Spatial patterns of cone serotiny in *Pinus banksiana* in relation to fire disturbance

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Abstract

Fire disturbance effects on tree species distribution and landscape pattern have been widely studied. However, the effects of differences among fire regimes on the spatial pattern of genetic variability within a tree species have received less attention. The objectives of this study were to examine (a) whether the marked gradient in serotiny in *Pinus banksiana* along its southern range limit is related to differences in fire regimes and (b) at what scale serotiny varies most strongly in *P. banksiana* in the US Midwest. *P. banksiana* in the 450,000 ha Pine Barrens area in northwestern Wisconsin, USA showed a marked broad scale pattern in serotiny. The percentage of serotinous trees was highest in the northeast (mean 83%, S.D. 13.5) and lowest in the southwest (mean 9%, S.D. 3.7). Historic fire regimes were inferred from pre-European settlement (mid-1800s) vegetation data. Serotiny was highest in pine forests that exhibited stand-replacing fires, and lowest in savannas where more frequent but less intense ground fires occurred. The data presented in this study suggest possible spatial control of genetic variability within a tree species by an ecological process (disturbance) at the landscape-scale.
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1. Introduction

Disturbance processes, such as fire, affect ecosystems at various scales. Locally, fires alter species competition (Moloney and Levin, 1996) and diversity (Turner et al., 1997), and at broader scales, landscape heterogeneity (Heinselman, 1973; Romme, 1982; Turner, 1987). On a global scale, fires change the forest carbon balance (Kasischke et al., 1995) and atmospheric properties by emitting trace gases (Cahoon et al., 1992), thus affecting climate. Due to the importance of fire,

landscape patterns generated under natural conditions have been suggested as a guideline for ecosystem management (Attiwill, 1994; Fulé et al., 1997). However, the effects of differences in fire frequency and fire intensity on the spatial pattern of genetic variability within a tree species have received less attention.

A polymorphic genetic trait that is closely related to fire disturbance is cone serotiny in several *Pinus* spp. (McCune, 1988; Lamont et al., 1991; Rodriguez-Trejo and Fulé, 2003). Serotinous cones are closed with resin and remain in the crown until opened by the heat from fire (Beaufait, 1960; Johnson and Gutsell, 1993). It was noted early that within a stand, cone morphology often varies between trees, but individual trees commonly possess either serotinous

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or non-serotinous cones (Clements, 1910; Mason, 1915). Stand-level variability of serotiny has been related to differences in fire disturbance, and it was reported that serotiny levels were highest where fires were frequent (Givnish, 1981; Muir and Lotan, 1985; Motzkin et al., 2002). Models showed that the variability in serotiny in *Pinus contorta* can be the result of variability in fire regimes (Hartl, 1979; Perry and Lotan, 1979) and the same was found for a serotinous Australian *Banksia* species (Enright et al., 1998). The variability found in stand-level serotiny can exhibit strong spatial pattern. Serotiny in North American *Pinus* spp. exhibits spatial gradients both at broad (100–300 km, Smith, 1970; Schoenicke, 1976; Despain, 2001) and fine scales (<20 km; Ledig and Fryer, 1972; Givnish, 1981).

Both *P. contorta* (lodgepole pine) and *Pinus banksiana* (jack pine) exhibit spatial pattern in serotiny across their range (Smith, 1970; Schoenicke, 1976). *P. contorta* exhibits high stand-level serotiny across its range in the Rocky Mountains in Canada and the United States, but serotiny levels are low near the West Coast, and a 100–300 km wide transition zone occurs between these areas (Smith, 1970). In the case of *P. banksiana*, serotiny levels are continuously high (90–100%) across the Canadian Shield, but decline sharply along a 100–200 km border region near the southern edge of jack pine's range in Minnesota, Wisconsin and Michigan, USA, where serotiny levels are low (0–40%; Schoenicke, 1976). The reasons for this broad scale pattern in the US Midwest are not well understood. Environmental gradients failed to fully explain the pattern found in *P. banksiana* (Schoenicke, 1976). The marked serotiny differences of *P. banksiana* in the US Midwest have been interpreted as an indicator for two separate glacial refugia (Critchfield, 1985). To our knowledge, the broad scale serotiny patterns in the US Midwest have not been explicitly related to fire disturbance regimes, which is surprising given that serotiny allows species to survive in fire-prone environments (Johnson and Gutsell, 1993).

