

Seed rain, safe sites, competing vegetation, and soil resources spatially structure white pine regeneration and recruitment

Martin Dovčiak, Peter B. Reich, and Lee E. Frelich

Abstract: We tested the effects of seed rain, safe sites, soil depth, overstory, and shrub layer on the establishment and recruitment of white pine (*Pinus strobus* L.) in aspen mixedwoods of the western Great Lakes region, U.S.A. Germinant and seedling densities were positively related to seed rain and safe site characteristics that indicate moist conditions: high overstory basal area, decaying wood, and moss cover. Germinant and seedling densities were highest under dense overstory (>16 m²/ha) and were unrelated to shrub cover. Sapling recruitment was greatest under low overstory density (<16 m²/ha) and low shrub cover (<55%). On shallow soil (~14 cm), germinants and seedlings commonly occurred on soil depths <5 cm, but large saplings almost always occurred on soil depths >5 cm. On deeper soil (~21 cm), overstory white pines occupied the shallowest soils (~18 cm) of all major overstory species, indicating that competition may cause white pine recruitment into the canopy to be lower on deeper soils. White pine populations in the study were initially spatially structured by seed rain and safe sites but sapling growth and recruitment was structured by overstory density, shrub cover, and soil depth.

Résumé : Nous avons testé les effets de la dispersion aérienne des graines, des refuges, de l'épaisseur du sol, de l'étage dominant et de la strate arbustive sur l'établissement et le recrutement du pin blanc (*Pinus strobus* L.) dans une forêt mixte de peuplier de l'ouest de la région des Grands Lacs, aux États-Unis. La densité des germinants et des semis était positivement reliée à la dispersion aérienne des graines et aux caractéristiques des refuges indicatrices de conditions humides : surface terrière élevée de l'étage dominant, bois en décomposition et tapis de mousses. La densité des germinants et des semis était la plus forte sous un étage dominant dense (>16 m²/ha) et n'était pas influencée par le couvert d'arbustes. Le recrutement de gaules était le plus élevé sous un étage dominant de faible densité (<16 m²/ha) et un faible couvert d'arbustes (<55 %). Sur sol mince (~14 cm), les germinants et les semis se trouvaient le plus souvent sur des sols de moins de 5 cm d'épaisseur mais les gaules de forte dimension se trouvaient presque toujours sur des sols de plus de 5 cm d'épaisseur. Sur les sols plus profonds (~21 cm), les pins blancs de l'étage dominant occupaient les sols les plus minces (~18 cm) comparativement à toutes les principales espèces de l'étage dominant, indiquant que la compétition peut être responsable du plus faible recrutement du pin blanc dans le couvert sur les sols plus profonds. Dans cette étude, la dispersion aérienne des graines et les refuges déterminaient initialement la structure spatiale des populations de pin blanc mais le recrutement et la croissance des gaules étaient déterminés par la densité de l'étage dominant, le couvert d'arbustes et la profondeur du sol.

[Traduit par la Rédaction]

Introduction

Species composition of any given forest-tree community results from an interplay among ecological processes that influence seed production and dispersal, germination and early survival of seedlings, and growth and recruitment of advanced regeneration of individual tree species (cf. Greene et al. 1999). The distribution of seed rain of individual tree species determines the area available for their successful

establishment and provides a template for subsequent processes influencing germination, survival, growth, and recruitment (Clark et al. 1998; Nathan and Muller-Landau 2000; Parciak 2002). While seed-limited community dynamics are more likely to occur in early successional habitats and in early successional species (Turnbull et al. 2000), forests are spatially structured by tree falls (Runkle 1981; Kneeshaw and Bergeron 1998), large-scale disturbances (Heinselman 1973, 1981; Turner et al. 1997, 1998), and underlying physical environment (Grigal and Ohman 1975; Host et al. 1987), and as a result they encompass species and habitats of different successional status. Within these habitats, microsites such as moss patches, decaying wood, root plate pits and mounds, different patches of understory herbs, pockets of different soil depths, and zones of different shading may vary in their suitability for germination and early seedling survival (Maguire and Forman 1983; Houle and Phillips 1989; Stewart and Rose 1990; Cornett et al. 1997; Kuuluvainen and Juntunen 1998; Wright et al. 1998). Population and community dynamics consequently may be lim-

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ited by the availability of safe sites (Harper 1977). Once seedlings are established, ensuing forest dynamics may be fueled by competition for light, since forest-tree species differ in their response to light (Pacala et al. 1994; Kobe et al. 1995; Reich et al. 1998) or by belowground competition (Peterson and Squiers 1995), which may occur under conditions of limited belowground space (McConnaughay and Bazzaz 1991).

Seed dispersal behaviour differs among tree species (Greene and Johnson 1989; Clark et al. 1999), as does their ability to colonize suitable habitats in patchy environments (Kneeshaw and Bergeron 1998; Tanaka et al. 1998). The ability of seeds to reach habitats suitable not only for germination but also for long-term growth and survival has been recognized as a crucial adaptation (Finegan 1984). Consequently, some models of forest dynamics currently incorporate the fine-scale spatial distribution of individual trees to predict both the spatial pattern of seed rain and the spatial variation of light within stands (Pacala et al. 1993). Forest-tree species with relatively low shade tolerance, fast growth in gaps, and abundant and well-dispersed seed can theoretically exhibit long-term dynamics characterized by particularly complex responses to spatial variation in within-stand light levels (Pacala and Deutschman 1995), although actual data are scarce. The long-term dynamics of intermediately shade-tolerant species may be even harder to predict, as they tend to be outcompeted by faster growing shade-intolerant species in large gaps and by shade-tolerant species in deep shade (e.g., Walters and Reich 1996; Kruger and Reich 1997; Reich et al. 1998). The key to understanding complex long-term dynamics of an intermediately shade-tolerant species, such as white pine (*Pinus strobus* L.), is to understand the variation in habitat conditions that allow for establishment, survival, and growth of the individual life stages of the species. A recent spatial pattern analysis of a population of white pine revealed that different size classes of this species can occupy different neighborhoods within the forest, likely because they are spatially structured by different habitat conditions (Dovčiak et al. 2001).

The objective of this paper is to describe possible causes of the complex population dynamics of an intermediately shade-tolerant forest-tree species by integrating the study of seed rain, safe sites, and broader scale habitat conditions that may spatially structure its regeneration and recruitment. To achieve these objectives we tested a set of environmental factors for their potential influence on the spatial distribution of different white pine size classes in forest stands.

First, we tested two alternative hypotheses (1 vs. 2) to determine what environmental factors are responsible for the initial spatial patterns in early regeneration stages.

- (1) Seed rain limitation hypothesis: The distribution of white pine germinants and seedlings is determined only by the distribution of seeds on the forest floor. Although the distribution of germinants, more so than seedlings, could be expected to be closely related to seed rain, seedling distribution integrates the variation in seed rain over several seed dispersal seasons, thus extending the temporal dimension of the analysis.
- (2) Safe sites limitation hypothesis: White pine germinant and seedling distributions depend on the distribution of microsites, which may differ in their suitability for ger-

mination and early survival (e.g., patches of moss, grass, different herbs, decaying wood, deep soil pockets), rather than on seed rain.

Second, we tested three additional independent (non-mutually exclusive) hypotheses (3–5), each related to one of the environmental factors tested in hypotheses 1 and 2 that may influence growth and recruitment among individual white pine size classes, and thus potentially reshape the spatial distribution of different sapling size classes relative to the initial patterns of germinants and seedlings:

- (3) Shallow soil refugia hypothesis: Regardless of the spatial pattern of early regeneration, white pine saplings recruit into larger size classes, and eventually into the canopy, more successfully on shallow soils where white pine can outcompete other tree species.
- (4) Negative canopy effects hypothesis: Regardless of the initial distribution of white pine germinants and seedlings, the recruitment of saplings into larger size classes is more successful in areas with sparse overstory canopy.
- (5) Shrub recruitment filter hypothesis: Regardless of canopy and soil depth effects, white pine recruitment into intermediate size classes is dependent on gaps in the understory woody layer.

Materials and methods

Study area

The study plots are located within upland areas of the western Great Lakes region centered at ~47°50'N and ~92°00'W. The region is a mosaic of wetlands, glacial lakes, rolling hills, and rock outcrops ranging in altitude from ~340 m to ~770 m above sea level. Substrate is mostly granitic Canadian shield covered with shallow and rocky soils (Ahlgren 1969). Upland soils, mostly Inceptisols and Entisols and a few Spodosols, are derived from sandy and gravelly loam glacial deposition (United States Department of Agriculture, Soil Conservation Service, Soil Survey Staff 1960). The climate is cold-temperate continental with an average length of frost-free season between 96 and 131 days (Heinselman 1996), mean July temperature 17 °C, mean January temperature -17 °C, and snow cover from early November to late April (Ahlgren 1969).

