^2/ha, SE = 0.7) than plantation tree densities (mean = 3,345 trees/ha, SE = 162) or BA (mean = 6.8 m^2/ha, SE = 0.5). This high tree density and basal area at Mack Lake resulted in lower levels of cover for all ground layer species at Mack Lake (mean = 24.2%, SE = 5.81) than in plantations (mean = 48.5%, SE = 2.6). Thus, forest plots at Mack Lake did not provide a good comparison of Kirtland's warbler habitat for plantations.

Plantations and Mack Lake sites were dominated by jack pine, whereas Hill's oak was of secondary importance (Table 4). Plantations contained low amounts of *Prunus serotina* (black cherry), *P. virginiana* (chokecherry), *P. pensylvanica* (pin cherry), *Populus grandidentata* (big-toothed aspen), and *P. tremuloides* (quaking aspen). Except for one individual of *Prunus virginiana*, no tree species other than jack pine and Hill's oak were found on Mack Lake sites.

Abrams and Dickmann (1982) reported that cover of *V. angustifolium* and *C. pensylvanica* are inversely related. Using the Pearson Product Moment Correlation, we found a significant negative correlation ($r^2 = 0.0258$, $p < 0.05$) between *V. angustifolium* and *C. pensylvanica* in forest plots across all sites. However, the relationship explained only 2.6% of the variation between the two variables. There was no significant relationship between *V. angustifolium* and *C. pensylvanica* in open plots ($r^2 = 0.0117$, $p > 0.05$). Thus we did not find strong evidence for an inverse relationship between *V. angustifolium* and *C. pensylvanica.*

Table 3. Mean percent cover and standard error for *Vaccinium angustifolium* and *Carex pensylvanica* for Mack Lake sites and prescribed burn forest sites with either 1-year delay or 3-year delay. A different letter indicates that means were significantly different ($p < 0.05$) for a given species.

	Forest	
	Vaccinium	*Carex*
Mack Lake	3.3 ± 0.6 a	0.4 ± 0.1 a
Burn/1-year delay	6.2 ± 1.0 a	1.7 ± 0.3 b
Burn/3-year delay	14.3 ± 2.5 b	0.6 ± 0.2 a

Site Ordinations

In open plots prescribed burning led to a clear separation of burned and unburned sites (Fig. 2). The first 3 axes explained 63% of the variation (axis 1 = 35%, axis 2 = 22%, and axis 3 = 6%). Prescribed burn sites tended to have high axis 1 scores, whereas unburned sites generally had low axis 1 and high axis 2 scores. Site 9 appeared to be an outlier in this ordination. However, we were unable to determine what led to the unusual ordination scores for this stand based on the variables we measured. Sites that were prescribed burned and experienced a delay of 3 years before planting were most similar to the Mack Lake reference sites in terms of ground cover species composition and abundance (Fig. 3). We examined site nutrients, stand age, and other treatment variables and found that only prescribed burning accounted for the patterns found in the ordinations.

Species Ordinations

In the species ordinations of ground cover plants in open plots (Fig. 3), the major delineation of species was the separation of sand prairie species in the lower right side of the ordination from those found in northern dry or boreal forests (as defined by Curtis 1959). Sand prairie species had high axis 1 and low axis 2 scores corresponding to the sites that experienced fire in the site ordination (Fig. 3). *V. angustifolium* and *C. pensylvanica* were located near the center of the ordination, suggesting that other species led to the separation of stands. The widespread occurrence and abundance of these two species in open and forest plots (Table 2) support this conclusion.

Discussion

Foresters involved in managing Kirtland's warbler habitat have proposed that among the environmental and disturbance factors affecting development of vegetation in Kirtland's warbler habitat, those with the greatest impact on ground cover species are the pre-harvest shade, the length of the interval between tree harvest and planting, and fire (J. Probst, personal communication). These factors are believed to be of vital impor-

Table 4. Density (trees/ha) for the 3 leading tree species on open and forest plots for plantations and Mack Lake sites. "Other" represents the summation of *Prunus serotina*, *Prunus virginiana*, *Prunus pensylvanica*, *Populus grandidentata*, *Populus tremuloides*.