Several studies examined serotiny differences in North American *Pinus* spp. at finer scales and correlated these to various environmental variables (Ledig and Fryer, 1972; Givnish, 1981; Muir and Lotan, 1985; Tinker et al., 1994; Gauthier et al., 1996). *P. contorta* serotiny is strongly correlated with the type

of stand-initiating disturbance (Muir and Lotan, 1985), and with elevation (Tinker et al., 1994). *P. banksiana* stands on islands with frequent but non-lethal fires exhibit lower serotiny than stands on the mainland that exhibit lethal fires (62% serotiny with non-lethal fires, 74% with lethal fires, Gauthier et al., 1996). *Pinus rigida* (pitch pine) in the New Jersey Pine Barrens exhibit high serotiny levels in the center of the area, but serotiny levels decline sharply towards the edges of the outwash plain and this decline has been related to differences in fire frequency (Givnish, 1981). Fire frequency was presumably lower at the edges of the region because fire could not spread from the more mesic forests.

In summary, previous studies of spatial pattern of serotiny in several North American *Pinus* spp. indicated strong gradients across 100–200 km regions as well as fine-scale heterogeneity in smaller study areas (20–100 km wide). The objective of this study was to examine (a) whether the gradient in serotiny in *P. banksiana* along its southern range limit is related to differences in fire regimes and (b) at what scale serotiny varies most strongly in *P. banksiana* in the US Midwest.

2. Methods

2.1. The northwestern Wisconsin Pine Barrens study area

Serotiny in *P. banksiana* was surveyed across the 450,000 ha Pine Barrens region in northwestern Wisconsin (Fig. 1a) which is part of the border region where serotiny in *P. banksiana* declines markedly from northeast to southwest (Schoenicke, 1976). The Pine Barrens soils mainly formed on outwash material and are sandy and well drained; eolian processes winnowed silt and clay out of the sandy material during the Pleistocene (Hole, 1980). The southernmost portion of the Pine Barrens contains sandy loams over acid gravelly and stony glacial drift (Hole, 1980). All soils in the Pine Barrens are prone to drought, and the vegetation types present before Euro-American settlement reflected a variety of fire disturbance regimes (Radeloff et al., 1998, 1999). The southern Pine Barrens contained open savannas with large-diameter *Quercus macrocarpa* (bur oak),
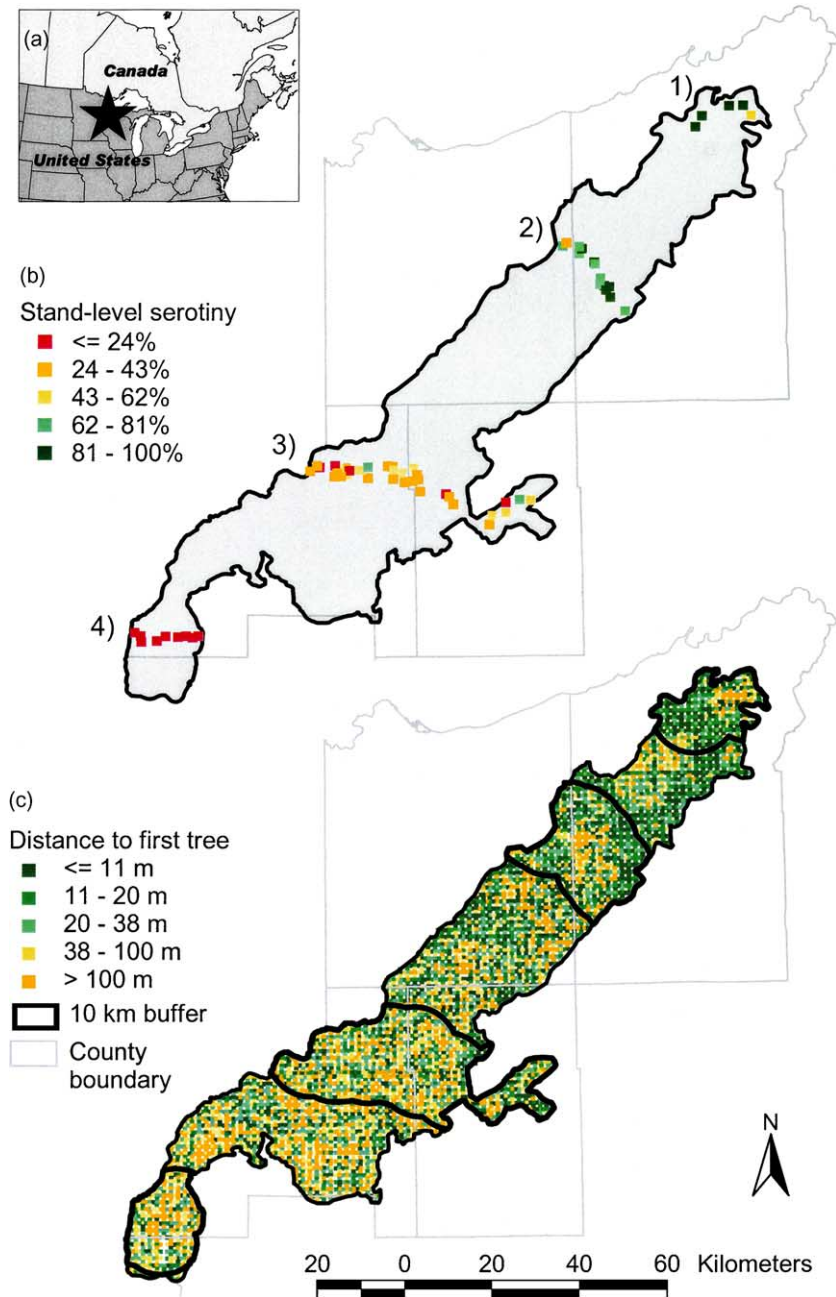
Fig. 1. (a) location of the study areas in North American marked with a star, (b) percentage of jack pine serotiny within stands along four transects the Pine Barrens outwash plain in northwestern Wisconsin, and (c) distances between section corner and first witness tree in the US General Land Office surveyor notes (~1855) with superimposed 10 km buffer surrounding the four transects. County boundaries are superimposed for reference.