Forests of the region are a mosaic of *Populus tremuloides* Michx., *Populus grandidentata* Michx., *Betula papyrifera* Marsh., *Pinus strobus* L., *Pinus resinosa* Aiton, *Pinus banksiana* Lambert, *Quercus rubra* L., *Acer rubrum* L., *Picea mariana* (Mill.) BSP, *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill., *Larix laricina* (DuRoi) K. Koch., and *Thuja occidentalis* L. (Grigal and Ohmann 1975). White pine often assumes a dominant canopy position, and prior to its extensive logging in the late 19th century it was the most dominant species in terms of basal area (20.1%) (Friedman et al. 2001). White pine stands had a complex fire regime before fire suppression occurred during late 19th century settlement of the area; light surface fires occurred every 20–40 years and stand-killing fires occurred every 150–200 years (Heinselman 1973, 1981). Dovčiak et al. (2001) provide further details on the study area and species.

Table 1. Basal area (BA; m²/ha) of tree species in the detailed plot and pooled plots.

| Species | Detailed plot BA | Pooled plots BA |
|----------------------------------|------------------|-----------------|
| <i>Populus</i> sp. | 7.2 | 12.8 |
| <i>Pinus strobus</i> L. | 5.0 | 3.0 |
| <i>Acer rubrum</i> L. | 7.8 | 2.5 |
| <i>Betula papyrifera</i> Marsh. | 0.8 | 2.0 |
| <i>Abies balsamea</i> (L.) Mill. | 0.6 | 2.0 |
| <i>Pinus banksiana</i> Lamb. | 0.4 | 1.2 |
| <i>Picea mariana</i> (Mill.) BSP | — | 1.0 |
| Other species | 1.2 | 1.6 |
| Total | 23.0 | 26.1 |

Table 2. Number of juvenile white pine individuals of different size classes per hectare in the detailed plot and pooled plots.

| Size class | Detailed plot | Pooled plots |
|------------------------|---------------|--------------|
| Germinants <1 year old | 2122 | 3959 |
| Seedlings <0.5 m tall | 4916 | 3541 |
| Saplings 0.5–1 m tall | 914 | 561 |
| Saplings 1–2 m tall | 824 | 218 |
| Saplings 2–4 m tall | 446 | 134 |
| Saplings >4 m tall | 143 | 124 |

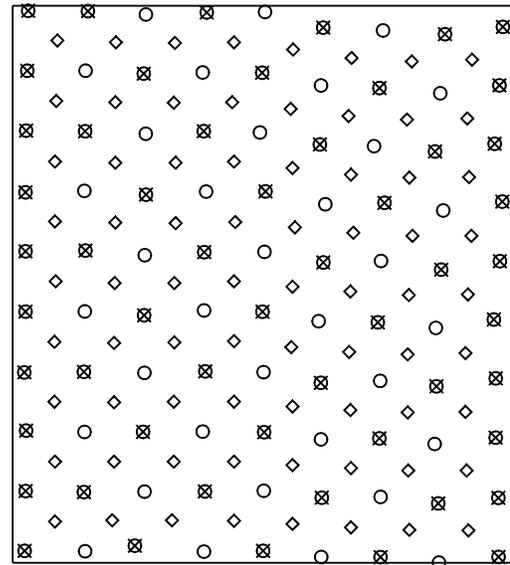
Study design and data collection

Five study plots were randomly placed within selected mature aspen stands that contained canopy white pines and white pine saplings in the understory, within ~30 km from the city of Ely in northeastern Minnesota, U.S.A. The greatest distance between any two plots was ~45 km. The largest plot (90 m × 80 m), used in a previous study (Dovčiak et al. 2001), will be referred to as the detailed plot. The four remaining plots are 90 m × 8–16 m belts (wider where white pine saplings were less abundant). These plots were pooled together to verify the generality of the observed patterns across the broader landscape, and they will be referred to as the pooled plots. Average overstory basal area was comparable in the detailed and pooled plots (~23 vs. 26 m²/ha, respectively). The upper canopy of both plots was dominated by aspen (mostly *Populus tremuloides* and some *Populus grandidentata* Michx.) and the lower canopy of the detailed plot was dominated by red maple (*Acer rubrum*). Other tree species had lower basal area (Table 1). The abundance of juvenile white pines by size class approximately followed an inverse J-curve in both the detailed and pooled plots (Table 2).

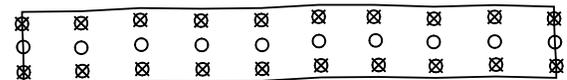
The environment of all plots was characterized using circular subplots (environmental subplots; radius = 1 m) in the summer of 1997. In the detailed plot, 90 environmental subplots were placed every 10 m on a 90 m × 80 m grid (10 m × 10 m mesh size). Seed traps were placed next to every other environmental subplot, except at the two north-south plot edges where seed traps were placed next to every subplot (a total of 56 traps). In 1998, the original grid was supplemented by 72 additional subplots (each located amidst

Fig. 1. Study plot layout of the detailed plot (A) and one of the belt pooled plots (B).

A Detailed plot



B One of the pooled plots



- environmental-overstory subplot
- × seed trap next to environmental subplot
- ◇ additional environmental subplot

four previously established subplots) (Fig. 1A). In each of the pooled plots, the environmental subplots were placed 10 m apart along the belt length (10 subplots over 90 m) and 4 m apart along the belt width (2–4 subplots over 8–16 m), for a total of 20–40 subplots per plot. Seed traps were placed along the belt length next to all 10 environmental subplots at both belt edges (20 seed traps per plot) (Fig. 1B). Seed traps were constructed from wire and milling bags and resembled an inverted cone with a catchment area of ~0.25 m². Traps were placed within plots in early August 1997 and seeds were collected in late October 1997. Since a low seed crop in 1997 resulted in only a few seeds, seed collection was repeated in 1998.

On all environmental subplots, percent cover was visually estimated to the nearest 5% for shrub layer vegetation (understory woody vegetation <2.5 m tall), tall herbs (>0.5 m), short herbs (<0.5 m), grass, moss, decaying wood, and bare rock. Percent cover was also estimated for those understory woody species that covered ≥25% of a subplot. Soil depth was measured using a steel rod with 0–40 cm scale at the

subplot center and at four locations ~30 cm away from the center along four cardinal directions. Depths >40 cm were unusual and were recorded as 41 cm. Overstory composition and basal area were characterized by the variable plot method (Bitterlich 1984) on overstory subplots centered on the environmental subplots. In the detailed plot, overstory basal area was measured only on the original 90 subplots and was interpolated (from four nearest neighbors) for the remaining 72 subplots. The variable plot method was selected because it weights trees based on their size (diameter); large trees with potentially greater significance (e.g., shading, competition) are sampled within a larger area than small trees. Since we used a basal area factor of 2, the majority of overstory trees were sampled within 7–10 m and large superdominant trees within 15 m from the center of each overstory subplot.

Juvenile white pine individuals (<20 cm DBH) were divided into six size classes: (1) germinants that germinated in the year of survey (1997) (GRM); (2) seedlings ≥ 1 year old and <0.5 m tall (SDL); (3) saplings ≥ 0.5 m and <1 m tall (SPL1); (4) saplings ≥ 1 m and <2 m tall (SPL2); (5) saplings ≥ 2 m and <4 m tall (SPL3); and (6) saplings ≥ 4 m tall (SPL4). Germinants and seedlings were counted within environmental subplots, and all environmental subplots and white pine saplings (SPL1–4) were mapped using a laser surveying station (DT-100, Topcon, Tokyo, Japan). All white pine saplings were tagged within pooled plots. Because of the large number of saplings in the detailed plot, saplings were tagged only within 90 m belts centered on nine parallel north–south transects that connected environmental subplots. Along these transects, saplings 0.5–1 m tall (SPL1), which were the most abundant sapling size class, were tagged within 1 m wide belts; saplings 1–2 m tall (SPL2), which were less abundant, were tagged within 2 m wide belts; and saplings >2 m tall (SPL3 and SPL4) (least abundant) were tagged within 4 m wide belts.

The approximate age of all tagged saplings was determined by counting the number of branch whorls or terminal bud scars. The length of the three annual height increments (terminal shoots) that preceded the uncompleted growing season (1997) was determined for tagged saplings <2 m tall (SPL1 and SPL2). Sapling height and basal diameter (~1 cm above the ground surface) were measured for tagged saplings <4 m tall (SPL1–SPL3), and DBH was measured for tagged saplings >4 m tall (SPL4). Soil depths were measured around all tagged saplings; a central soil depth measurement was located immediately next to the sapling stem. Circular subplots (sapling subplots; radius = 1 m) were established around tagged saplings 0.5–2 m tall (SPL1 and SPL2) so that a sapling was at the subplot center, and shrub cover layer was characterized in the same way as in the environmental subplots. All saplings occurred within 5 m of the nearest overstory subplot center and thus they were assigned the overstory basal area of that overstory subplot (radius ~7–15 m).

Data analysis

We tested 10 environmental factors (seed rain density and nine habitat characteristics) for their potential to influence the spatial patterns of white pine germinants and seedlings (hypotheses 1 and 2). The nine habitat characteristics tested

were overstory basal area, soil depth, and percent cover of tall herbs, short herbs, moss, decaying wood, rock surface, shrub layer, and *Corylus cornuta*. The most significant predictors among these factors were identified.