	Open		*Forest*	
	Plantations	*Mack Lake*	*Plantations*	*Mack Lake*
Pinus banksiana	6.46 ± 0.51	12.93 ± 0.66	2889.7 ± 142.0	8577.6 ± 1380.7
Prunus serotina	0.05 ± 0.02	0.00 ± 0.00	102.3 ± 38.2	0.0 ± 0.0
Quercus ellipsoidalis	0.24 ± 0.06	0.65 ± 0.47	353.4 ± 74.9	372.8 ± 196.5
Other	0.06 ± 0.03	0.00 ± 0.00	87.4 ± 41.8	8.0 ± 0.0
Total	6.81 ± 0.52	13.58 ± 0.68	3345.4 ± 162.3	8950.4 ± 1339.8

tance to the relationship between *Carex pensylvanica* and *Vaccinium angustifolium.*

Shade

Our results indicated that the pre-harvest shade did not significantly affect the cover of *V. angustifolium* or *C. pensylvanica.* The shade-tolerance of *V. angustifolium* is supported by Hall (1955), who determined that *V. angustifolium* persisted at light intensities of 0.5% of full sunlight under a spruce-fir canopy. Hoefs and Shay (1981) found that intermediate shade provided favorable conditions for *V. angustifolium* in Manitoba where high ground temperatures and reduced soil moisture occurred in open areas during the summer, similar to conditions occurring in northern Michigan. Moreover *V. angustifolium* generally reproduces poorly from seeds (Vander Kloet 1976, 1985; Wesley et al. 1986; Matlack et al. 1993), and colonization occurs mostly by rhizomatous growth (Martin 1954; Barker & Collins 1963*b*; Kender & Eggert 1966; Vander Kloet 1976; Carroll & Bliss 1982). Although jack pine plantations in northern Michigan are usually harvested 40–60 years after planting, *V. angustifolium* clones can be long-lived (Vander Kloet 1976) and persist as rhizomes for many years (Martin 1954). Thus, the amount of *V. angustifolium* present on a site, including belowground organs, prior to tree harvest is likely a key factor in determining increased levels of cover and colonization of this species following harvest (Hall 1955; Ahlgren 1960; Moore & Wein 1977; Hoefs & Shay 1981). Our results indicate that although site history may contribute to the amount of *V. angustifolium* cover, pre-harvest shade apparently did not limit the amount of *V. angustifolium* that developed on a site following harvest.

Carex pensylvanica can persist at high frequency but with low cover in the shade of mature jack pine plantations (Buell & Cantlon 1953; Abrams & Dickmann 1984). Following tree harvest, *C. pensylvanica* is capable of spreading rapidly by seed and rhizomes (Rowe & Scotter 1973) in response to the increased light, space, soil temperature, and moisture (Abrams & Dickmann 1983). Thus, pre-harvest shade levels may have little effect on *C. pensylvanica* in these plantations.

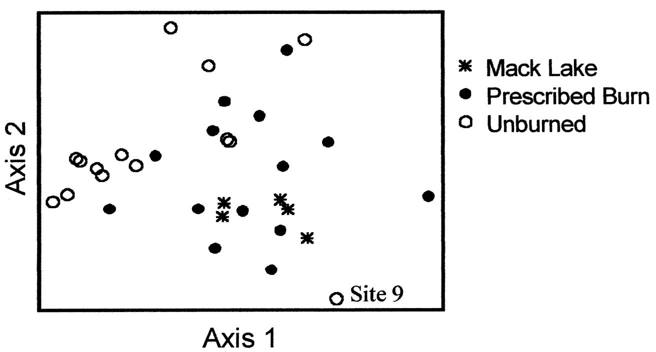

Figure 2. Detrended Correspondence Analysis of 28 plantation forest plots and 5 Mack Lake sites. An asterisk represents Mack Lake sites, a solid diamond represents prescribed burned sites, and open circles represents unburned sites.

