

PATHWAYS IN OLD-FIELD SUCCESSION TO WHITE PINE: SEED RAIN, SHADE, AND CLIMATE EFFECTS

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Abstract. Trees slowly colonize old fields on sandy outwash in the prairie–forest ecotone of the north-central United States, and in the absence of fire, succession is expected to proceed toward oak woodland. We analyzed whether a case of unusually rapid and spatially extensive invasion by white pine (*Pinus strobus*) could be explained by the presence of specific temporal or spatial opportunity windows suitable for such invasion. We tested whether the invasion was temporally restricted to the period immediately after abandonment or to periods of favorable climate, and whether it was spatially restricted to areas of high seed rain or high forest-edge shade. White pine invasion into the field occurred in two waves separated from each other by a 1987–1989 drought period. The first wave (1980–1985) occurred during a period of average climate and led to the establishment of dense sapling patches in shade near forest edges. The second wave (1991–1994) occurred during a period of high precipitation and cooler than normal temperature, and resulted in colonization of the unshaded field center. In addition to the two temporal windows, white pine invasion occurred within two spatial windows: in areas highly sheltered by forest edge and in areas receiving high white pine seed rain. Overall these windows produced three different successional pathways: (1) a slow, creeping white pine invasion into highly shaded areas with low seed rain near forest edges; (2) a rapid, discrete-step invasion in areas where seed rain was abundant enough to overcome mortality in lower shade and where early arrivals facilitate filling in by later arrivals; and (3) a deferred invasion in the field center where low seed rain and lack of shade allowed the persistence of a grassland stage until favorable climate resulted in a white pine recruitment pulse. Temporal variation in climate can accelerate or decelerate any of the three successional pathways.

Key words: *climate fluctuations; forest edge; forest–prairie ecotone; invasion; old field; recruitment pulse; savanna; seed dispersal; succession; white pine; Pinus strobus.*

INTRODUCTION

Successional change during periods between disturbances can be driven by various mechanisms, such as amelioration of high insolation and droughtiness (Finegan 1984, Kitzberger et al. 2000), incremental soil improvement (Bormann and Sidle 1990), and gradual competitive displacement favoring superior competitors for light on N-rich soils (Tilman 1988, Canham 1989) or nitrogen in N-depleted soils (Gleeson and Tilman 1990). However, successional trajectory may be significantly influenced by the availability of propagules of potential colonists (Egler 1954). While many herbaceous species may be present in the soil seed bank, most forest tree species depend on seed rain from the surrounding landscape. Thus the appearance of tree species in the course of succession may be related to seed source distribution and seed dispersal as much as it is to other successional mechanisms. Seed dispersal is crucial for understanding forest dynamics (Ribbens et al. 1994, Clark et al. 1999) and historical and future

migrations of tree species (Clark 1998). However, since detailed study of forest tree seed rain is a complex endeavor (Greene and Johnson 1996, Clark et al. 1999), and is impossible to do retrospectively, the majority of studies of secondary succession either disregard seed rain of forest trees or use distance to forest edge as its inaccurate surrogate (e.g., McClanahan 1986, Inouye et al. 1994).

In addition to seed rain, environmental conditions can also be spatially structured. Current models of forest dynamics bring together spatial variation in seed rain and environmental conditions (Pacala et al. 1993, LePage et al. 2000). In regions where native forest has been partially removed, forest edges inherently impose spatial variation; they shade nearby areas and moderate climatic extremes, potentially facilitating colonization by forest trees sensitive to climatic extremes (cf. Finegan 1984). On the other hand, shade may slow down tree growth (Reich et al. 1998) and decrease longer term survival, leading to better recruitment of forest trees some distance away from the forest edge. In large forest openings, the distance to forest edge can influence the composition of secondary forest communities (e.g., McClanahan 1986, Golley et al. 1994, Fastie 1995).

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Successional systems vary not only in space, but also in time. As interspecific interactions intensify during the course of succession, the availability of establishment microsites declines, and the resistance to further invasions from the surrounding area may increase (Foster and Tilman 2000). Alternatively, harsh climatic conditions of short duration (e.g., droughts) may set back succession by several years (Tilman and El Haddi 1992, Tilman 1996), while favorable conditions may accelerate it (Kitzberger et al. 2000).

Thus important successional processes, such as tree invasions, may operate on restricted temporal scales that function as temporal opportunity windows (e.g., years with high precipitation or early successional stages with abundant suitable microsites), and on restricted spatial scales that function as spatial opportunity windows (e.g., along shaded forest edges or nearby abundant seed sources). Successional processes within these restricted opportunity windows may easily go unnoticed unless they are specifically investigated. Ample replication used in chronosequence and short-term experimental studies may average these processes out, since the majority of the successional system is likely to experience different processes than those that occur within the opportunity windows. However, successional processes within the restricted opportunity windows may lead to successional states that can eventually persist in time and increase their spatial extent through positive feedback switches or neighborhood effects (Wilson and Agnew 1992, Frelich 2002). For example, once seedlings reach a certain size they may be more drought tolerant, and tree regeneration within forest-edge shade may eventually create a new, advanced forest edge, casting its shade and supporting new regeneration farther in the field. If restricted opportunity windows occur frequently enough over broad spatial and temporal scales, they may eventually come to represent the dominant successional pathway in a given region.

In this paper, we investigate an unusually rapid and spatially extensive white pine invasion into a large old field in a water-limited and nutrient-poor sand plain upland in the prairie-forest ecotone in the north-central United States. Abandoned fields in this area have experienced only limited tree invasion (Inouye et al. 1987, Lawson et al. 1999), and in the absence of fire they are expected to proceed toward oak woodland (White 1983), possibly through an intervening prairie stage (Gleeson and Tilman 1990, Knops and Tilman 2000). The objective of this paper is to test whether the unusual successional direction (i.e., the white pine invasion) could be explained by the presence of specific temporal or spatial opportunity windows. We test the temporal opportunity window hypothesis by testing two alternative subhypotheses: (1) that the invasion occurred mostly within several years after the abandonment, and declined since; and (2) that the invasion fluctuated over time, responding to fluctuation in precipitation and temperature. We test the spatial oppor-

tunity window hypothesis by testing whether (1) the invasion occurred in close proximity to an abundant white pine seed source; and (2) the invasion occurred within the shaded habitat near forest edges, which moderate the climatic extremes that occur in the open field.

METHODS

Study area and species

The study took place in the Boot Lake Scientific and Natural Area (hereafter Boot Lake), in east-central Minnesota (45°20' N, 93°11' W, ~300 m above sea level). Climate summaries (1961–1990) from weather stations located <15 km from Boot Lake give mean July and January temperatures of 22.3°C and –11.8°C. Average annual precipitation is 758 mm, of which ~41% falls in June–August and only ~9% in December–February; ~50% is approximately equally split between the two remaining parts of the year. The median length of the season with continuous temperatures >0°C is 139 days (Midwestern Climate Center 2000).