At sapling stage not all environmental factors were tested, as some of them are hard to interpret. Testing the sapling-seed rain relationship would not be accurate, given the temporal lag between seed rain measurements and the time since sapling establishment (~9–23 years ago; Dovčiak et al. 2001). Testing the influence of ground cover (e.g., tall herbs, short herbs, decaying wood, rock surface, moss) on saplings using short-term data would also not be conclusive. Saplings occupied their locations long enough, and are large enough (up to 20 cm DBH) that any association between them and ground cover could be due to either ground-cover effects on sapling survival and growth, or sapling effects on ground cover (personal observation; cf. Kuuluvainen and Pukkala (1989) for effects of larger trees). Thus, only three of the 10 environmental factors (i.e., soil depth, overstory basal area, shrub cover) were tested at sapling stage (hypotheses 3–5).

The role of seed rain and safe site characteristics in the early stages of white pine regeneration (hypotheses 1 and 2) was studied by regressing response variables — germinant and seedling densities within environmental subplots — against environmental factors separately for the detailed and pooled plots. The analysis of germinant densities in the pooled plots could be done for only two out of the original four plots. A tree harvest precluded seed collection in one of the plots in 1998, and another plot was excluded from the analysis because of an extremely and unusually low number of germinants (only three germinants, all of them in a single subplot). Before running the regressions, safe site characteristics were transformed where needed to best approximate a normal distribution, yielding the following predictors: Tukey-transformed seed density (per square metre); square root transformed short herb cover; natural logarithm transformed covers of *Corylus cornuta*, moss, tall herbs, rock surface, and decaying wood; and untransformed average soil depth, overstory basal area of live trees, and overall shrub layer cover. The response variables — germinant and seedling counts on environmental subplots — were transformed using natural logarithms. Since the number of predictors and two-way interactions was high relative to the number of data points, we used stepwise regression with mixed selection of variables to select only those individual predictors that were significant at $p = 0.1$. The selected variables were then used in multiple linear regression analyses that incorporated all relevant interaction terms.

Field data often display a high degree of spatial autocorrelation, potentially leading to violation of the assumption of independence. Regardless of the spatial structure of variables, spatial structure in regression residuals has been widely used in ecological studies to distinguish between independence regression models versus autoregressive (AR, SAR, CAR) or geostatistic (i.e., exponential, Gaussian) models (Keitt et al. 2002). The spatial structure of residuals is described by residual variograms or correlograms (e.g., Verdú and García-Fayos 1998; Gumpertz et al. 2000; Keitt et al. 2002). A lack of residual spatial structure (flat variogram or correlogram) indicates that residuals are spatially independent (independence model) and regression coefficients

Table 3. Best linear regression models for the density of white pine germinants and seedlings relative to seed rain and habitat characteristics in the detailed plot and pooled plots.

| Analysis | Predictors | Coefficient estimates | Coefficient standard error | Predictor p | Partial r^2 | Overall regression | |
|-----------------------------|------------------------------|-----------------------|----------------------------|---------------|---------------|--------------------|---------|
| | | | | | | R_{adj}^2 | p |
| Germinants on detailed plot | Tukey (seed density) | 0.0386 | ± 0.0148 | 0.0107 | 0.06 | 0.18 | <0.0001 |
| | ln(decaying wood) | 0.1624 | ± 0.0426 | 0.0002 | 0.14 | | |
| Seedlings on detailed plot | Overstory BA | 0.0419 | ± 0.0078 | <0.0001 | 0.22 | 0.32 | <0.0001 |
| | ln(moss cover) | 0.2217 | ± 0.0693 | 0.0019 | 0.07 | | |
| | BA \times moss interaction | 0.0241 | ± 0.0241 | 0.0056 | | | |
| Seedlings on pooled plots | Tukey (seed density) | 0.0856 | ± 0.0291 | 0.0047 | 0.09 | 0.15 | 0.0027 |
| | ln(moss cover) | 0.2784 | ± 0.0900 | 0.0202 | 0.10 | | |

Note: Only R_{adj}^2 values are reported to adjust for the number of predictors. BA, basal area.

are unbiased estimates of their true value. If regression residuals show spatial structure (spatial dependence), then an appropriate autoregressive or geostatistic model should be used to produce a valid regression fit (e.g., Keitt et al. 2002). In testing the significance of correlation coefficients between any two variables, spatial autocorrelation in variables, instead of in residuals, needs to be explicitly incorporated to prevent underestimation of type I errors (e.g., Dutilleul 1993; Legendre et al. 2002). If this is not done, the significance test of the correlation coefficient of the variables may be invalid (if both variables are spatially autocorrelated), although the significance is not affected if one of the variables is not spatially autocorrelated (Legendre et al. 2002). In our case, checks using variograms and Moran's I correlograms show that both the residuals and the response variables (germinant and seedling densities) are not spatially autocorrelated at the scale of the study, and thus the independence regression model produces unbiased coefficient estimates and correct p values.

To clarify the role of soil depth and overstory density in white pine recruitment (hypotheses 3 and 4) we tested whether individual white pine size classes were associated with different values of these variables using the nonparametric Wilcoxon rank sum test. Using this test, we further examined whether sapling age, diameter (basal area, DBH), or average annual height increment differs according to high vs. low overstory density and high vs. low understory shrub cover (hypotheses 4 and 5).

Results

Regeneration relative to seed rain and safe sites

Germinant density in the detailed plot was positively related to seed rain density and cover of decaying wood (Table 3, Fig. 2). The partial r^2 from added variable analysis shows that most of the explained variation could be accounted for by the decaying wood cover, followed by seed rain density (Table 3, Figs. 2A and 2B). The semivariogram of residuals from the complete model with both predictors does not show any spatial structure (Fig. 2C) implying spatial independence of residuals. In the analysis of germinant densities in the pooled plots, no significant predictors emerged, probably because sample size was significantly reduced because of missing seed rain data and low germinant number in one of the study plots.

In the detailed plot, seedling density was positively related to overstory basal area of living trees (all species pooled), moss cover, and the positive interaction of these two predictors (Table 3). Most of the explained variation could be accounted for by the overstory basal area of living trees, while moss cover explained less variation (Table 3, Figs. 3A and 3B). This model may be considered final since the residuals are not spatially correlated (Fig. 3C). Although seed rain density does not seem to be an important predictor of seedling density in this analysis, seed rain is positively correlated with live overstory basal area (Pearson's correlation coefficient is 0.46), suggesting that seed rain may be partially responsible for the significance of live overstory basal area as a predictor. Replacing the live overstory basal area by seed rain density still yields a significant fit ($p < 0.0002$) but it explains less variation ($R_{\text{adj}}^2 = 0.16$). Thus, it appears that live overstory basal area (in addition to seed rain) positively influences seedling density in this plot.

In the pooled plots, seedling density was positively related to seed rain density and moss cover (Table 3). Seed rain and moss explained approximately equal amounts of variation (Table 3, Figs. 4A and 4B), producing spatially uncorrelated model residuals (Fig. 4C). Notably, moss cover was related to seedling density in the same way in the pooled plots as in the detailed plot, and it explained a similar amount of variation in seedling density in both analyses (cf. coefficient estimates and partial r^2 , Table 3). In addition, the influence of seed rain on seedling density in the pooled plots was not significantly different from the influence of seed rain on germinant density in the detailed plot (cf. coefficient estimates and their standard errors, Table 3).

White pine distribution relative to soil depth

Overall overstory density was not significantly related to soil depth in either of the plot types (Fig. 5A). However, in the pooled plots, which had greater average soil depth (~21 cm) than the detailed plot (~14 cm), the major species of adult overstory trees were associated with different average soil depths: white pine with the shallowest soils (~18 cm), red maple with the deepest soils (~24 cm), and aspen with soils of intermediate depth (~22 cm) (Fig. 5B; pooled plots). On soil depths <15 cm, ~40% of overstory white pines and only ~20% of overstory red maples occurred, whereas on depths >25 cm, just ~25% of white pines but as many as ~52% of red maples occurred. Thus, it ap-

Fig. 2. Regression model for germinant density in the detailed plot. Added variable plots show the influence of significant predictors — decaying wood cover (A) and seed density (B) — upon germinant density. Semivariogram (C) shows that model residuals do not have any spatial structure.