Quercus ellipsoidalis (northern pin oak) and *Pinus resinosa* (red pine). The central Pine Barrens was almost exclusively dominated by jack pine forest of varying densities. Stem diameters were on average smaller than in the southern Pine Barrens. The northern Pine Barrens contained a mixture of *P. resinosa*, *P. banksiana* and *Pinus strobus* (white pine) forests interspersed with some hardwood species such as *Quercus rubra* (red oak), all of them exhibiting relatively large stem diameters (Radeloff et al., 1999).

Beginning in 1860, land cover and disturbances regimes in the Pine Barrens were altered drastically due to human land use (Radeloff et al., 1999). Extensive logging and farming removed almost the entire forest cover in the period between 1860 and 1930 (Murphy, 1931). Since the 1930s, natural forest regeneration, forest plantations and active fire suppression shaped the landscape and resulted in increased forest cover and higher forest densities (Radeloff et al., 1999).

2.2. Cone serotiny and fire disturbance data analysis

We sampled jack pine cone serotiny along four transects (Fig. 1b). Sampling plots were selected from county forest compartment maps and forest inventory data. All stands older than 30 years within 5 km of each transect were sampled. Younger stands were not sampled because serotinous cones do not always appear on juvenile trees (Gauthier et al., 1993). Known or suspected plantations were avoided because of uncertain seed origins. A total of 66 sampling points were located along four transects across our study area (Fig. 1b, transect 1: $n = 5$, 2: $n = 17$, 3: $n = 35$, 4: $n = 12$). A single forest stand could contain only one plot to avoid pseudoreplication. Plots were placed in the interior of jack pine stands that had regenerated naturally. Plots were sampled in late summer (August–September) of 1997. Plot size varied based on tree density. At each of the 66 sampled plots, the 50 mature trees that were closest to the plot center were visually classified into three classes: 'serotinous' (<30% open cones in the canopy), 'non-serotinous' (>70% open), or 'mixed' (30–70% open cones). Serotinous cones were identified by their closed scales; binoculars aided the examination of cones in the upper crown.