Boot Lake is a part of the 269 000-ha Anoka Sand Plain, a gently undulating glacial outwash. Over 70% of the Anoka Sand Plain is well to excessively drained (Department of Soil Science, University of Minnesota et al. 1980). The first vegetation surveys (1850–1905) described most of the upland forests as oak savanna dominated by *Quercus macrocarpa* Michx., with occasional pines (*Pinus* spp.) within a tallgrass prairie matrix (Marschner 1974). Later much of the area was converted to agriculture, but currently many fields are abandoned, and their soil nitrogen and carbon supplies are significantly depleted (Knops and Tilman 2000).

Mature white pines are often the largest trees in the region (>45 m in height, >100 cm dbh, Wendel and Smith 1990) and assume dominant canopy position. Seeds are dispersed by wind in August and September and can travel >60 m in a forest and >210 m in the open (Wendel and Smith 1990). In a forest, the majority of seeds fall and germinate near their parent trees (<20 m, Ribbens et al. 1994). Mast years occur every 3–10 years (Wendel and Smith 1990). Young white pines grow slowly and compete poorly in both high and low light (Reich et al. 1998), and white pine regeneration is best on sites where competition is reduced due to low soil quality (Wendel and Smith 1990) or low-intensity surface fires (Frelich and Reich 1995).

Study design

We chose a former hayfield that was abandoned ~20 years prior to our study. Previous observations by the authors suggested that white pine was the only species aggressively invading the abandoned field and that there were almost no other woody species present within the field. The field is located on Zimmerman fine sand (0–6% slopes, Chamberlain 1977) and surrounded by a closed oak forest with white pine patches. We measured the basal area of all white pines >20 cm dbh

within a 60-m buffer around a chosen ~5.2-ha tract of the field (~75% of the entire field, Fig. 1A). The buffer was not established around the entire field as its parts would have encompassed swampy areas near the lake that were difficult to access and contained few white pines.

All white pine saplings (dead or alive) >0.2 m tall were surveyed within the ~5.2-ha tract (Fig. 1A), except in two small disturbed areas (each <125 m²) near forest edges. For saplings <4 m tall, we measured sapling height, terminal shoot length (1997 shoots), approximate total sapling age, and approximate age when the sapling reached 0.5 m in height (by counting the number of branch whorls along the sapling's entire stem and along the bottom 0–0.5 m section of the stem). It took these saplings, irrespective of their size class, ~4 years to reach 0.5 m in height. Counting branch whorls in the thick bottom stem sections may be inaccurate for saplings >4 m tall, and thus we counted only branch whorls >0.5 m above the ground, and then added 4 years. If branch whorl counts >10 on tall (>4 m) saplings in dense sapling clumps were difficult because the view of their crown top was obstructed by neighboring saplings, such saplings were recorded in the >10-whorl category. These measurements were done for all individually standing saplings, but saplings located in extremely dense patches (total patch area ~0.5 ha) near the forest edge were subsampled using a continuous grid of 5 × 5 m plots. The density of saplings >2 m tall within these patches was 10–100 saplings/plot, and thus measuring them all was not feasible. The closest sapling to the northwest corner of each plot was measured in each of four size classes (0.2–1 m, 1–2 m, 2–4 m, and >4 m). For each size class, densities ≤10 individuals/plot were determined by counting, and densities >10 were estimated using several density classes (11–20, 21–30, 31–40, 41–50, and 51–100 individuals/plot).

Using a laser surveying station (Topcon, DT-100, Topcon Corporation, Tokyo, Japan), supplemented within the dense sapling clumps by tape measures, we mapped (1) all white pine saplings outside of the plot grid placed in the dense sapling clumps, (2) all plots within the plot grid, (3) all measured white pines within the 60-m buffer, and (4) the forest edge. The individually mapped saplings were pooled into 5 × 5 m plots, to match the sampling in the dense clumps (Fig. 1A). The forest edge followed visible straight lines well defined by stems >20 cm dbh. The average height of the forest edge was measured from the field center at 10-m intervals with a clinometer and a laser range finder.

Seed rain model

Seed rain within the field was estimated using a mechanistic model for seed dispersal from forests to clearings (Greene and Johnson 1996). Using relatively well-studied geometry of seed fall and wind flow, the model simulates average trajectories of seeds from in-

dividual trees for any site with known wind regime, species-specific seed descent velocity, and site geometry (e.g., stand height, spatial distribution of trees). Greene and Johnson (1996) validated a general version of this model across several conifer species and sites, and we parameterized it for white pine at the Boot Lake old field (Fig. 1B). While the model cannot describe detailed variation in seed rain over the course of succession, it provides a seed rain index that describes broad seed rain patterns within the old field. We use the term “seed rain” throughout the text for brevity.

Dominant or codominant white pine trees with dbh >20 cm (mean dbh ~43 cm) and with live crown tops were defined as potentially seed-bearing pines (cf. Greene and Johnson 1994, Ribbens et al. 1994). While fecundity of any single tree may vary among years, we assumed that variability among individual trees and years cancelled each other, given that our analyses involved broad time periods rather than annual variation. The approximate annual seed production (Q) of each tree was estimated from an allometric relationship derived for temperate forest tree species:

$$Q = 0.0107m_s^{-0.58}m_L^{1.08} \quad (1)$$

where m_s is mean individual seed mass (grams), m_L is leaf mass (grams), and

$$m_L = 113\,000BA^{0.855} \quad (2)$$

where BA is basal area (in square meters) (Greene and Johnson 1994). Mean individual seed mass for white pine is 0.0172 g/seed (Young and Young 1992:257).

Since the seed source distribution was heterogeneous, we used formulas for estimating seed deposition from individual seed-bearing trees (Eqs. 3–6, Greene and Johnson 1996). The number of seeds dispersing from a tree at any given wind speed, u (in meters per second), is

$$\frac{dQ}{du} = Q(\sqrt{2\pi}\sigma_{\ln}u)^{-1} \exp\left\{-\left[(\sqrt{2}\sigma_{\ln})^{-1} \ln\left(\frac{u}{u_{g^*}}\right)\right]^2\right\} \quad (3)$$

where Q is from Eq. 1, σ_{\ln} is the standard deviation of the natural logarithms of the horizontal wind speeds, and u_{g^*} is the median horizontal wind speed corrected for the preferential abscission of seeds at higher wind speeds:

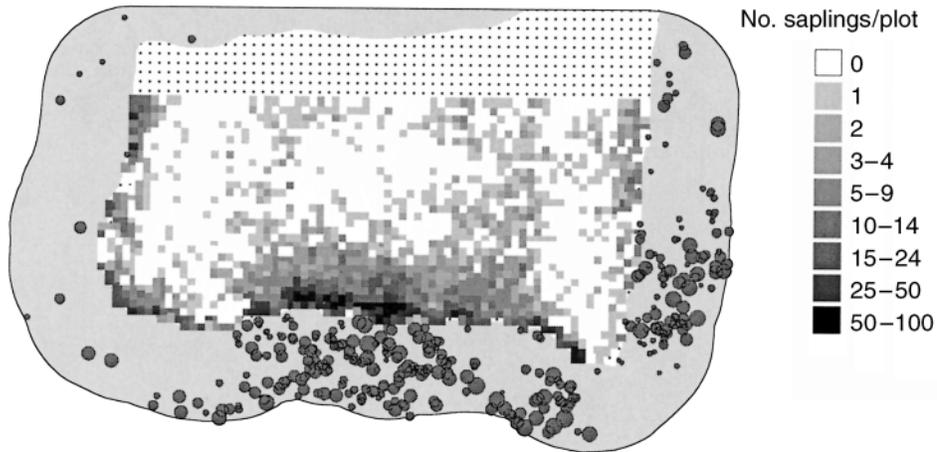
$$u_{g^*} = u_g[\exp(\sigma_{\ln}^2)]^2 \quad (4)$$

where u_g is the median wind speed from measurements. Using mechanistic formulas for seed fall and wind behavior within and outside of a forest in full leaf, the wind speed, u , in Eq. 3 is

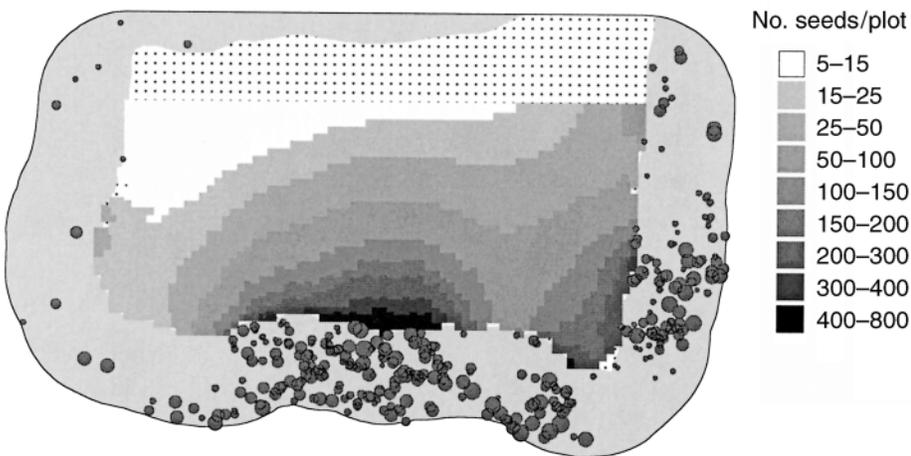
$$u = (v_f z_r^{0.14}/z_a)\{[0.38^{-1}x_0^{0.814}z_h^{0.186}(z_a/2)^{-0.14}] + (0.116^{-1}x_f z_h^{-0.14})\} \quad (5)$$

where v_f is the mean descent velocity (meters per second) of a seed in still air, z_r is anemometer height (meter) at a reference station, z_a is the mean abscission

A) Sapling density



B) Simulated seed rain



C) Forest-edge shade

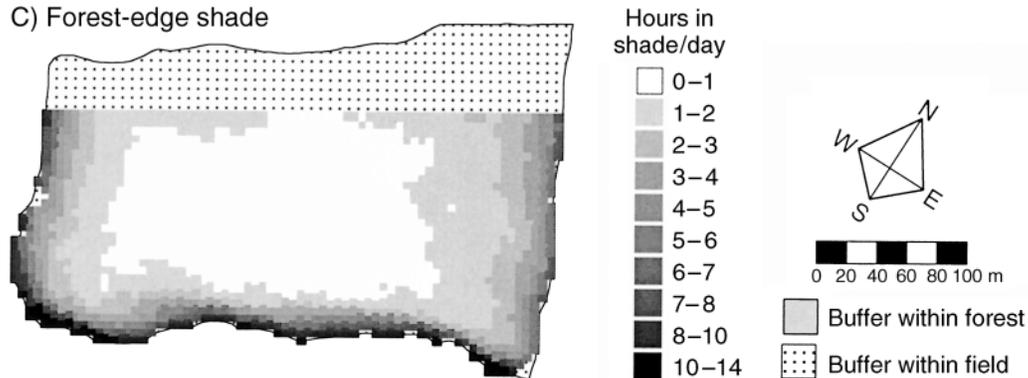


FIG. 1. (A) Distribution of white pine seed-bearing trees and saplings at the study site. Seed-bearing trees (dark gray circles) are drawn in proportion to their dbh. Sapling numbers are sums for all size classes (both dead and alive) per 5×5 m survey plot. (B) Simulated seed rain based on formulas adapted from Greene and Johnson (1994, 1996). Seed numbers are given per 5×5 m plot. (C) Forest-edge shade during the growing season (May–September) within the sampled tract of the field. For each plot, the average number of hours spent in shade per day was calculated using formulas for solar angle and azimuth in Campbell and Norman (1998). A wind rose gives dominant wind directions during the seed dispersal season.

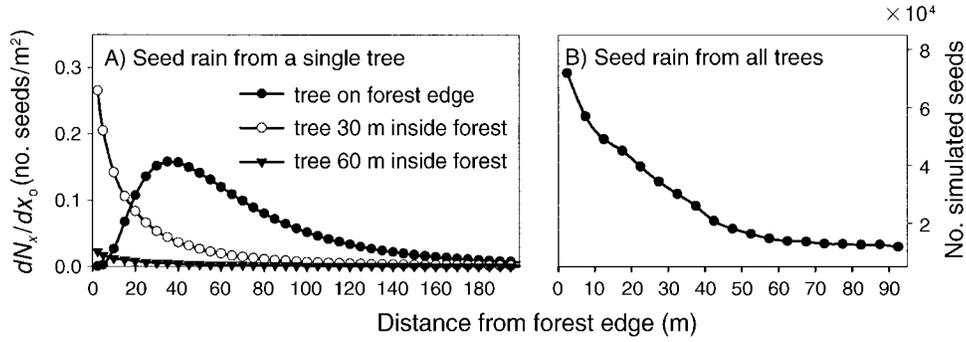


FIG. 2. White pine seed rain from the forest edge into the field. (A) Seed rain within the field from an average seed-bearing white pine tree (dbh \sim 43 cm, height \sim 30 m). Wind speed within the open field increases with distance from the forest edge; thus seeds dispersed from trees located on the forest edges experience higher wind speeds during their descent and are deposited farther (and at lower density at peak deposition) than seeds dispersed from trees located within the forest (where wind speed is low). While a significant proportion of seeds is deposited at 60 m from a tree located on the forest edge (seeds travel only above the field), less than half of that amount is deposited 60 m away from a tree located 30 m into the forest (seeds travel 30 m inside the forest and 30 m above the field) because the majority of seeds land within the forest or near the forest edge. Single trees located 60 m inside the forest (i.e., at the edge of the mapped forest buffer) do not contribute significant seed rain within the field. (B) Total seed rain within the field from all white pine seed-bearing trees within the 60-m buffer. Since more seed-bearing white pines are located farther inside the forest than near the forest edge, the shape of the curve resembles an exponential curve.