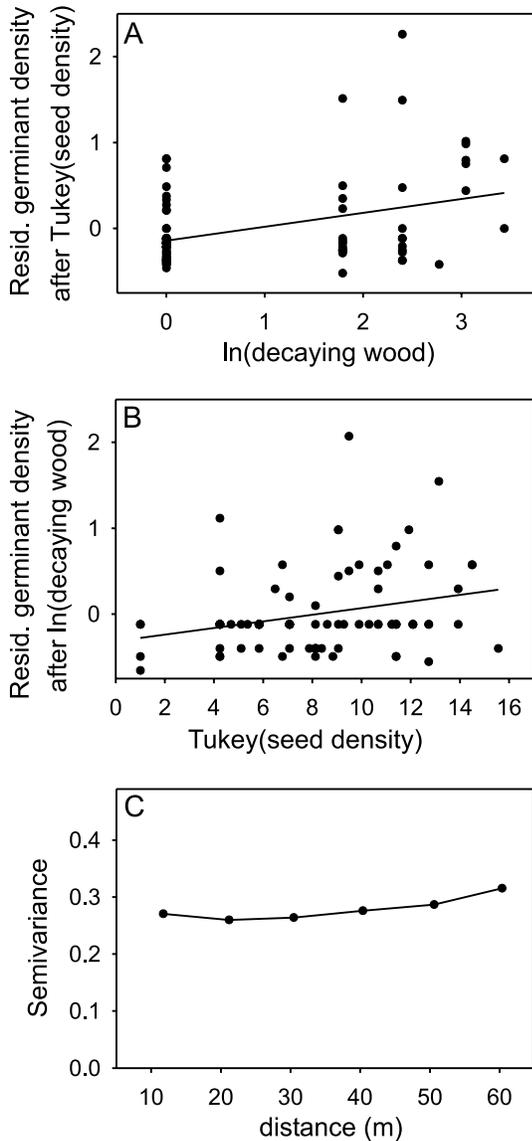
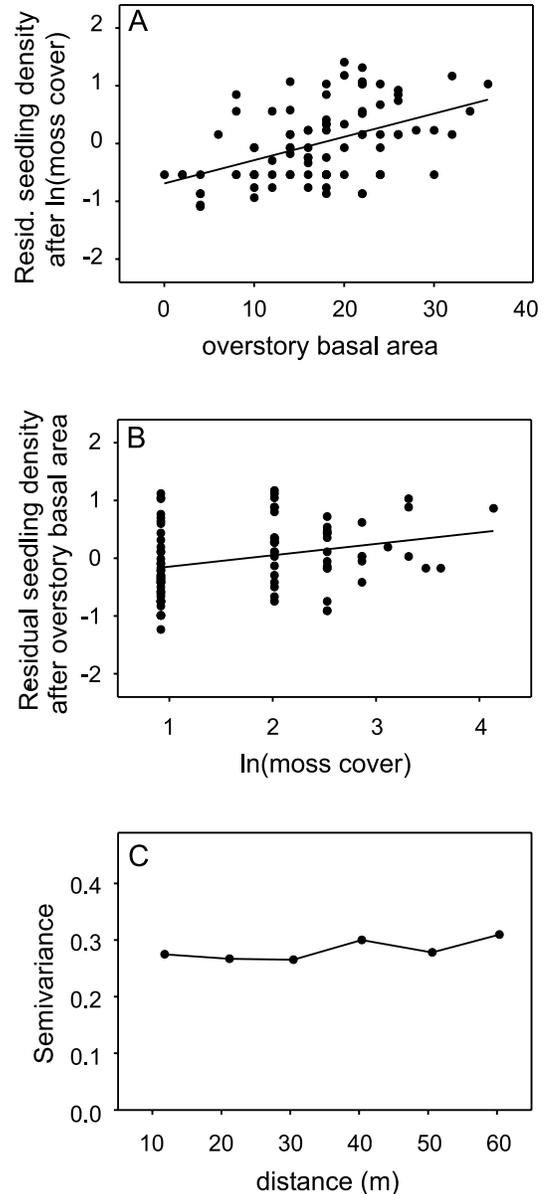


Fig. 3. Regression model for seedling density in the detailed plot. Added variable plots show the influence of significant predictors — overstory basal area (A) and moss cover (B) — upon seedling density. Semivariogram (C) shows that model residuals do not have any spatial structure.

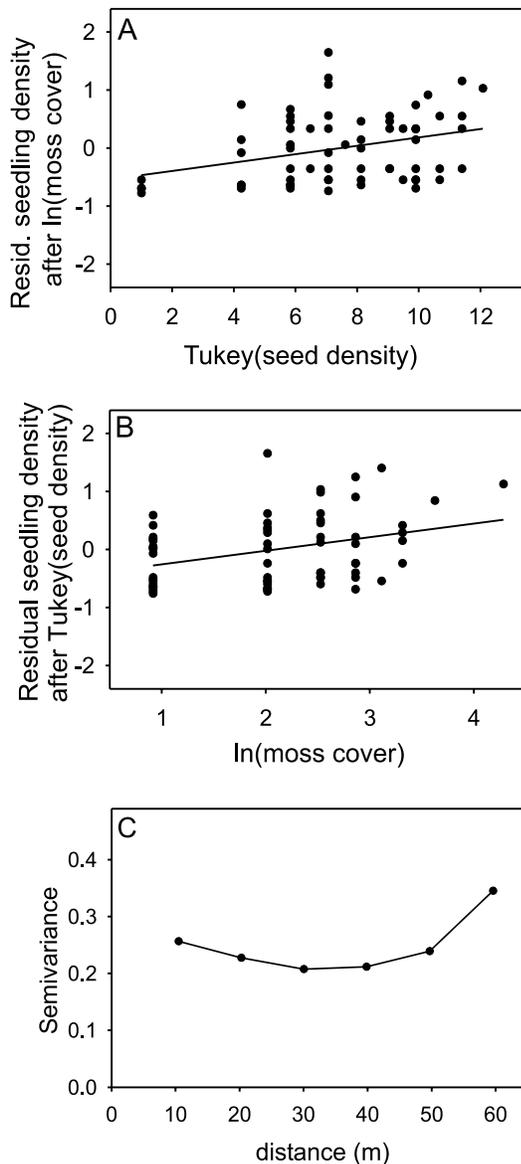


pears that white pine has a competitive advantage over red maple and aspen on shallower soil. Soil depth influence on major species of adult overstory trees was not observed in the detailed plot (Fig. 5B; detailed plot). This could be due to the fact that soil depth measurements were not possible directly underneath adult overstory trees because of difficulties in distinguishing bedrock from large tree roots; overstory subplot soil depth measurements were used instead. These measurements may have missed spatially restricted deep soil pockets directly underneath adult overstory red maple and aspen.

Although overstory white pines were associated with the shallowest soils of all overstory tree species in the pooled plots, extremely shallow soil may limit white pine recruitment in earlier stages. In the generally shallow detailed plot,

saplings were associated with progressively deeper soils as they increased in size (Fig. 5C; detailed plot). The average soil depth increased from 14 cm (under seedlings) to 18 cm (under large saplings). While 20% of the area has extremely shallow soil (<5 cm) and contains 15% of seedlings, only ~2.5% of tall saplings (>2 m) occur there. Thus, it appears that seedlings occurring on extremely shallow soils cannot recruit to advanced sapling stage. On the deeper soil of the pooled plots, juvenile white pine size classes were not associated with differing soil depths. Instead, they all occurred on average soil depths (~21 cm; Fig. 5C; pooled plots). Soil depth associations of saplings and adult overstory trees were not compared because different methods were employed in

Fig. 4. Regression model for seedling density in the pooled plots. Added variable plots show the influence of significant predictors — seed rain density (A) and moss cover (B) — upon seedling density. Semivariogram (C) shows that model residuals do not have any spatial structure.



measuring soil depths. Soil depths were measured directly under each sapling but, as mentioned above, soil depth measurements for overstory trees were taken from overstory subplots (i.e., not directly next to the tree stem).

Sapling recruitment relative to overstory density

In the pooled plots, the mean basal area of live trees was approximately equal above all seedling and sapling size classes; however, in the detailed plot, mean basal area significantly decreased with increasing size class (Fig. 6). In the detailed plot, 30–40% of seedlings (SDL and GRM), as opposed to only ~10% of the largest saplings (SPL4), occurred within high forest density (32–48 m²/ha) (Fig. 7A). The majority (~55–70%) of each size class grew under the intermediately dense overstory (16–32 m²/ha), which occupied most

of the detailed plot (Fig. 7B) and most of the pooled plots. In the detailed plot, low overstory density (<16 m²/ha) represented ~20% of sapling habitat but contained as much as ~35% of the largest saplings (SPL4) (Fig. 7C). In the pooled plots, only 4.5% of the overstory was low density, which may explain the lack of a higher percentage of large saplings in this overstory density category.

To further examine the influence of overstory density on sapling recruitment, we studied size and age distributions of saplings in individual size classes in the three different overstory density categories. In the detailed plot, the size (basal area and DBH) of saplings 2–4 m and >4 m tall (SPL3 and SPL4) was significantly greater under low overstory density (<16 m²/ha) than under high overstory density (>32 m²/ha), while saplings 0.5–2 m tall (SPL1 and SPL2) did not significantly differ in size under different overstory densities (Fig. 8A; detailed plot). In addition, in the detailed plot, saplings >1 m tall (SPL2–4) that grew under low overstory density were younger than those under medium or high overstory density (Fig. 8B; detailed plot). In the pooled plots, we could only analyze medium and high overstory density categories, since no saplings where we measured size and age occurred under the rare low overstory density category. The lack of difference in size or age of saplings 0.5–4 m tall (SPL1–3) between these two overstory densities in the pooled plots shows the same trend as was observed in the detailed plot for these two overstory density categories (Figs. 8A and 8B; pooled plots). Moreover, the DBH of the tallest saplings (SPL4) in the pooled plots was significantly greater under medium than high overstory density, further confirming the trend visible in the detailed plot.