Only cones >3 m above the ground were assessed, because heat reflected from the ground may open lower serotinous cones. Serotiny levels were calculated per plot as the percentage of serotinous trees out of all trees sampled. Differences in serotiny levels across the Pine Barrens area were examined using ANOVA between transects.

To our knowledge, no direct data on historic fire regimes exist for the Pine Barrens region. Current forests reflect approximately 150 years of European settlement and their stand structure does not reflect pre-settlement disturbance regimes (Radeloff et al., 1999). Stumps that might have contained historic fire scars are no longer present. Therefore, historic fire disturbance regimes were inferred from pre-European settlement forest structure (Radeloff et al., 1998, 1999, Fig. 1c) and data on dominant tree life histories (Heinselman, 1973). A database in a Geographical Information System (GIS) was developed containing data for 5,367 survey points established by the US General Land Office in the 1850s. Surveyors recorded tree species, diameter, and distance to survey points for two–four trees per survey point (Radeloff et al., 1998). Distance to the first witness tree was used as a proxy of forest density (Cottam and Curtis, 1956). Average and standard deviation of this distance was calculated in 10 km buffers surrounding the four transects (Fig. 1c, transect 1: number of witness trees $n = 367$, 2: $n = 644$, 3: $n = 1168$, 4: $n = 352$).

It was also conceivable that differences in historic forest densities were not caused by differences in fire regimes but due to other environmental factors such as climate or soil type. Current forest densities were examined to test this alternative hypothesis. It was assumed that climatic limitations would persist in the current landscape if they were a direct cause for different tree densities at pre-settlement times. Forest densities in current forests of the white pine/red pine/jack pine forest types in our study area were derived from the US Forest Service Eastwide Forest Inventory Analysis (FIA; Smith, 1983). The FIA database contains standardized forest inventory information collected in randomly places in forest stands throughout our study area. Tree density (no. of trees/ha) were calculated by dividing the number of all live trees >12.5 cm dbh by the area of these stands.

Previous research on another serotinous pine species found a strong pattern in stand-level serotiny,

which was lowest in close proximity to the border of an sandy outwash plane (Givnish, 1981). We tested for significant spatial patterns within transects by calculating correlograms for transects 2 and 3. Spatial patterns, such as higher levels of serotiny in the center of transects, and lower levels at its ends, would result in positive spatial autocorrelation between plots. Significance of autocorrelation was tested using the method developed by Clayton and Hudelson (1995). The number of sampling points in transects 1 and 4 were limited by the availability of naturally regenerated jack pine stands >30 years old and did not permit calculation of correlograms.

3. Results

Mean serotiny levels in *P. banksiana* among transects 2, 3, and 4 were significantly different (Fig. 2a–c, $P < 0.0001$, $F = 110$, transect 1 was not included due to limited sample size, but was consistent with the serotiny gradient). The highest mean serotiny levels occurred in the northeast (transect 1: 82%) and lowest in the southwest (transect 4: 9%, Fig. 2a). Single trees with both serotinous and non-serotinous cones were uncommon (<2.5%) in all transects, except transect 3 (12.8%c).

Forest stand density prior to European settlement, estimated from US General Land Office survey notes, also exhibited a gradient across the study area, being highest in the northeast and lowest in the southwest Figs. 1c and 2d). Forest densities in the current landscape did not exhibit this gradient. Pine forest density in the southernmost county of the Pine Barrens (Burnett, 1,151 trees/ha) were similar to those in the northernmost County (Bayfield, 912 trees/ha).