height (meter) set as \sim 75% of the mean seed-bearing tree height, z_h is the mean height (meter) of the top of the canopy, x_o is the distance (meter) that seeds travel in the open from the forest border to the site of deposition, and x_f is the distance (meter) traveled within the forest from a seed-bearing tree to the forest border. Assuming uniform distribution of wind directions during seed dispersal, the number of seeds per square meter (N_x) deposited from any seed-bearing tree at any distance x_o within the field is

$$\frac{dN_x}{dx_o} = [2\pi(x_o + x_f)]^{-1} \left(\frac{dQ}{du} \right) \times \left\{ 0.814 v_f z_h^{0.186} z_r^{0.14} \left[0.38 z_a \left(\frac{z_a}{2} \right)^{0.14} x_o^{0.186} \right]^{-1} \right\} \quad (6)$$

where dQ/du is from Eq. 3, u_{gs} is from Eq. 4, and u is from Eq. 5 (Fig. 2). Since the assumption of uniform wind directions is false for our site, we incorporated wind directionality into the original Eq. 6 of Greene and Johnson (1996). The seed deposition from each seed-bearing tree was calculated for four main wind directions, each time allowing seeds to disperse in a particular direction in proportion to the number of hours when wind was blowing in that direction:

$$\frac{dN_{xDir}}{dx_o} = 4 \sum_{Dir} \frac{H_{Dir}}{H_{Dir}} \left(\frac{dN_x}{dx_o} \right) \quad (7)$$

where dN_x/dx_o is from Eq. 6, and H_{Dir} is the number of hours during dispersal season when wind was blowing in a particular direction (Dir = north, east, south, or west). Summing the seed deposition from all four wind directions and all seed-bearing trees gives the total number of seeds deposited per 5×5 m plot:

$$N_{plot} = \sum_{m=1}^M \sum_{Dir} 25 \left(\frac{dN_{xDir}}{dx_o} \right) \quad (8)$$

where m is the number of a seed-bearing tree, and M is the total number of seed-bearing trees.

The 1976–1995 hourly wind speed observations for August and September from the closest wind recording station (Minneapolis–St. Paul International Airport, \sim 65 km away over flat terrain) were used to calculate u_g (3.9 m/s) and σ_{in} (0.54) for Eqs. 3 and 4 (Midwestern Climate Information System 2000). For Eqs. 5 and 6, $v_f = 0.93$ m/s (Greene and Johnson 1995); $z_r = 10$ m (Minnesota State Climatology Office); $z_a \sim 20$ m and $z_h \sim 20$ m (measured); and x_o and x_f were calculated from the coordinates of plots, forest border, and seed-bearing trees. The H_{dir} values for Eq. 7 were obtained from the airport data, and indicated that wind blew most frequently from the south (\sim 34% of the time) and less frequently from the other directions: west (\sim 23%), east (\sim 21%), and north (\sim 20%).

Shade model

Forest-edge shade could not be directly measured, since the current shade regime within the field is modified by large patches of tall white pine saplings near forest edges. Thus the distribution of shade along forest edges was modeled using site location, site geometry (forest-edge shape and height), and basic equations for solar movement (Campbell and Norman 1998).

We simulated shadow movement along the field's edge during the period from May to September (beginning of late spring to end of early fall [Baker and Strub 1963]). In order to simplify the calculations, we simulated the location of the shadow at 1-h intervals one day in the middle of each month and calculated

the maximum number of hours that each plot spent in the shade that day. The average from these monthly calculations was used to derive the number of hours that individual plots spent in the shade during an “average day” of this period (Fig. 1C).

In order to determine if a plot within the field was in the shade at any particular time when shadow was simulated, sun altitude angle (solar elevation angle, the elevation angle above the horizon) and sun azimuth angle (the angle from true south measured in the horizontal plane) were calculated using equations from Campbell and Norman (1998). The solar altitude angle, β (degrees), was calculated as

$$\beta = \arcsin\{\sin \phi \sin \delta + \cos \phi \cos \delta \cos[15(t - t_0)]\} \quad (9)$$

where ϕ is the latitude (degrees), δ is solar declination (degrees), t is standard local time (hours, 0–24), and t_0 is time of local solar noon (hours, 0–24). Solar declination, δ , was calculated as

$$\delta = \arcsin\{0.39785 \sin[278.97 + 0.9856J] + 1.9165 \sin(356.6 + 0.9856J)\} \quad (10)$$

where J is a Julian day, with $J = 1$ at 1 January. Solar noon, t_0 , was calculated as

$$t_0 = 12 - LC - ET \quad (11)$$

where LC is the longitude correction (± 4 minutes for each degree east or west of the standard meridian), and ET is the equation of time calculated as

$$ET = 3600^{-1}(-104.7 \sin f + 596.2 \sin 2f + 4.3 \sin 3f - 12.7 \sin 4f - 429.3 \cos f - 2 \cos 2f + 19.3 \cos 3f) \quad (12)$$

where $f = 279.575 + 0.9856J$ (degrees). The solar azimuth angles (degrees) before solar noon were calculated as

$$AZ = \arccos\left[-\frac{\sin \delta - \cos(90 - \beta)\sin \phi}{\cos \phi \sin(90 - \beta)}\right] \quad (13)$$

and the solar azimuth angles after solar noon were calculated as $AZ^* = 360 - AZ$.

From forest-edge height and distances between plots and the forest border, vertical angles were calculated between each plot and the top of the forest edge along the horizontal angle equal to the sun azimuth at each time for which shadow location was being calculated. A plot was in shade if the vertical angle to the top of the forest edge was greater than solar altitude at that time.

Reconstructions and data analysis

Sapling arrivals and climate.—The approximate age and establishment year of live saplings was determined

from branch whorl counts. For dead saplings, branch whorl count gave only approximate age at death, and the determination of their establishment year was not possible. Thus we integrated sapling approximate age, size class, and health status (dead vs. live), and defined broad categories of saplings that established in different time periods (see *Results* for more detail). Sapling invasion into the field was compared with long-term drought and temperature data from nearby weather stations. Droughtiness was expressed as a dimensionless, 12-month standardized precipitation index (SPI) that describes droughts (negative values) and wet periods (positive values) in terms of precipitation deficit relative to “normal” historical precipitation for a given location (Heim 2000). Temperature was expressed as a dimensionless standardized temperature index (STI) that gives absolute differences between average monthly maximum temperature and long-term monthly mean, from May to September, in units of standard deviation.