Sapling recruitment relative to understory shrub layer

Since both overstory and understory modify the light regime and compete directly with saplings 0.5–2 m tall, we compared the effects of four combinations of overstory basal area (high and low, defined as equal or greater than and less than the median value of 24 m²/ha) and understory cover (high and low, defined as equal or greater than and less than the median value of 55% cover) on average sapling height increments (calculated for individual saplings from three terminal shoot lengths). Across both the detailed plot and pooled plots, height growth was better in the combination of low overstory basal area and low understory cover than in either of the combinations with high understory cover (Fig. 9). This difference in height growth was statistically significant in the detailed plot when tested against all the other overstory–understory combinations together ($p = 0.0328$). In the pooled plots, the sapling height increments were greater in areas with low understory cover than in areas with high understory cover, regardless of overstory basal area (Fig. 9). The lack of influence of the overstory in the pooled plots may be due to the fact that the pooled plots lack the open, low forest density (<16 m²/ha) that was shown in the preceding sections to play an important role in sapling growth and recruitment.

To control for the influence of sapling size, these analyses were done separately for saplings 0.5–1 m tall and 1–2 m tall. There were no statistically significant trends in the detailed plot where height increments were measured for a subsample of saplings, but in the pooled plots, where height

Fig. 5. Mean soil depth associated with (A) different overstory density classes, (B) major canopy tree species, and (C) different white pine seedling and sapling size classes. Broken line gives mean plot soil depth. High forest density is defined as 32–48 m²/ha, medium as 16–32 m²/ha, and low as 0–16 m²/ha; the pooled plots contained almost no low forest density. Abbreviations for major canopy tree species are as follows: *Populus* sp. (POPSP), *Acer rubrum* (ACRU), *Pinus strobus* (PIST). White pine size classes are as follows: germinants that germinated in the year of the survey (GRM), seedlings >1 year old but <0.5 m tall (SDL), saplings ≥0.5 and <1 m tall (SPL1), saplings ≥1 and <2 m tall (SPL2), saplings ≥2 and <4 m tall (SPL3), saplings ≥4 m tall but <20 cm DBH (SPL4). The differences in soil depths were tested using the Wilcoxon rank sum test. Statistically significant differences were marked with different letters above their corresponding bars. Where the same letter occurs above two different bars there is a lack of statistically significant difference between the two bars. Letters were omitted for the sake of simplicity if there were no significant differences between any bars in a single graph. An asterisk marks results that were significant at Bonferoni corrected significance levels.

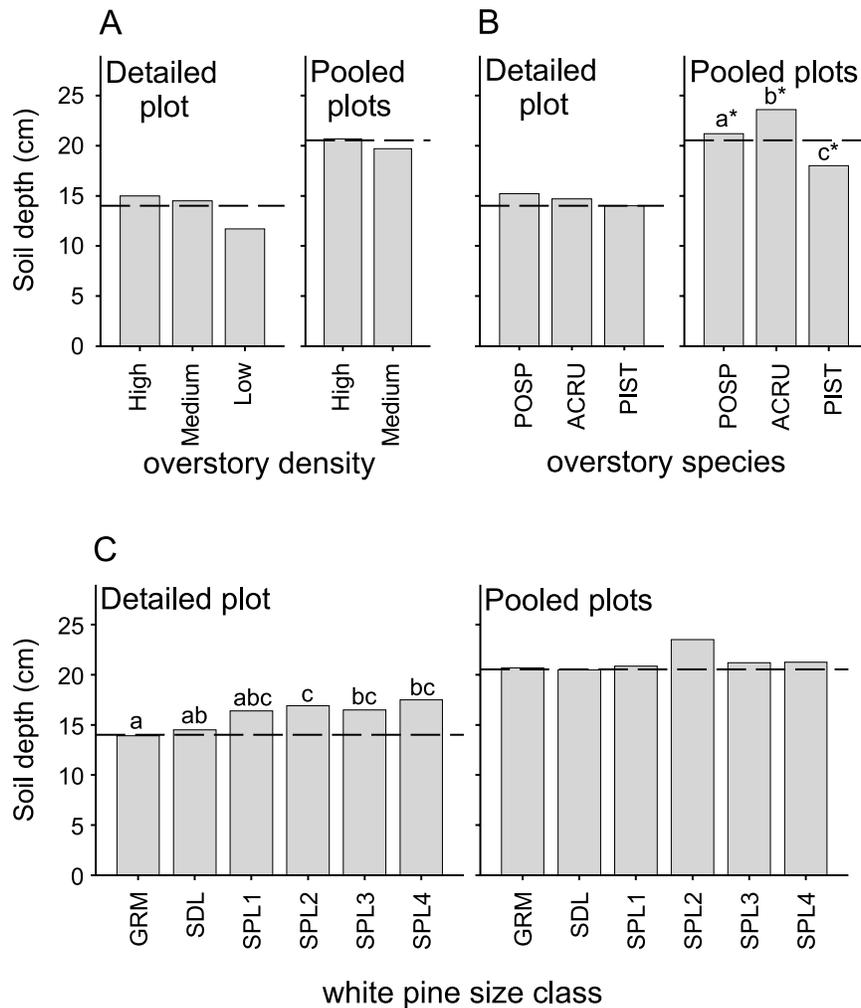
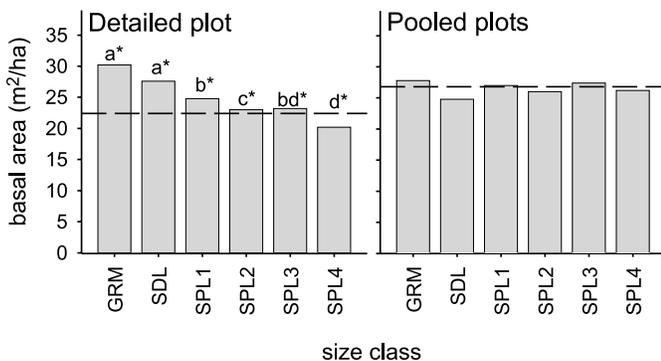


Fig. 6. Mean basal area above individual white pine size classes. White pine size classes and significance testing are the same as in Fig. 5. Broken line gives mean plot basal area.

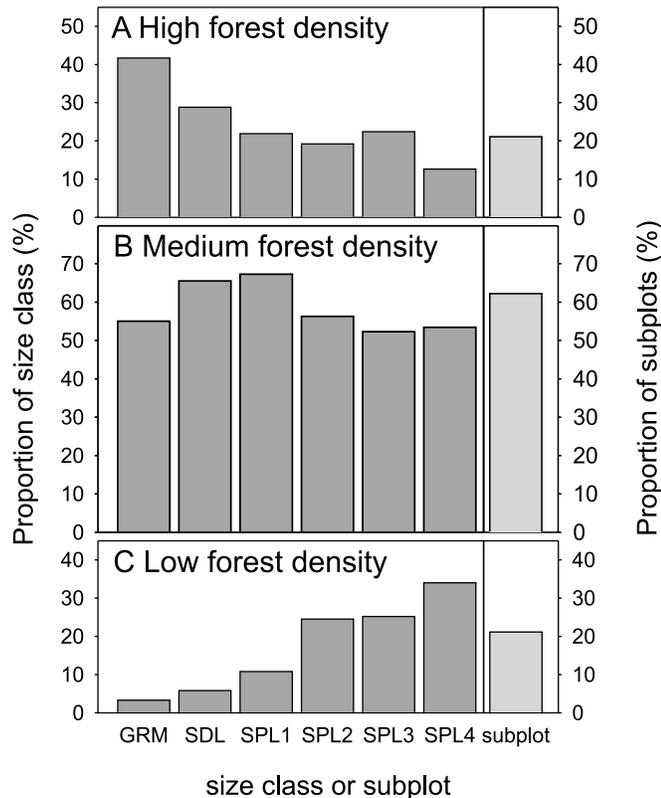


increments were measured for all saplings, the results differed between the two sapling size classes. The height increment of saplings 0.5–1 m tall in the pooled plots (data not shown) had virtually the same trend as that shown in Fig. 9 (pooled plots) for all saplings 0.5–2 m tall, whereas the height increment of the saplings 1–2 m tall in the pooled plots (data not shown) had the same trend as was observed for saplings 0.5–2 m tall in the detailed plot (Fig. 9). Interestingly, the pattern given for the detailed plot for both sapling size classes (Fig. 9) probably more greatly reflects the pattern of saplings 1–2 m tall than saplings 0.5–1 m tall, as the former were almost twice as abundant in the subsample.

Discussion

The results indicate that white pine invasion–retraction

Fig. 7. Proportion of germinants, seedlings and different sapling size classes within different forest density classes in the detailed plot. Overstorey density classes and sapling size classes are the same as in Fig. 5. Subplot category at the right of the graphs gives the proportion of subplots (plot area) that belongs to each particular forest density class. Summing the proportions of each size class or subplot (plot area) across the three forest density levels adds up to 100% (the total population of each individual size class or all subplots).



population dynamics (Dovčiak et al. 2001) in aspen mixedwoods may be initiated by positive effects of seed rain and safe sites on the distribution of germinants and seedlings on the forest floor. In aspen mixedwoods that contain overstorey white pine, the initial distribution of white pine seedlings may be quite broad, but later negative effects of overstorey basal area and shrub cover, and complex effects of soil depth, influence sapling recruitment from one size class to another, eventually leading to a more spatially restricted distribution of advanced saplings and adult white pines within the forest.