Planting Delay and Prescribed Burning

We found an interaction between planting delay and burning for *V. angustifolium* in forest plots. Sites that received prescribed burning but were not planted for three or more years had higher cover of *V. angustifolium* than sites that were prescribed burned and planted within one year. There are several possible biological explanations for this result. Many studies have demonstrated a positive response of *V. angustifolium* to burning (Hall 1955; Trevett 1956; Barker & Collins 1963*a*; Smith & Hilton 1971; Matlack et al. 1993). This positive growth response results in the colonization of new areas by the horizontal spread of *Vaccinium* spp. (Matlack et al. 1993). Because *V. angustifolium* rarely reproduces from seed on these sites, asexual reproduction and colonization are vital to increased cover (Vander Kloet 1976, 1985; Wesley et al. 1986; Matlack et al. 1993). A longer delay between burning and planting may allow *V. angustifolium* to respond initially to burning without the added competition of *Pinus banksiana* seedlings.

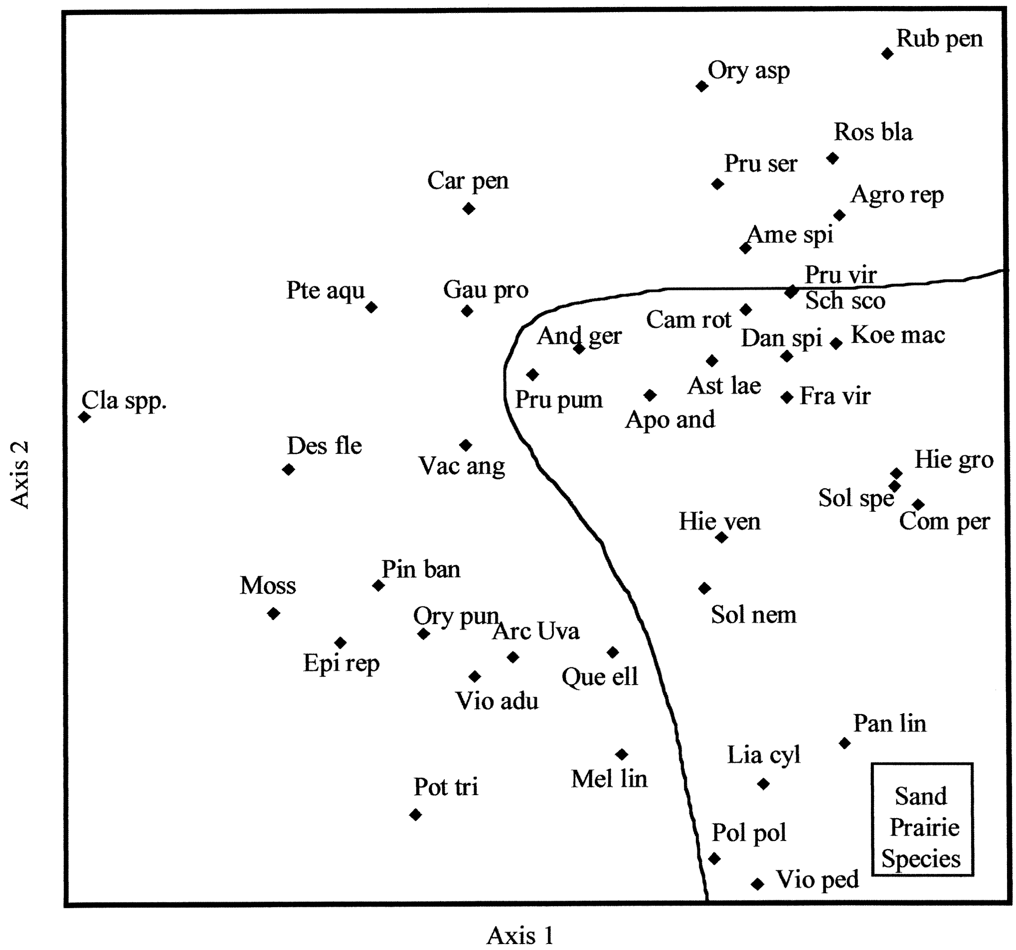

Figure 3. DCA species ordination of species sampled in open plots. Gau pro (*Gaultheria procumbens*), Cla spp (*Cladonia* spp.), Hei ven (*Hieracium venosum*), Vio ped (*Viola pedata*), Pin ban (*Pinus banksiana*), Ory pun (*Oryzopsis pungens*), Arc Uva (*Arctostaphylos Uva-ursi*), Pan lin (*Panicum linearifolium*), Vac ang (*Vaccinium angustifolium*), Que ell (*Quercus ellipsoidalis*), Epi rep (*Epigaea repens*), Pot tri (*Potentilla tridentata*), Pru pum (*Prunus pumila*), And ger (*Andropogon gerardii*), Apo and (*Apocynum androsaemifolium*), Pte aqu (*Pteridium aquilinum*), Sch sco (*Schizachyrium scoparium*), Sol spe (*Solidago speciosa*), Mel lin (*Melampyrum lineare*), Sol nem (*Solidago nemoralis*), Des fle (*Deschampsia flexuosa*), Car pen (*Carex pensylvanica*), Ame spi (*Amelanchier spicata*), Ast lae (*Aster laevis*), Cam rot (*Campanula rotundifolia*), Fra vir (*Fragaria virginiana*), Dan spi (*Danthonia spicata*), Vio adu (*Viola adunca*), Com per (*Comptonia peregrina*), Pru vir (*Prunus virginiana*), Ros spp (*Rosa* spp.), Ory asp (*Oryzopsis asperifolia*), Pru ser (*Prunus serotina*), Hie gro (*Hieracium gronovii*), Agr rep (*Agropyron repens*), Rub pen (*Rubus pensilvanicus*), Pol pol (*Polygala polygama*), Koe mac (*Koeleria macrantha*), and Lia cyl (*Liatris cylindracea*).

A second possibility is that when prescribed burning is followed by planting within one year, the *V. angustifolium* does not have time to capitalize fully on the facilitation of the prescribed burn before the physical disturbance associated with planting occurs. The furrow created by mechanical planting is approximately 8–15 cm deep and 46–61 cm wide (R. Marzolo, personal communication) and may dislodge many of the rhizomes of *V. angustifolium.