Invasion relative to forest edge, seed rain, and shade.—We compared the distribution of all sapling size classes relative to forest edge using nonparametric pairwise Wilcoxon rank-sum tests. We tested whether saplings differed in their distribution relative to the nearest forest edge by size class or by health status (live or dead). Z scores were reported using Bonferroni-corrected significance levels. The effect of seed rain and shade on sapling densities was studied by dividing the field into areas with plots that received low or high seed rain (<100 and ≥ 100 seeds·plot⁻¹·yr⁻¹, respectively) and were in low, medium, or high shade (<4 , 4–8, and >8 h/d, respectively), resulting in six different combinations of seed rain and shade. In addition, seed rain and shade (both log-transformed to approximate normality) were tested against distance to forest edge as predictors for sapling density, using conditional spatial autoregression (CAR). Final fits for the two competing models, the Seed and Shade Model (SSM) and Distance-Based Model (DBM), were determined by a forward stepwise procedure from full models that included centered quadratic terms and interactions. The models and individual terms were tested by likelihood ratio tests on nested models (Cressie 1993:562).

Recent invasion relative to earlier invasion.—Average densities of live small (0.2–1 m tall) saplings from recent invasion were compared under different density classes of large (>2 m tall) saplings from earlier invasion (0, 1–5, 6–10, 11–20, and >20 large saplings/plot). This analysis was restricted to high seed rain plots (≥ 100 seeds/plot) because only these plots contained high densities of large saplings (>10 saplings per plot). To control for the forest-edge shade, the analysis was carried out separately within each of the three predefined shade categories. Arrival of new saplings to the plots with large saplings was considered to be facilitated if small-sapling density there was greater than on plots without large saplings, and inhibited if it was lower. These analyses were repeated

for the density of dead small saplings, which reflect mortality on large sapling plots. The association between live small and large saplings and their spatial patterns on the low seed rain plots (<100 seeds/plot) in the field center (~100 × 280 m area, >30 m away from the forest edge) was studied using Standard Normal Deviates (SND) that characterize spatial relationships within and between different types of points in space (Sokal and Oden 1978, Cliff and Ord 1981, Dovčiak et al. 2001). SND were calculated for prespecified distance classes (0–4 m, 4–8 m) as the difference between the observed and expected number of between- and within-size class point pairs in units of standard deviation (assuming random assignment of size classes on the given set of spatial locations). SND > 2 indicate clumping or positive association, while SND < -2 indicate overdispersion or negative association. The relationship of small-sapling density to large-sapling density across the entire field was tested by including the density of large saplings as an additional predictor in the CAR models.

Growth and recruitment relative to shade.—To corroborate changes in sapling densities, short- and long-term growth were studied in each of the three forest-edge shade categories for live saplings in 0.2–1, 1–2, and 2–4 m size classes. Short-term growth was approximated by the average length of 1997 terminal shoots, which reflect a slightly less optimal than average season. Long-term growth was approximated by the average number of branch whorls (approximate age) since, for a fixed height of each individual size class, a greater number of branch whorls indicates a greater number of shorter yearly height increments, and thus slower growth over a period of years. To minimize the influence of competition between saplings, we analyzed the growth of each size class only on plots where no taller size classes were present; in addition, for this analysis we used only plots with a maximum of five saplings <2 m tall and a maximum of three saplings 2–4 m tall.

RESULTS

Timing of sapling arrivals

Climatic conditions during the course of succession at Boot Lake were characterized by mostly above-average precipitation (SPI positive) and below-average or average temperature (STI ≤ 0), with the exception of one extreme drought centered on 1988 (documented for the whole region) and a minor drought during early successional stages in 1980 (Fig. 3A). The first large invasion into the field may have occurred in 1980 (Fig. 3B). The number of living saplings in the 12–17 yr old annual cohorts is approximately constant, potentially indicating continuing abundant invasion into the field in the 1980–1985 period. Except for the year 1980, precipitation was above average or average, and temperature fluctuated around average values during this

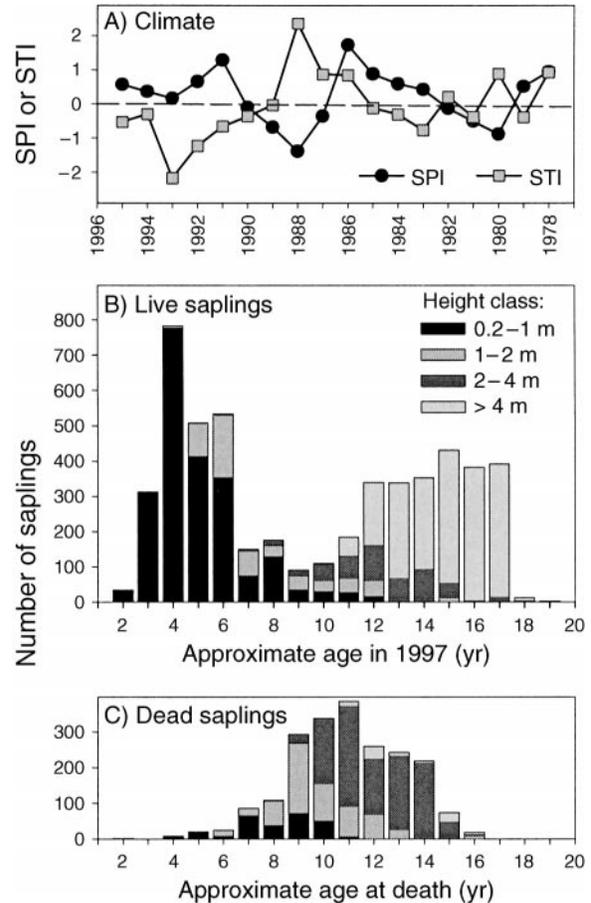


FIG. 3. Age structure of invading white pine relative to climate. (A) Growing-season climate (May–September) during the course of succession (1978–1995). SPI gives the average 12-month standardized precipitation index (a drought index) for each growing season. STI gives the average monthly standardized temperature index based on average monthly maximum temperature for each growing season. SPI and STI values above zero indicate wetter and hotter conditions than average; values below zero indicate drier and cooler conditions than average. (B) Total number of all living saplings within the surveyed area by approximate age and height classes. (C) Total number of all dead saplings within the surveyed area by approximate age at death and height classes; sapling height classes are as in (B).

period (Fig. 3A). After the initial invasion in 1980–1985, there was a decrease in successful establishment during the 1987–1989 period of below-average precipitation and above-average temperatures (Fig. 3A), as indicated by the low number of ~7–11 yr old living saplings in 1997 (Fig. 3B). The year 1988 had the fifth lowest regional growing-season precipitation in ~100 years (Inouye et al. 1987), and the lowest precipitation and highest temperature during the course of invasion at the study site (Fig. 3A). The following period of mostly well below average temperatures and above-average precipitation (1991–1994) coincided with rapid sapling invasion into the field and considerable sub-