Seed rain and microhabitat effects on seedling establishment

White pine seed rain density and microhabitat characteristics, such as immediate overstorey basal area and decaying wood and moss cover, were positively related to white pine germinant and seedling densities. The importance of bare mineral soil and decaying wood for successful germination and early survival of tree seedlings has been demonstrated in numerous studies (Stewart and Rose 1990; Cornett et al. 1997; Kuuluvainen and Juntunen 1998). In this study, bare mineral soil was virtually absent and did not play a major role, but germinant density was positively related to decay-

ing wood. The positive association of older seedlings with moss cover may be indicative of better seedling survival on logs and stumps in advanced stages of decay where greater moss cover tends to be common.

Discrepancies between spatial patterns of seeds and seedlings documented for various species (e.g., Houle 1998; Lamont et al. 1993) can be explained by the dependence of germination and seedling establishment success on the quality of microsites, provided that the microsites are not randomly arranged relative to seed rain density. Microsites were nonrandomly arranged relative to seed rain in our detailed plot. Overstorey basal area was positively correlated with seed rain density and, in addition, the positive effect of moss on seedling density was higher under higher overstorey basal area. Under aspen canopy, safe sites such as logs and stumps can provide moister substrate than the surrounding forest floor (Cornett et al. 1997), while rock outcrop communities that are unprotected by dense forest canopy may be prone to disruptions due to seasonal droughts (Houle and Phillips 1989). In the pooled plots, overstorey basal area did not reach values as low as those on the rock outcrop of the detailed plot, and it was not related to seedling density.

Variations in white pine seedling and sapling dispersion patterns around individual seed sources have been noted earlier but microhabitat characteristics were not simultaneously studied (Rudis et al. 1978). In addition to seed rain, microsite-related establishment success has been found to influence the seedling distributions of 14 canopy tree species in southern Appalachian forests, but actual microsite characteristics were not identified (Clark et al. 1998). In the present study, we quantify the contribution of seed rain and different habitat characteristics to the variation in white pine germinant and seedling densities within aspen mixedwoods of the western Great Lakes region. Our results lead us to conclude that approximating actual seed dispersal curves by seedling dispersion curves in forest dynamics models (cf. Pacala et al. 1993; Ribbens et al. 1994) may not be accurate because of spatial variations in seedling density resulting from microsite induced differences in germination and seedling survival (cf. LePage et al. 2000; Wright et al. 1998).

Soil depth effects on white pine distribution

On generally deeper soil (~21 cm), overstorey white pine occupied the shallowest soils (~18 cm) of the three major overstorey species (aspen, white pine, red maple), indicating that white pine recruitment into the canopy may be lower on deeper soils due to competition. Thus, the distribution of overstorey tree species relative to soil depth lends some support to our shallow soil refugia hypothesis (3). Various authors have suggested that white pine regenerates and recruits into the canopy most successfully in areas where competition from other vegetation is limited, such as on rocky soils, sandy soils, or areas burned by surface fires (Wendel and Smith 1990; Frelich and Reich 1995a; Tester et al. 1997).

Contrary to this hypothesis, however, on generally shallow soils large saplings were associated with deeper soils more than small saplings or seedlings; on generally deeper soils, no difference in soil depth was found among seedling and sapling size classes. Large white pine saplings “avoid” extremely shallow soil (<5 cm); and, on generally shallow soil (~14 cm), they tend to be associated with somewhat deeper

Fig. 8. Mean size (A) and mean age (B) of different sapling size classes (based on height) within different forest density categories in the detailed plot and pooled plots. Forest density categories are the same as in Fig. 5, but note that only high and medium forest density categories are present in the pooled plots. The subsample of the largest saplings (SPL4) used to determine age was smaller than that used to determine DBH, thus age comparisons for this size class could not be made. Sapling size classes are the same as in Fig. 5. Size was measured as basal diameter for SPL1–3, and as DBH for SPL4. Age was approximated by branch whorl counts. Significance testing is the same as in Fig. 5.

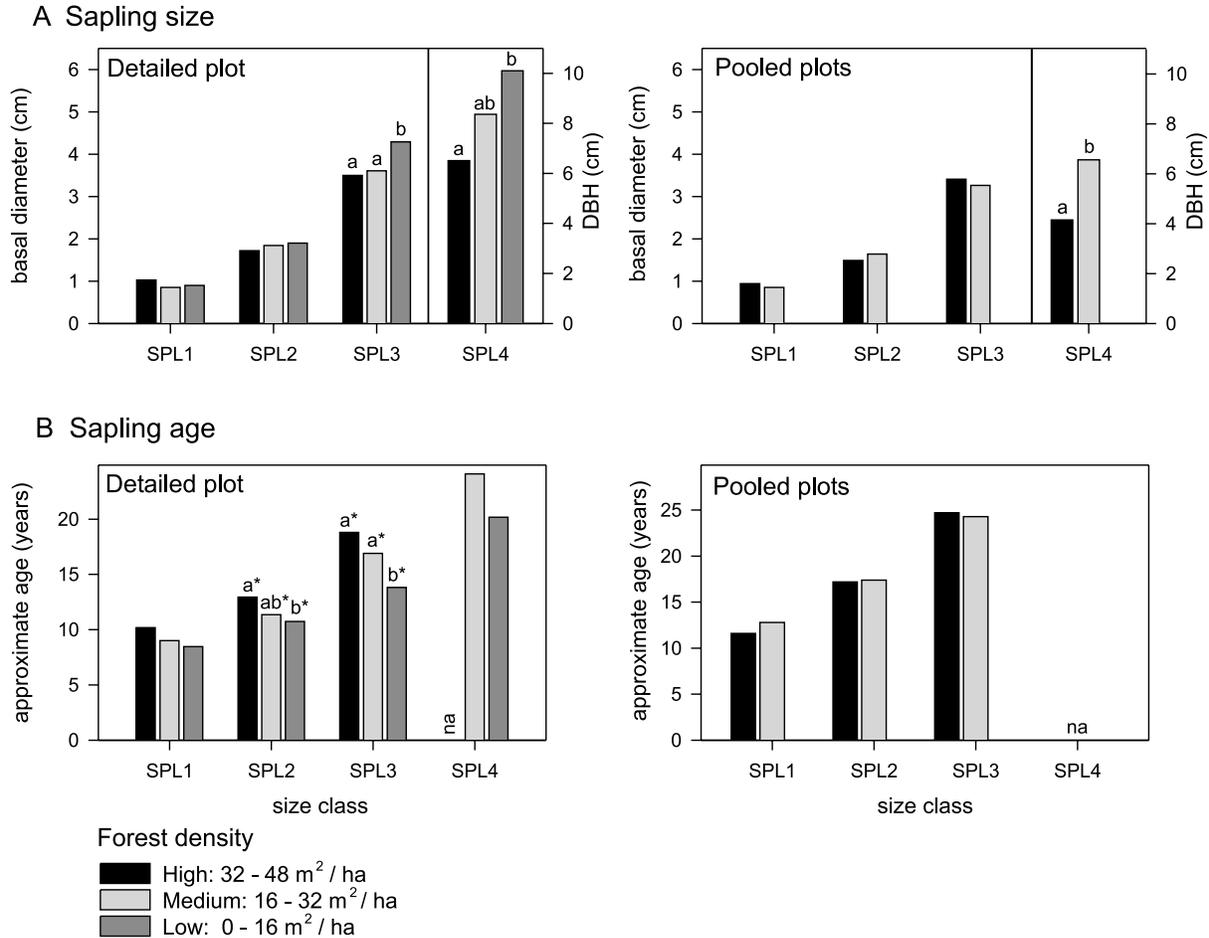
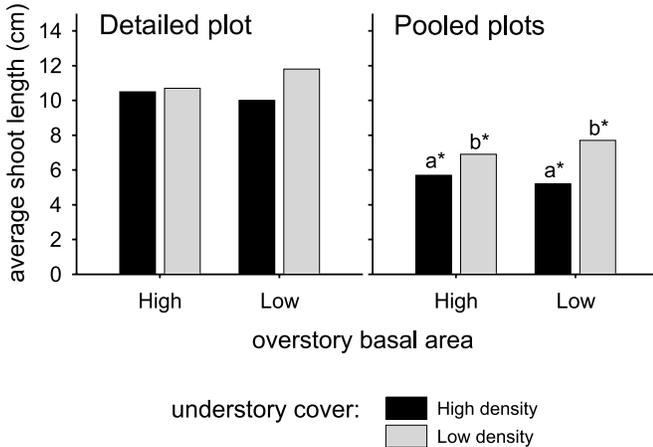


Fig. 9. Average terminal shoot length of saplings 0.5–2 m tall (SPL1–2) occurring in four different combinations of high and low overstory basal area and high and low understory shrub cover density. Significance testing is the same as in Fig. 5. The median values of overstory basal area (24 m²/ha) and understory shrub cover (55%) were used to divide these variable values into high and low levels.



soil pockets (~18 cm). Thus, on extremely shallow soil, white pine recruitment may be limited by soil depth rather than by competition from the overstory. On such soil, a difference of even a few centimetres may be biologically significant for seedlings and saplings because it significantly influences their ability to hold onto the substrate as well as the amount of available physical belowground space (McConaughay and Bazzaz 1991). Extremely shallow soils may be drought prone and moisture availability may become the limiting factor for certain plant species (Houle and Phillips 1989), including white pine, even though white pine saplings are tolerant of soil moisture deficits of >20% (Caspersen and Kobe 2001). Other soil characteristics such as pH, ion concentration, and soil texture may vary with soil depth and influence the distribution of plant species (Bigelow and Canham 2002; van Breemen et al. 1997).