Within transects, no spatial pattern of serotiny levels could be detected. The serotiny levels within the two longest transects (2 and 3) were not significantly autocorrelated ($P < 0.05$) at any distances (Fig. 3).
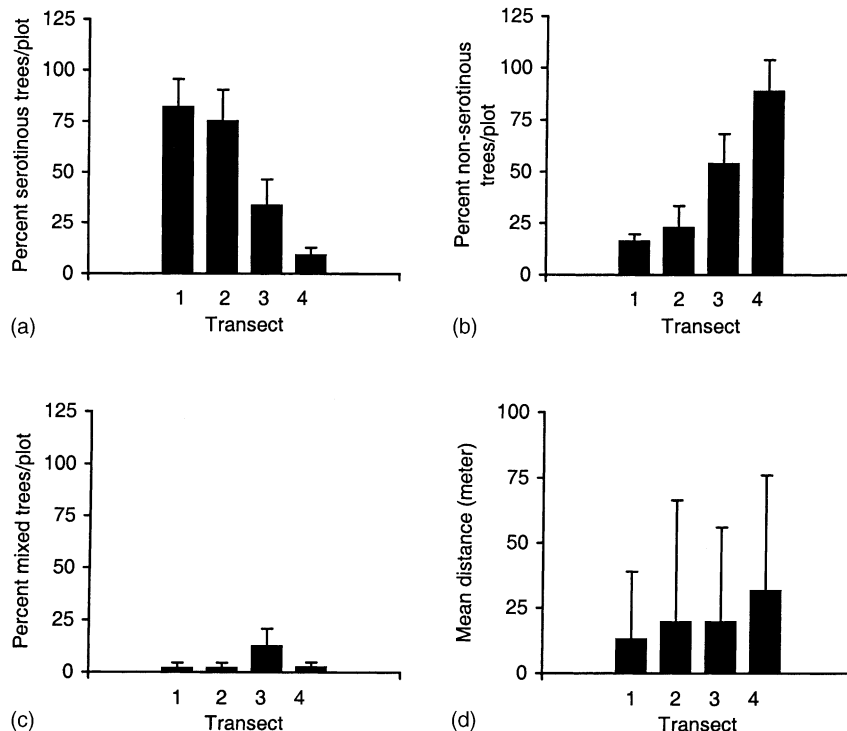

Fig. 2. Jack pine serotiny levels and forest density along the four transects. Mean percent (a) serotinous, (b) non-serotinous, (c) mixed-serotinous jack pine, and (d) mean distance to first witness tree (error bars represent one standard deviation).
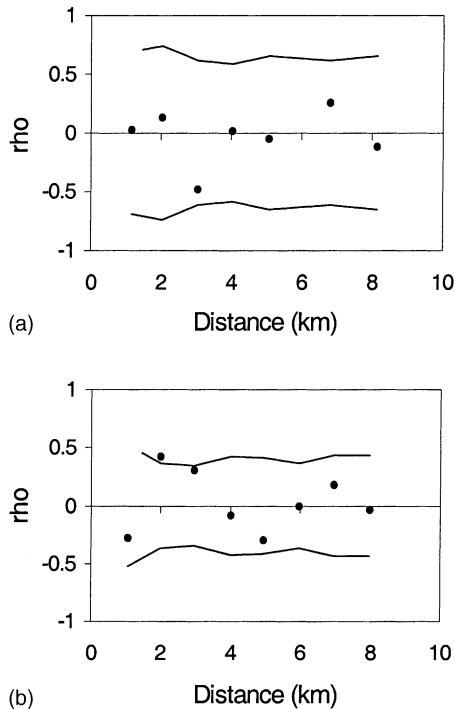
Fig. 3. Correlograms of stand-level serotiny in transects (a) 2 and (b) 3. Points between the lines indicate non-significant (*P* > 0.05) levels of spatial autocorrelation (Clayton and Hudelson, 1995).

4. Discussion and conclusions

Our results showed a strong gradient in stand-level serotiny in *P. banksiana* across our study area, with lowest serotiny levels in the southwestern portion and highest in the northeast, but no gradient in serotiny levels within each of the four transects. What can potentially explain these patterns?

The historical vegetation data, especially the observed forest density gradient, suggest a pre-settlement savanna-type landscape in the southwest Pine Barrens that was shaped by frequent, non-lethal ground fires (Radeloff et al., 1998). Tree cover here generally was too sparse to permit crown fires to spread. Higher tree density in the northeastern Pine Barrens was compatible with occurrence of lethal, stand-replacing crown fires (Fig. 1c).