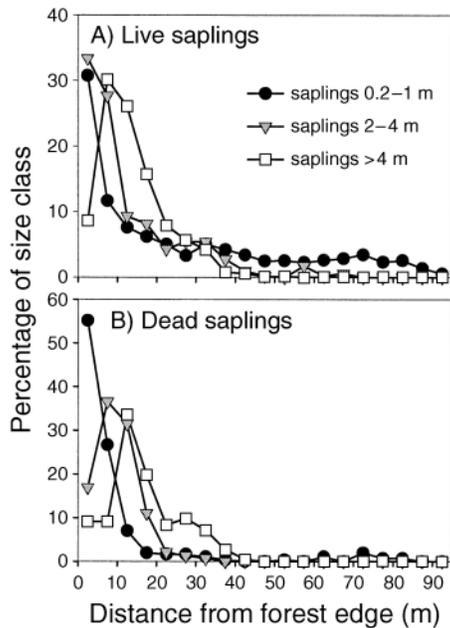


FIG. 4. Distribution of white pine height classes within the field relative to the forest edge. (A) Dispersion of live saplings; (B) dispersion of dead saplings. Height class 1–2 m was omitted for clarity because it is least common and its dispersion is intermediate between the dispersion of height classes 0.2–1 and 2–4 m. Percentages instead of absolute numbers of saplings are given to facilitate comparison of dispersion of the individual size classes (the sum of percentages at all distances is 100% for a given size class). The absolute sapling numbers were as follows: for 0.2–1 m class, ~2200 live and ~300 dead saplings; for 2–4 m class, ~500 live and ~1100 dead saplings; and for >4 m class, ~1900 live and ~100 dead saplings. Percentages were adjusted for varying area between distance classes.

sequent recruitment to the 1–2 m size class (Fig. 3A, B). Observations in 1998 and 1999 confirmed that mortality within the recent invasion wave appeared low and that saplings were growing and recruiting to taller size classes (M. Dovčiak, *personal observation*).

The majority of all dead saplings were ~9–14 years of age at death, and the majority of 0.2–1 m tall dead saplings were 7–10 years of age at death (Fig. 3C). The majority of 0.2–1 m tall dead saplings were dead for <7–10 years (since the abundant invasion started 17 years prior to investigation) and >2–3 years (as indicated by their missing or bleached bark). Saplings were not likely to originate during the drought period, since only a few live saplings appeared to originate from that time (Fig. 3A, B). Thus the majority of dead saplings had been dead for at least 3 but at most 10 years (i.e., died either during or after the drought) and were mostly of pre-drought origin (Fig. 3B, C). The greater number of dead saplings in the 2–4 m size class (~1100 saplings) vs. the 0.2–1 m size class (~300 saplings) may have resulted from either the disappearance of shorter dead saplings over time after they

died, or from low initial mortality of pre-drought saplings (at the 0.2–1 m size class), followed by their increasing mortality as they grew larger and competition for resources increased. The age approximations show that saplings can be conservatively pooled in two broad categories that originated in different periods: “pre-drought” saplings (all saplings >2 m tall) and “post-drought” saplings (live saplings 0.2–1 m tall).

Spatial pattern of invasion relative to forest edge

White pine size classes differed in their dispersion relative to the forest edge (Fig. 4). Young 0.2–1 m tall live saplings were present at all distances from the forest edge, and, on average, they were distributed farther from the forest edge than older >2 m tall live saplings, which were abundant only within ~35 m of the forest edge (Table 1, Fig. 4A); thus it appears that either the post-drought invasion during the period of lower temperatures and higher precipitation was more successful in the field center than was the pre-drought invasion during a somewhat less favorable climate, or that any pre-drought saplings that may have established in the field center died. However, there were almost no dead saplings of any size class present >35 m from the forest edge, while many were present near the forest edge, including dead 0.2–1 m tall saplings (Fig. 4B). Thus it appears that dead saplings either did not persist in the field center and persisted disproportionately well near forest edges, or more likely, pre-drought saplings never recruited to >0.2 m height within the field center. Taller dead sapling size classes were distributed progressively farther out into the field than were shorter ones (Fig. 4B, Table 1), suggesting that mortality in the pre-drought invasion wave started in densely colonized and heavily shaded areas closest to the forest edge and moved progressively outward into the field following the outward shift in the density of surviving saplings as saplings grew and recruited to taller size classes (Fig. 4A). As a consequence, live saplings >4 m tall were distributed farther from the forest edge than were dead saplings in size classes <4 m and live 2–4 m tall saplings (Table 1). The density of >4 m tall live saplings followed a unimodal distribution, with low density in the immediate vicinity of the forest edge and a peak at ~10 m from the forest edge (Fig. 4A).

Invasion relative to seed rain and shade

The division of the field into the six seed rain–shade categories produced reasonable combinations. The number of hours spent in shade within each shade category did not differ between the high and low seed rain plots (Fig. 5A). Seed rain density was uniform across shade categories on the low seed rain plots, and although it increased with shade on the high seed rain plots (Fig. 5B), it still provided a clear contrast between the two seed rain categories.

The density of pre-drought saplings (saplings >2 m tall in 1997) incrementally increased with shading on

TABLE 1. Distribution of individual height classes relative to forest edge.

Height class	Live saplings			Dead saplings			
	1–2 m	2–4 m	>4 m	0.2–1 m	1–2 m	2–4 m	>4 m
Live							
0.2–1 m	-0.9	8.5*	6.1*	12.2*	12.0*	11.5*	0.7
1–2 m		9.0*	9.1*	11.6*	12.5*	12.6*	3.9*
2–4 m			-7.9*	6.9*	2.4	-1.4	-7.9*
>4 m				15.4*	14.8*	12.4*	-5.5*
Dead							
0.2–1 m					-6.5*	-10.8*	-12.9*
1–2 m						-5.9*	-13.1*
2–4 m							-11.9*

Notes: Table contains z scores from pairwise Wilcoxon rank-sum tests (normal approximation) of the distances of the individual height classes to the nearest forest edge. The z scores that are significant on a Bonferroni-corrected level ($P < 0.05/28 = 0.0018$) are marked with an asterisk. A positive z score means that the height class in the corresponding row is distributed relatively farther from the forest edge than the height class in the corresponding column. A negative z score indicates that the height class in the corresponding row is distributed relatively closer to the forest edge than the height class in the corresponding column.

the low seed rain plots; on the high seed rain plots, it peaked in medium shade where it was greater than in either low or high shade (Fig. 5C), in spite of the higher seed rain in high shade (Fig. 5B). Compared to low seed rain plots, plots with high seed rain displayed considerably increased density of pre-drought saplings in medium and low shade, but additional seed rain did not make a large difference in high shade (Fig. 5C), an observation that corresponds with the pattern of high sapling mortality close to the forest edge (Fig. 4B). Overall, pre-drought sapling density was related positively to both seed rain and shade and negatively to their interaction (driven by the decrease in sapling density in high shade–high seed rain plots), and these terms constituted a more likely model (Seed and Shade Model, SSM; Table 2) than one based on distance to forest edge (Distance-Based Model, DBM; Table 2). Moreover, the SSM was not improved by adding the significant DBM terms (likelihood ratio test: $\chi^2 = 1.25$, $df = 2$, $P = 0.74$), but the DBM was significantly improved by adding the significant SSM terms ($\chi^2 = 66.13$, $df = 4$, $P < 0.00001$).