Therefore, while shallow soils (such as rock outcrops) may indeed provide good habitat for successful white pine recruitment into the canopy, as also described by Ziegler (1995), the soil cannot be too shallow, or it may limit seedling recruitment to an advanced sapling stage. Studies of associations between soil depth and tree saplings or adult overstory trees are not very frequent, and our data contribute

to understanding of the basic variability of tree – soil depth associations within aspen mixedwoods of the western Great Lakes region.

Overstory effects on white pine recruitment

We can accept in part our negative canopy effects hypothesis (4) since the recruitment of white pine saplings into larger size classes was indeed more successful under low overstory density. Negative overstory effects and gap phase regeneration (where most recruitment occurs within canopy gaps) play an important role in the dynamics of mesic temperate late successional forests, mixed early successional deciduous–conifer forests, and southeastern boreal forests (Runkle 1981; Frelich and Reich 1995*b*; Kneeshaw and Bergeron 1998). White pine recruitment in boreal forests was found to be mostly restricted to relatively open habitats (Carleton et al. 1996) and pollen analyses suggest that white pine arrival in Minnesota 7000 years ago occurred mostly within open savanna-like forests (Jacobson 1979). Other studies, however, documented white pine recruitment in aspen-dominated forests with overstory densities similar to the intermediate density category in our study (Sharik et al. 1989; Palik and Pregitzer 1993, 1995; Peterson and Squiers 1995). We found that although white pine saplings were able to recruit into larger size classes (>4 m height) in medium forest density (16–32 m²/ha), their growth was better, recruitment was faster, and their density was disproportionately higher under the lowest overstory density (<16 m²/ha). In the past, a simplified “Swiss cheese” canopy gap model that contrasts tree recruitment in gap and nongap environments has been used (cf. Lieberman et al. 1989). In the present study, we offer a more detailed elucidation of the dynamics of white pine within aspen-dominated mixed forests, wherein gradual variation in canopy density (in combination with other noncanopy factors) determines the success of the regeneration and recruitment of the species.

Understory shrub effects on sapling growth

As hypothesized, white pine recruitment into intermediate size classes was dependent on the density of the understory shrub layer. A dense shrub layer, more so than high overstory basal area, slowed the height growth of saplings 0.5–1 m tall. The growth of saplings 1–2 m tall was poor when either shrub cover or overstory basal area were high. Thus, even if an abundant white pine seedling layer occurs beneath a low overstory density, competition from shrubs may slow white pine recruitment into intermediate sapling size classes. Our results corroborate suggestions from other authors that both overstory and understory competition have a negative effect on sapling recruitment (Smidt and Puettmann 1998; Saunders and Puettmann 1999). In boreal forests, understory woody vegetation, including shrubs, can increase in abundance if light levels increase because of a decrease in overstory density (Lieffers et al. 1999). The susceptibility of white pine saplings to competition has been widely recognized (e.g., Wendel and Smith 1990; Machado 1999) and management strategies that include controlling competition from more shade-tolerant saplings in the forest understory have been suggested (Abrams et al. 1995; Tester et al. 1997). According to our results, after white pine saplings reach >1 m in height, if the overstory density in aspen

mixedwoods is too high, shrub elimination will successfully aid recruitment only if coupled with the reduction of overstory density.

Conclusions

Although white pine regeneration in the Canadian portion of the Great Lakes region appears to be regulated by habitat limitations on seedling survival and growth rather than by seed dispersal (Carleton et al. 1996), we have shown in this paper that white pine seed rain can limit early white pine regeneration in aspen mixedwoods of the western Great Lakes region. In addition, suitable microhabitats, such as decaying wood and moss within the shade of a canopy, are equally important for early regeneration in these forests. In the later stages of white pine regeneration, recruitment is faster and disproportionately more abundant in areas of lower overstory density and low shrub cover, provided that soil is sufficiently deep. Shallow soil above some minimum depth (~5 cm) may provide a suitable habitat where white pine recruitment into the canopy is more successful than is the recruitment of some co-occurring tree species.

Understanding the interplay between seed rain density and microhabitat effects on regeneration and recruitment among individual white pine life stages can explain the discordance in spatial patterns of individual white pine life stages in aspen mixedwoods of the Great Lakes region. Interactions between seed dispersal and spatial distribution of suitable habitat has been addressed in theoretical mathematical models (Green 1983; Geritz et al. 1984), computer simulations using simplifying assumptions (e.g., Pacala et al. 1993), and conceptual models (Janzen 1970; Connell 1971), but because of its complexity it has typically been only partially addressed in field ecology studies (e.g., Stewart and Rose 1990; Bergelson et al. 1993; Moer 1993; Tanaka et al. 1998; Wright et al. 1998; Barot et al. 1999; LePage et al. 2000). Our study helps to fill this gap by describing the dynamics of regeneration and recruitment in several white pine populations occurring in aspen mixedwoods, and examining the capacity of a number of habitat characteristics to function as potential regeneration and recruitment filters.

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References

- Abrams, M.D., Orwig, D.A., and Demeo, T.E. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white-pine-mixed-oak forest in the southern Appalachians, USA. *J. Ecol.* **83**: 123–133.
- Ahlgren, C.E. 1969. Eighteen years of weather in the Boundary Waters Canoe Area. Quetico-Superior Wilderness Research Center, Minnesota Agricultural Experiment Station, St. Paul, Minn. Misc. Rep. 88.
- Barot, S., Gignoux, J., and Menaut, J.-C. 1999. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. *Ecology*, **80**: 1987–2005.
- Bergelson, J., Newman, J.A., and Floresroux, E.M. 1993. Rates of weed spread in spatially heterogeneous environments. *Ecology*, **74**: 999–1011.
- Bigelow, S.W., and Canham, C.D. 2002. Community organization of tree species along soil gradients in a north-eastern USA forest. *J. Ecol.* **90**: 188–200.
- Bitterlich, W. 1984. The relascope idea: relative measurements in forestry. Commonwealth Agricultural Bureaux, Slough, U.K.
- Carleton T.J., Maycock, P.F., Arnup, R., and Gordon, A.M. 1996. In situ regeneration of *Pinus strobus* and *P. resinosa* in the Great Lakes forest communities of Canada. *J. Veg. Sci.* **7**: 431–444.
- Caspersen, J.P., and Kobe, R.K. 2001. Interspecific variation in sapling mortality in relation to growth and soil moisture. *Oikos*, **92**: 160–168.
- Clark J.S., Macklin, E., and Wood, L. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecol. Monogr.* **68**: 213–235.
- Clark, J.S., Silman, M., Kern, R., Macklin, E., and HilleRisLambers, J. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**: 1475–1494.
- Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *In* Dynamics of populations. Edited by P.J. den Boer and G.R. Gradwell. Center for Agricultural Publication and Documentation, Wageningen, Netherlands. pp. 298–312.
- Cornett, M.W., Reich, P.B., and Puettmann, K.J. 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer–deciduous forests. *Écoscience*, **4**: 353–364.
- Dovčiak, M., Frelich, L.E., and Reich, P.B. 2001. Discordance in spatial patterns of white pine (*Pinus strobus*) size-classes in a patchy near-boreal forest. *J. Ecol.* **89**: 280–291.
- Dutilleul, P. 1993. Modifying the *t* test for assessing the correlation between two spatial processes. *Biometrics*, **49**: 305–314.
- Finegan, B. 1984. Forest succession. *Nature (London)*, **312**: 109–114.
- Frelich, L.E., and Reich, P.B. 1995a. Neighborhood effects, disturbance, and succession in forests of the western Great Lakes region. *Écoscience*, **2**: 148–158.
- Frelich, L.E., and Reich, P.B. 1995b. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecol. Monogr.* **65**: 325–346.
- Friedman, S.K., Reich, P.B., and Frelich, L.E. 2001. Multiple scale composition and spatial distribution patterns of the north-eastern Minnesota presettlement forest. *J. Ecol.* **89**: 538–554.
- Geritz, S.A.H., de Jong, T.J., and Klinkhamer, P.G.L. 1984. The efficacy of dispersal in relation to safe site area and seed predation. *Oecologia*, **62**: 219–221.
- Green, D.S. 1983. The efficacy of dispersal in relation to safe site density. *Oecologia*, **56**: 356–358.
- Greene, D.F., and Johnson, E.A. 1989. A model of wind dispersal of winged or plumed seeds. *Ecology*, **70**: 339–347.
- Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., and Simard, M.-J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Can. J. For. Res.* **29**: 824–839.
- Grigal, D.F., and Ohmann, L.F. 1975. Classification, description, and dynamics of upland plant communities within a Minnesota wilderness area. *Ecol. Monogr.* **45**: 389–407.
- Gumpertz, M.L., Wu, C., and Pye, J.M. 2000. Logistic regression for southern pine beetle outbreaks with spatial and temporal autocorrelation. *For. Sci.* **46**: 95–107.
- Harper, J.L. 1977. Population biology of plants. Academic Press, London.
- Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quat. Res.* **3**: 329–382.
- Heinselman, M.L. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. *In* Fire regimes and ecosystem properties. U.S. For. Ser. Gen. Tech. Rep. WO-26. pp. 7–57.
- Heinselman, M. 1996. The Boundary Waters Wilderness Ecosystem. University of Minnesota Press, Minneapolis, Minn.
- Houle, G. 1998. Seed dispersal and seedling recruitment of *Betula alleghaniensis*: spatial inconsistency in time. *Ecology*, **79**: 807–818.
- Houle, G., and Phillips, D.L. 1989. Seed availability and biotic interactions in granite outcrop plant communities. *Ecology*, **70**: 1307–1316.
- Host, G.E., Pregitzer, K.S., Ramm, C.W., Hart, J.B., and Cleland, D.T. 1987. Landform-mediated differences in successional pathways among upland forest ecosystems on northeastern lower Michigan. *For. Sci.* **33**: 445–457.
- Jacobson, G.L., Jr. 1979. The palaeoecology of White pine (*Pinus strobus*) in Minnesota. *J. Ecol.* **67**: 697–726.
- Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**: 501–528.
- Keitt, T.H., Bjørnstad, O.N., Dixon, P.M., and Citron-Pousty, S. 2002. Accounting for spatial patterns when modeling organism–environment interactions. *Ecography*, **25**: 616–625.
- Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology*, **79**: 783–794.
- Kobe, R.K., Pacala, S.W., Silander, J.A., Jr., and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* **5**: 517–532.
- Kruger, E.L., and Reich, P.B. 1997. Responses of hardwood regeneration to fire in mesic forest openings. III. Whole-plant growth, biomass distribution, and nitrogen and carbohydrate relations. *Can. J. For. Res.* **27**: 1841–1850.
- Kuuluvainen, T., and Pukkala, T. 1989. Effect of Scots pine seed trees on the density of ground vegetation and tree seedlings. *Silva Fenn.* **23**: 159–167.
- Kuuluvainen, T., and Juntunen, P. 1998. Seedling establishment in relation to microhabitat variation in a windthrow gap in a boreal *Pinus sylvestris* forest. *J. Veg. Sci.* **9**: 551–562.
- Lamont, B.B., Witkowski, E.T.F., and Enright, N.J. 1993. Post-fire litter microsites: safe for seeds, unsafe for seedlings. *Ecology*, **74**: 501–512.
- LePage, P.T., Canham, C.D., Coates, K.D., and Bartemucci, P. 2000. Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. *Can. J. For. Res.* **30**: 415–427.
- Legendre, P., Dale, M.R.T., Fortin, M.-J., Gurevitch, J., Hohn, M., and Myers, D. 2002. The consequences of spatial structure for