Historic mean tree distances and current mean serotiny levels of the four transects were inversely related. Serotiny was lowest in the southwestern savannas, where historical tree densities were lowest

and non-lethal fires were common. In the denser northeastern forests, where lethal fires shaped vegetation pattern, serotiny levels were highest. Medium cone serotiny levels occurred in transect 3, located in the transition zone where both fire types could occur (Fig. 1b). Transect 3 also had the highest level of jack pine trees with both serotinous and non-serotinous cones (Fig. 2). We speculate that this may have allowed *P. banksiana* to survive and reproduce under varying fire intensities, however, this result was not statistically significant (*P* > 0.05).

No direct evidence of pre-settlement fire conditions, such as different stand structures or fire scars, exist in the current Pine Barrens. Instead, tree distance was used as a proxy for forest density and fire regimes were inferred from these data. The underlying assumption is that the historical forest density gradient across the Pine Barrens was caused by differences in the disturbance regimes.

Three other lines of evidence support this assumption. First, vegetation types at pre-settlement times (∼1850) indicate strong differences in fire frequency and intensity (Curtis, 1959). The southwestern Pine Barrens contained oak and red pine savannas and had a high abundance of herbaceous species commonly found in prairies dominated by very frequent fires (3–10 years return interval) that are non-lethal to fire adapted tree specie, such as oaks (Vogl, 1964). In contrast, the central Pine Barrens area was characterized by closed canopy *P. banksiana* ecosystems as well as large openings, a landscape pattern that is typical for frequent (10–70 years return interval) stand-replacing fires followed by dense regeneration (Heinselman, 1973) also typical for boreal forests (Johnson, 1992) and lodgepole pine forests in the western US (Turner et al., 1997). The northeastern Pine Barrens contained relatively dense forests of *P. resinosa*, *P. banksiana* and *P. strobes* forests interspersed with some hardwood species such as *Q. rubra* (Radeloff et al., 1999). Such a species mixture is typically found in areas where lethal, stand-replacing fires occur at lower frequencies (70–300 years return interval; Heinselman, 1973).

A second line of evidence is that the Pine Barrens region is part of a larger transition zone between dense forests to the North and northeast, in Canada and in the Upper Peninsula of Michigan, and open prairies to the southwest in southern Minnesota and Iowa

(Curtis, 1959). The SW–NE tree density gradient observed in this study is in agreement with these regional patterns (Ricketts et al., 1999).

And third, bark thickness in *P. banksiana* also exhibits a continental gradient, being significantly thicker in the southern part of its range (Schoenicke, 1976). This may be another species trait that permits tree survival where frequent, low-intensity ground fires occur that are not necessarily lethal to trees. An analysis of fire-adaptive traits across all pine species found that that serotinous pine species were not more likely to have thicker bark (Schwilk and Ackerly, 2001) suggesting that bark thickness and serotiny are adaptations to different fire regimes.

This leads to the conclusion that the Pine Barrens study areas exhibited at pre-settlement times three distinct fire regimes: very frequent but non-lethal ground fires in the South, frequent, lethal crown fires in the center and a medium frequency, lethal, crown fires in the North. There are several reasons for this gradient in fire frequency. First, the northern Pine Barrens are close to Lake Superior and precipitation is highest in this portion of the study area (Curtis, 1959). This potentially limits the number of days where fires can spread. Second, the northern Pine Barrens are hilly, whereas the central and southern Barrens have little topography (Murphy, 1931). The topographic variability in the North results in fine-scale soil variability and mesic valley bottoms that can form potential firebreaks. Third, soil productivity, while altogether low, is relatively highest in the southwestern portion of the Pine Barrens and prairie grasses are most abundant here (Vogl, 1964, Radeloff et al., 1998). This means that fire fuel for ground fires is available within a few years after a previous fire, whereas ground fires are less likely to spread soon after a fire in the Central and Northern Pine Barrens.