Unlike the density of pre-drought saplings, the density of post-drought saplings (live saplings 0.2–1 m tall in 1997) incrementally increased with shading in both seed rain levels. While this density increased solely with forest-edge shading in low seed rain plots, it increased with both seed rain and shade in high seed rain plots (Fig. 5D). Thus overall white pine invasion into the field was structured by shade and seed rain, but the role of shade differed between high and low seed rain plots. On the low seed rain plots, shade facilitated the invasion, as sapling density generally increased with increasing shade (Fig. 5C, D). On these plots, mean sapling density was low, the majority of saplings were alive (~92%), most were established in the second invasion wave (~60%), and only a few (~15%) were >4

m tall. Thus the post-drought invasion on the low seed rain plots took advantage of suitable sites left unoccupied by the previous invasion wave. In contrast, mean sapling density on high seed rain plots was ~2.5 times higher than on the low seed rain plots, the majority of saplings (~75%) were established during the pre-drought invasion, a smaller number (~62%) of saplings were alive, and many living saplings (~50%) were >4 m tall. Thus the abundant pre-drought invasion on the high seed rain plots left a relatively small proportion of suitable sites unoccupied for the post-drought invasion.

Pattern of post-drought relative to pre-drought invasion

Although the density of large (pre-drought) saplings was positively related to seed rain (Fig. 6A–C, Table 2), it explained additional patterns in the density of small (post-drought) saplings. Within high shade, any presence of large saplings had a negative effect on the density of live small saplings; the density of live small saplings was highest on plots with no large saplings, and it decreased as the density of large saplings increased (Fig. 6D). In medium and low shade, large saplings appeared to have a negative effect on the post-drought new arrivals only at high densities (≥ 11 large saplings/plot), and a positive effect at low densities (1–10 large saplings/plot), compared to plots with zero large saplings (Fig. 6E, F). On the other hand, sapling mortality during the invasion appeared to be greatest on the plots with the highest density of large saplings (>20/plot) as evidenced by the patterns in the density of dead small saplings (Fig. 6G–I). Since small dead saplings were mostly from the pre-drought invasion, and potentially from the same cohorts as the large saplings, their relationship may indicate density-dependent mortality due to competition for resources in dense pre-

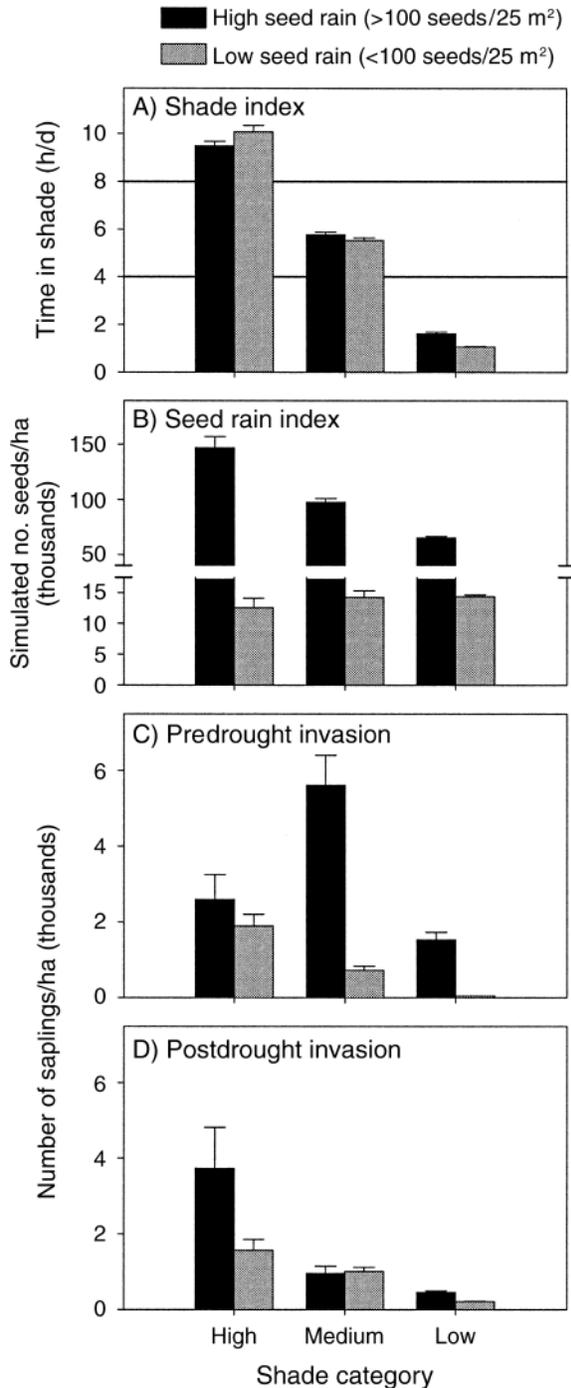


FIG. 5. Pattern of sapling invasion relative to strong gradients in shade and seed rain. Since shade and seed rain indices may not perfectly represent the actual shade and seed rain values within the field, the entire field was divided into areas that distinctly differ in their shade and seed rain. (A) The shade index was used to divide the field into areas of low shade (≤ 4 hours in shade/day), medium shade (4–8 hours in shade/day), and high shade (> 8 hours in shade/day). (B) The seed rain index was used to divide the field into areas of low seed rain (≤ 100 seeds/plot) and high seed rain (> 100 seeds/plot). These categories were chosen so that there are > 30 plots in each combination. Sapling density within these distinct areas was studied separately for (C) pre-drought and (D) post-drought invasion. Error bars show $+SE$.

drought sapling clumps. The spatial association between live small and large saplings in the field center where the amount of shade from the forest edge was very low (< 2 hours of shade) was negative at fine spatial scales (0–4 m), and it was neutral at slightly broader scales (4–8 m, Table 3). Within-size class spatial patterns were random at the broader scales and aggregated at the fine scales. The clumping was stronger for large saplings, indicating stronger environmental structuring of the older size class (Table 3).

Overall, the post-drought sapling density was related positively to shade, negatively to shade–seed rain interaction, and in a complex way to pre-drought sapling density, and these terms constituted a more likely model (SSM) than the model based on distance to forest edge (DBM) (Table 4). Unlike shade, seed rain did not influence the density of post-drought invasion directly (Table 4), probably because it was positively related to pre-drought sapling density (Table 2), and pre-drought saplings colonized a large proportion of the high seed rain plots. On the other hand, in both the SSM and the DBM models, pre-drought sapling density had a negative quadratic effect on post-drought sapling density (Table 4), which is consistent with the negative effects of pre-drought saplings at very high densities and their positive (facilitative) effects at medium and low shade (Fig. 6E, F). The SSM was not improved by adding the significant distance terms from the DBM ($\chi^2 = 1.19$, $df = 2$, $P = 0.55$), but the DBM was improved by adding the additional SSM terms ($\chi^2 = 47.30$, $df = 4$, $P < 0.00001$).