- the design and analysis of ecological field surveys. *Ecography*, **25**: 601–615.
- Lieberman, M., Lieberman, D., and Peralta, R. 1989. Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology*, **70**: 550–552.
- Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., and Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. *Can. J. For. Res.* **29**: 796–811.
- Machado, J.L. 1999. The role of resource availability in the growth, distribution, survival, and physiology of cold temperate tree species. Ph.D. thesis, University of Minnesota, St. Paul, Minn.
- Maguire, D.A., and Forman, R.T.T. 1983. Herb cover effects on tree seedling patterns in a mature hemlock–hardwood forest. *Ecology*, **64**: 1367–1380.
- McConnaughay, K.D.M., and Bazzaz, F.A. 1991. Is physical space a soil resource? *Ecology*, **72**: 94–103.
- Moer, M. 1993. Characterizing spatial patterns of trees using stem-mapped data. *For. Sci.* **39**: 756–775.
- Nathan, R., and Muller-Landau, H.C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Tree*, **15**: 278–285.
- Pacala, S.W., and Deutschman, D.H. 1995. Details that matter: the spatial distribution of individual trees maintains forest ecosystem function. *Oikos*, **74**: 357–365.
- Pacala, S.W., Canham, C.D., and Silander, J.A., Jr. 1993. Forest models defined by field measurements: I. The design of a north-eastern forest simulator. *Can. J. For. Res.* **23**: 1980–1988.
- Pacala, S.W., Canham, C.D., Silander, J.A., Jr., and Kobe, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. For. Res.* **24**: 2172–2183.
- Palik, B.J., and Pregitzer, K.S. 1993. The repeatability of stem exclusion during even-aged development of bigtooth aspen dominated forests. *Can. J. For. Res.* **23**: 1156–1168.
- Palik, B.J., and Pregitzer, K.S. 1995. Height growth of advance regeneration under an even-aged bigtooth aspen (*Populus grandidentata*) overstory. *Am. Midl. Nat.* **134**: 166–175.
- Parciak, W. 2002. Seed size, number, and habitat of a fleshy-fruited plant: consequences for seedling establishment. *Ecology*, **83**: 794–808.
- Peterson, C.J., and Squiers, E.R. 1995. Competition and succession in an aspen–white-pine forest. *J. Ecol.* **83**: 449–457.
- Reich, P.B., Tjoelker, M.G., Walters, M.B., Vanderklein, D.W., and Buschena, C. 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Funct. Ecol.* **12**: 327–338.
- Ribbens E., Silander, J.A., Jr., and Pacala, S.W. 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology*, **75**: 1794–1806.
- Rudis, V.A., Ek, A.R., and Balsiger, J.W. 1978. Within-stand seedling dispersal for isolated *Pinus strobus* within hardwood stands. *Can. J. For. Res.* **8**: 10–13.
- Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology*, **62**: 1041–1051.
- Saunders, M.R., and Puettmann, K.J. 1999. Effects of overstorey and understorey competition and simulated herbivory on growth and survival of white pine seedlings. *Can. J. For. Res.* **29**: 536–546.
- Sharik, T.L., Ford, R.H., and Davis, M.L. 1989. Repeatability of invasion of eastern white pine on dry sites in northern lower Michigan. *Am. Midl. Nat.* **122**: 133–141.
- Smidt, M.F., and Puettmann, K.J. 1998. Overstorey and understorey competition affect underplanted eastern white pine. *For. Ecol. Manage.* **105**: 137–150.
- Stewart, G.H., and Rose, A.B. 1990. The significance of life history strategies in the developmental history of mixed beech (*Nothofagus*) forests, New Zealand. *Vegetatio*, **87**: 101–114.
- Tanaka, H., Shibata, M., and Nakashizuka, T. 1998. A mechanistic approach for evaluating the role of wind dispersal in tree population dynamics. *J. Sustain. For.* **6**: 155–174.
- Tester, J.R., Starfield, A.M., and Frelich, L.E. 1997. Modelling for ecosystem management in Minnesota pine forests. *Biol. Conserv.* **80**: 313–324.
- Turnbull, L.A., Crawley, M.J., and Rees, M. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos*, **88**: 225–238.
- Turner, M.G., Romme, W.H., Gardner, R.H., and Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol. Monogr.* **67**: 411–433.
- Turner, M.G., Baker, W.L., Peterson, C.J., and Peet, R.K. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems*, **1**: 511–523.
- U.S. Department of Agriculture, Soil Conservation Service, Soil Survey Staff. 1960. Soil classification — a comprehensive system, 7th approximation. U.S. Government Printing Office, Washington, D.C.
- van Breemen, N., Finzi, A.C., and Canham, C.D. 1997. Canopy tree-soil interactions within temperate forests: effects of soil elemental composition and texture on species distributions. *Can. J. For. Res.* **27**: 1110–1116.
- Verdú, M., and García-Fayos, P. 1998. Old-field colonization by *Daphne gnidium*: seedling distribution and spatial dependence at different scales. *J. Veg. Sci.* **9**: 713–718.
- Walters, M.B., and Reich, P.B. 1996. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology*, **77**: 841–853.
- Wendel, G.W., and Smith, H.C. 1990. *Pinus strobus* L. Eastern white pine. In *Silvics of North America. Conifers. Edited by R.M. Burns and B.H. Honkala*. U.S. Dep. Agric. Agric. Handb. 654. pp. 476–488.
- Wright, E.F., Coates, K.D., and Bartemucci, P. 1998. Regeneration from seed of six tree species in the interior cedar–hemlock forests of British Columbia as affected by substrate and canopy gap position. *Can. J. For. Res.* **28**: 1352–1364.
- Ziegler, S.S. 1995. Relic eastern white pine (*Pinus strobus* L.) stands in southwestern Wisconsin. *Am. Midl. Nat.* **133**: 88–100.