Factors other than the fire regime are unlikely to have been a direct cause for the observed gradients of tree density. Environmental factors that conceivably could cause lower tree density are soil productivity and climatic limitations. We observed lowest tree densities at pre-settlement times in the southwestern Pine Barrens. However, among the four transects, soil productivity is lowest in proximity to transect 2 in the northeastern Pine Barrens (Radeloff et al., 1998). This makes it unlikely that the observed tree density gradient is directly related to soil nutrient limitations.

Climate data exhibit a gradient, with higher precipitation in the North near Lake Superior and possible greater drought stress in the South (Curtis, 1959). However, this climate gradient does not result in lower tree density in the southern Pine Barrens in current forests. On the contrary, current pine forest densities in the southernmost county of the Pine Barrens was 26% higher than in the northernmost county. This suggests that drought stress is not a cause for the observed tree density gradient at pre-settlement times. However, climatic variation may be the cause for the observed differences in pre-settlement fire regimes and thus be an indirect cause for the pre-settlement forest density gradient. Also, climate itself cannot account for the observed cone serotiny gradient; maximum air temperatures in the SW Pine Barrens are not high enough to melt the resin of serotinous cones >3 m above the ground (Johnson and Gutsell, 1993).

At the regional scale, the difference in cone serotiny in Minnesota, Wisconsin and Michigan (Schoenicke, 1976) has been interpreted as an indication that two distinct jack pine populations migrated into the Lake States from different glacial refugia (Critchfield, 1985). We offer a more parsimonious explanation for the serotiny differences; our results suggest that differences in disturbance regimes over relatively short distances can explain the observed serotiny gradient. Furthermore, serotiny in a related North American pine species, *P. contorta* was correlated with stand-initiating disturbance (Muir and Lotan, 1985), suggesting that the frequency of cone serotiny can change within a few generations as stands regenerate following different disturbance regimes. It seems unlikely that serotiny differences among populations could have persisted since the last glaciation.

No evidence was found for fine-scale spatial pattern of serotiny within transects, there was no significant spatial autocorrelation within transects 2 and 3 (Fig. 3). Fine-scale spatial pattern of serotiny had previously been reported for *P. rigida* in the central New Jersey Pine Barrens, leading to the hypothesis that distance to outwash plain border determines fire frequency and thus serotiny level (Givnish, 1981). This hypothesis was rejected for *P. banksiana* in the study area. Even the six sampling plots that were almost isolated at the eastern edge of transect 3, an area that is divided by the Namekagon river, did not exhibit lower serotiny levels than the rest of that transect (Fig. 1b). It is unclear why

P. banksiana does not exhibit fine-scale patterns comparable to *P. rigida*. Possible reasons could be differences in gene flow between the two species, or steeper climatic gradients—and thereby also disturbance regimes—in the New Jersey Pine Barrens. Another possible difference is the dominant wind direction (SW) during fires. Wind direction may override the effect of location within the outwash plain.

It has previously been speculated that very high fire frequencies may not permit enough fuel accumulation thus resulting in fires that are not hot enough to open serotinous cones, and may therefore favor non-serotinous reproduction (Heinselman, 1973; Muir and Lotan, 1985). Decreasing levels of serotiny with increasing levels of non-lethal fires were reported by Gauthier et al. (1996), but the majority of *P. banksiana* (62%) was still serotinous in their study. Our data suggest that serotiny levels in *P. banksiana* can decrease to 0–20% in areas that are affected by very frequent, but non-lethal ground fires. A linear relationship between serotiny levels and fire frequency can only be assumed where crown fires prevail.

Variation in cone serotiny in our region corresponds to variation in fire disturbance regimes that occurred before this landscape was greatly altered by Euro-American settlement. Maintaining the genetic variability of species is crucial for their conservation and marginal habitat at range edges may exhibit higher rates of adaptive evolution (Holt, 1997) and thus deserve particular attention (Lesica and Allendorf, 1995). A mix of non-serotinous and serotinous trees ensures jack pine regeneration after both lethal or non-lethal fire disturbance. *P. banksiana* plantations, often created using seed from a single provenance, lack this diversity. Such stands are probably less resilient to future changes in fire regimes that may be induced by climate change (Clark, 1988, 1990).

Acknowledgements

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