* Barker and Collins (1963*b*) found that *V. angustifolium* rhizomes ceased growth even when briefly exposed to sunlight. Thus the positive growth response of the *V. angustifolium* colony may be disrupted by the physical disturbance of planting. Because some studies have indicated that *Vaccinium* spp. increases in the second and succeeding years after a burn (Ahlgren 1960; Barker & Collins 1963*a*), the increased development of *Vaccinium* spp. colonies for three years before tree planting may compensate for the negative effect of the physical disturbance associated with planting. This hypothesis is supported by Kender and Eggert (1966), who found that *V. angustifolium* had greater aerial and underground stem growth when planted in undisturbed soil than in soil that had been homogenized before planting. Physical disturbances to the soil may also disrupt the mycorrhizal association of *V. angustifolium*, which has been shown to enhance the uptake of nutrients by *Vac-*

cinium spp. in nutrient-poor soils such as those found in northern lower Michigan (Pearson & Read 1973; Read & Stribley 1973; Stribley & Read 1974).

Sites with a three-year delay following a prescribed burn and Mack Lake sites had similar *C. pensylvanica* cover, but the sites with a three-year delay had higher cover of *V. angustifolium* than Mack Lake sites. The low cover of *V. angustifolium* is likely reflective of the general reduction of understory cover in Mack Lake forest plots compared to plantations probably resulting from the suppressive effects of high tree density and basal area of Mack Lake sites.

Competition Between *C. pensylvanica* and *V. angustifolium*

We found no evidence for an inverse relationship between the abundance and occurrence of *C. pensylvanica* and *V. angustifolium. C. pensylvanica* and *V. angustifolium* were both found on all sites and in nearly all plots. It appeared that *C. pensylvanica* and *V. angustifolium* were competing at some level on these sites, but there was only a weak inverse relationship between the cover of the two species on forest plots. As previously noted, Abrams and Dickmann (1982, 1984) reported that *C. pensylvanica* formed dense mats that excluded all other species. Forest managers suspect that planting delays may foster *C. pensylvanica*, leading to exclusion of *V. angustifolium.* In some cases, we found *C. pensylvanica* "mats" with little or no *V. angustifolium.* However, these mats were not the result of three-year delays in planting. The difference between our results for the two species compared with those reported by other workers (Abrams & Dickmann 1982, 1984) might be due to the difference in scale at which sampling occurred in our study and in those of previous workers. Our summary unit was the 5 × 10–m plot, whereas other workers (Abrams & Dickmann 1982, 1984) have summarized occurrence of the two species along line transects. At a small scale, competitive interactions between the two species may be expressed, but we did not find this pattern at our sampling scale.

Community Response

Jack pine is the dominant tree species of barrens in northern Michigan. In natural jack pine barrens, the distribution of trees is highly aggregated (Curtis 1959; Voss & Crow 1976). This is the pattern we found at the Mack Lake sites, where natural jack pine regeneration had occurred following a wildfire. The openings that developed following wildfire were also highly variable in size and were often continuous with other openings.

The ground cover in jack pine barrens is a unique combination of sand prairie, northern dry forest, and boreal forest species (Curtis 1959). The sand prairie species from all sites clustered together in the ordinations of open plots and forest plots. Northern dry forest and boreal forest species were interspersed across the ordinations. The combination of ground cover species is likely related to historical burning and regeneration patterns (Hall 1955; Ahlgren 1960; Moore & Wein 1977; Hoefs & Shay 1981), the size of the opening, and the relative amount of tree cover. Open sites that were burned were generally most similar in overall species composition to the open plots found on Mack Lake reference sites.

The stand ordination suggested that prescribed burning and the delay factor were important factors for the response of the ground cover as hypothesized by local managers. However, the pre-harvest shade did not seem to be a strong controlling factor.

Implications for Restoration and Management

Our results indicate that managers should conduct prescribed burns to enhance the development of *V. angustifolium* in forest plots. Planting should be delayed for three years to allow for the response of *V. angustifolium* to the facilitation of fire. The effect of fire would also facilitate the growth of barrens species in openings. If it is not possible to conduct a prescribed burn, then sites should be planted within one year of tree harvest. Restoration and maintenance of barrens species in openings would also benefit from addition of native seed in the openings. This practice would help overcome seed limitation that may have occurred during the last century of management.

The openings created in jack pine plantations are of vital importance to the maintenance of jack pine barrens species. Historically, jack pine barrens were part of a spatially shifting, vegetational mosaic on sandy sites in northern lower Michigan that was maintained by wildfires with return intervals of 20–40 years. As jack pine stands matured, tree densities increased. When fire swept through old, dense jack pine stands, there likely was a large seed release and high germination resulting in high tree densities as reported by Voss and Crow (1976) and found in many areas after the Mack Lake wildfire. After wildfire, openings that are essential for maintenance of jack pine barrens ground cover were numerous and random in size and space.

Because nearly all of the original jack pine barrens have been converted to pine plantations or alternative uses, it is important for managers to integrate conservation strategies into the creation of these plantations. Maintaining jack pine on a single site for 50 years likely eliminates many of the sand prairie species associated with barrens. These species are probably maintained during later phases of the 50-year rotation cycle in the openings. Thus, openings that are created to improve nesting and foraging habitat for Kirtland's warblers ensure that every site has some openings so that the floristic elements of jack pine barrens can be maintained. Although the species composition of open and forest plots was similar in this study, many of the barrens species will likely disappear as the 8–18 year jack pine stands mature, creating more shady conditions.

Because the success of Kirtland's warblers is dependent upon vegetational composition, further research and monitoring is needed. Special attention should be given to the abundance of ground cover species before harvest. Ideally, long-term monitoring plots would be established to quantify changes in species composition and abundance during the different stages of stand development. The effect of the extensive furrows used to prepare the site for jack pine seedlings on jack pine barren ecosystem components needs to be carefully examined. The furrowing disrupts soil systems, causes potential loss of seed banks, and destroys above- and belowground ecosystems components. Over several rotation periods a large portion of the plantation could be subjected to the disrupting effects of the furrows.

Stimulating recurring wildfires is the only way to ensure that jack pine barrens are maintained as a functioning community (Pregitzer & Saunders 1999). However, societal demands for forest products have resulted in the establishment of extensive areas of jack pine plantations. In these areas management should be conducted in a way to ensure personal safety and encourage production of jack pine. Nevertheless, preservation of barrens flora and Kirtland's warbler habitat is dependent upon plantation management strategies that simulate natural processes and maintain the constituent barren components.

Acknowledgments

This research was supported financially by a Michigan Natural Heritage Grant and grants from the Beta Lambda Chapter of the Phi Sigma Honor Society and Illinois State University Graduate School. We thank Carol Bocetti, Charles Thompson, Angelo Capparella, and two anonymous reviewers for helpful comments on the manuscript. We also thank the Kirtland's Warbler Advisory Committee, and the USFS, MDNR, and the AuSable Institute for logistic support.

LITERATURE CITED

Abrams, M. D., and D. I. Dickmann. 1982. Early revegetation of clear-cut and burned jack pine sites in northern Lower Michigan. Canadian Journal of Botany **60:**946–954.

Abrams, M. D., and D. I. Dickmann. 1983. Response of understory vegetation to fertilization on mature and clear-cut jack pine sites in northern Lower Michigan. American Midland Naturalist **110:**194–200.

Abrams, M. D., and D. I. Dickmann. 1984. Floristic composition before and after prescribed fire on a jack pine clear-cut site in northern Lower Michigan. Canadian Journal of Forest Research **14:**746–749.

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

Barbour, M., J. Burk, W. Pitts, F. Gilliam, and M. Schwartz. 1999. Terrestrial plant ecology, 3rd edition. Addison Wesley Longman, Inc., New York.

Barker, W. G., and W. B. Collins. 1963*a*. Growth and development of the lowbush blueberry: apical abortion. Canadian Journal of Botany **41:**1319–1324.

Barker, W. G., and W. B. Collins. 1963*b*. The blueberry rhizome: in vitro culture. Canadian Journal of Botany **41:**1325–1329.

Bocetti, C. I. 1994. Density, demography, and mating success of Kirtland's warblers in managed and natural habitats. Ph.D. dissertation. Ohio State University, Columbus.

Boyle, J. R. 1973. Forest soil chemical changes following fire. Communications in Soil Science and Plant Analysis **4:**369–374.

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

Buell, M. F., and J. E. Cantlon. 1953. Effects of prescribed burning on ground cover in the New Jersey pine region. Ecology **34:**520–528.

Carroll, S., and L. C. Bliss. 1982. Jack pine-lichen woodland on sandy soil in northern Saskatchewan and northeastern Alberta. Canadian Journal of Botany **60:**2270–2282.

Curtis, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison.

Green, D. C., and D. F. Gringal. 1980. Nutrient accumulations in jack pine stands on deep and shallow soils over bedrock. Forest Science **26:**325–333.

Greig-Smith, P. 1964. Quantitative plant ecology. Butterworths, London.

Hall, I. V. 1955. Floristic changes following the cutting and burning of a woodlot for blueberry production. Canadian Journal of Agricultural Science **35:**143–152.

Heikens, A. L., and P. A. Robertson. 1994. Barrens of the Midwest: a review of the literature. Castanea **59:**184–194.

Hill, M. O., and H. G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio **42:**47–58.

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. Canadian Journal of Botany **59:**166–174.

Houseman, G. R. 1998. Effects of various management practices in jack pine plantations on ground cover preferred by Kirtland's warblers. M. S. thesis. Illinois State University, Normal.

Kender, W. J., and F. Eggert. 1966. Several soil management practices influencing the growth and rhizome development of the lowbush blueberry. Canadian Journal of Plant Science **46:** 141–149.

Lapin, M. C., and B. V. Barnes. 1995. Using the landscape ecosystem approach to assess species and ecosystem diversity. Conservation Biology **9:**1148–1158.

Martin, J. L. 1954. The vegetation characteristics of certain forest burn communities on the southern upland of Nova Scotia with observations on secondary succession. Dalhousie University, Halifax, Nova Scotia, Canada.

Matlack, G. R., D. J. Gibson, and R. E. Good. 1993. Clonal propagation, local disturbance, and the structure of vegetation: ericaceous shrubs in the pine barrens of New Jersey. Biological Conservation **63:**1–8.

McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data. Version 3.0. MjM Software Design, Gleneden Beach, Oregon.

Moore, J. M., and R. W. Wein. 1977. Viable seed populations by soil depth and potential site recolonization after disturbance. Canadian Journal of Botany **55:**2408–2412.

Pearson, V., and D. J. Read. 1973. The biology of mycorrhiza in the ericaceae: II. The transport of carbon and phosphorus by the endophyte and the mycorrhiza. New Phytologist **72:** 1325–1331.

Pregitzer, K. S., and S. C. Saunders. 1999. Jack pine barrens of the northern Great Lakes region. Pages 343–361 in R. Anderson, J. Fralish, and J. Baskin, editors. Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, New York.

Probst, J. R. 1988. Kirtland's warbler breeding biology and habitat management. United States Department of Agriculture, United States Forest Service General Technical Report NC-122. North Central Forest Experiment Station, St. Paul, Minnesota.

Probst, J. R., and J. P. Hayes. 1987. Pairing success of Kirtland's warblers in marginal vs. suitable habitat. Auk **104:**234–241.

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

Read, D. J., and D. P. Stribley. 1973. Effect of mycorrhizal infection on nitrogen and phosphorus nutrition of ericaceous plants. Nature **244:**81–82.

Rowe, J. S., and G. W. Scotter. 1973. Fire in the boreal forest. Quaternary Research **3:**444–464.

Scheiner, S. M. 1993. MANOVA: Multiple response variables and multispecies interactions. Pages 94–112 in S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York.

Simard, A. J., D. A. Haines, R. W. Bath, and J. S. Frost. 1983. The Mack Lake fire. United States Department of Agriculture, United States Forest Service General Technical Report NC-83. North Central Experiment Station, St. Paul, Minnesota.

Smith, D. W., and R. J. Hilton. 1971. The comparative effects of pruning by burning or clipping on lowbush blueberries in North-Eastern Ontario. Journal of Applied Ecology **8:**781–789.

Smith, E. 1979. Analysis of Kirtland's warbler breeding habitat in Ogemaw and Roscommon counties, Michigan. M. S. Thesis. Michigan State University, East Lansing.

Stribley, D. P., and D. J. Read. 1974. The biology of mycorrhiza in the ericaceae: IV. The effect of mycorrhizal infection on uptake of ^{15}N from labelled soil by *Vaccinium macrocarpon* Ait. New Phytologist **73:**1149–1155.

Trevett, M. F. 1956. Observations on the decline and rehabilitation of lowbush blueberry fields. Anonymous Maine Agricultural Experiment Station. Miscellaneous Publication 626.

Vander Kloet, S. P. 1976. A comparison of the dispersal and seedling establishment of *Vaccinium angustifolium* (the lowbush blueberry) in Leeds County, Ontario and Pictou County, Nova Scotia. Canadian Field Naturalist **90:**176–180.

Vander Kloet, S. P. 1985. Differences in vegetative and reproductive growth among Ontario, Nova Scotia and Newfoundland populations of *Vaccinium angustifolium* Aiton. American Midland Naturalist **113:**397–400.

Voss, E. G. 1996. Michigan flora. Cranbrook Institute of Science, Bloomfield Hills, Michigan.

Voss, E. G., and G. E. Crow. 1976. Across Michigan by covered wagon: a botanical expedition in 1888. Michigan Botanist **15:**3–71.

Walkinshaw, L. H. 1983. Kirtland's warbler: the natural history of an endangered species. Cranbrook Institute of Science, Bloomfield Hills, Michigan.

Wesley, S. L., N. M. Hill, and S. P. Vander Kloet. 1986. Seed banks of *Vaccinium angustifolium* Aiton on managed and unmanaged barrens in Nova Scotia. Le Naturaliste Canadien **113:**309–316.

Whitney, G. G. 1986. Relation of Michigan's presettlement pine forests to substrate and disturbance history. Ecology **67:**1548–1559.

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.