Growth and recruitment relative to shade

For 0.2–1 m, 1–2 m, and 2–4 m size classes, height growth incrementally declined and average age in-

TABLE 2. Spatial regression models for the density of saplings from the pre-drought white pine invasion into the Boot Lake old field.

Best predictors	Coefficient	SE
Seed and Shade Model, SSM ($\chi^2_4 = 140.0478^{***}$)		
Seeds	0.0635	0.0627
(Seeds) 2 †	0.1156 ***	0.0300
Shade	0.6471 ***	0.0696
Seeds \times shade	-0.2316 ***	0.0514
Distance-Based Model, DBM ($\chi^2_2 = 75.1645^{***}$)		
minDist	-0.0143 ***	0.0027
(minDist) 2 ‡	0.0002 ***	0.0001

Notes: The best fits were determined by forward stepwise procedure for two alternative models, the Seed and Shade Model (SSM) and the Distance-Based Model (DBM). Full models included quadratic terms and interactions of all potential predictors: seed rain (seeds) and shade for the SSM and closest distance to forest edge (minDist) for the DBM. All variables except distance were log transformed to approximate normality. The error structure was modeled by conditional spatial autoregression (CAR). The models were tested by likelihood-ratio tests (χ^2_{df}) due to Cressie (1993:562).

$^{***} P \leq 0.001$.

† Quadratic terms in the full SSM were (Seeds) 2 and (Shade) 2 .

‡ Quadratic terms in the full DBM were (minDist) 2 .

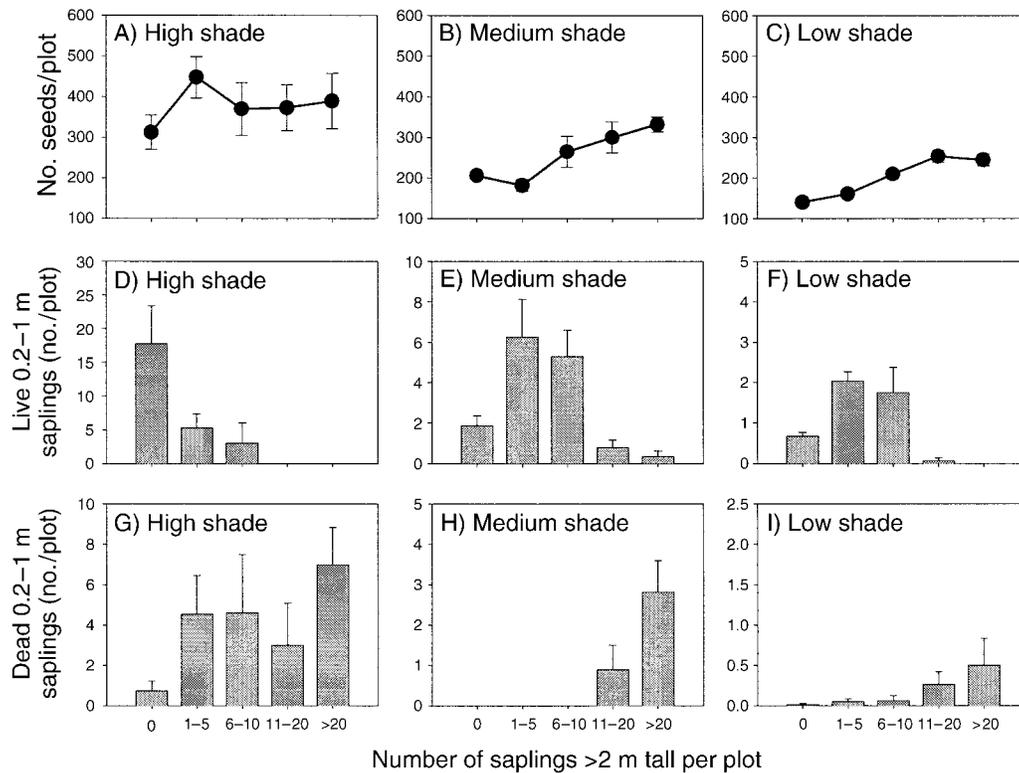


FIG. 6. Pattern of post-drought invasion relative to pre-drought invasion, seed rain, and shade. (A–C) Seed rain at different densities of saplings established during the pre-drought invasion wave (>2 m tall in 1997) and in different shade categories. (D–F) Mean number of saplings established during the post-drought invasion wave (live 0.2–1 m tall saplings in 1997) relative to the density of saplings established during the pre-drought invasion wave (>2 m tall in 1997), by shade category. (G–I) Mean number of dead 0.2–1 m tall saplings (established pre- or post-drought) at different densities of saplings >2 m tall and in different shade categories. Shade categories are defined as in Fig. 5. Only plots with high seed rain (>100 seeds/25 m²) were considered since only they contained greater densities of large saplings (>10 per plot). Error bars show \pm SE.

creased with increasing shade (Fig. 7). In low shade, we observed \sim 30 cm average height increments of 0.2–1 m tall saplings, which would lead to saplings being recruited to the next size class in approximately the third growing season after they reach 0.2 m in height. In high shade, however, we observed an average height increment of only \sim 10 cm, implying that the average sapling residence time in the 0.2–1 m size class is eight growing seasons (Fig. 7A). Sapling residence time in the 1–2 m size class appears to be less than two growing seasons in low shade (\sim 65 cm average height increment) but it could not be calculated in high shade because no plots satisfied the low sapling density criteria (Fig. 7B). Sapling residence time in the 2–4 m size class appears to be less than three growing seasons in low shade (\sim 75 cm average height increment) and approximately seven seasons in high shade (\sim 30 cm average height increment) (Fig. 7C). If we add individual residence times to the 2–3 years required for seedlings to reach 0.2 m height, 2–4 m tall saplings should be 7–11 years old in low shade and 12–19 years old in high shade (using a conservative low-shade residence time for the 1–2 m size class instead of the missing high-shade residence time). The measured average age of the 2–4 m tall saplings was \sim 10 years in low shade

and \sim 12–13 years in high shade (Fig. 7F), suggesting that slowly growing saplings in high shade died (cf. Fig. 4B).

DISCUSSION

The old fields within the oak savanna system of the drought-prone and nutrient-poor Anoka Sand Plain in the north-central United States have been characterized by slow and limited tree establishment (Inouye et al. 1987, 1994, Lawson et al. 1999, Foster and Tilman 2000). Although the locally extensive and rapid white pine invasion into the abandoned field near Boot Lake differs from other studies in the Anoka Sand Plain, pines are generally capable of invading xeric grasslands (Richardson and Bond 1991), and life history traits rank white pine among potentially more invasive pines (Grotkopp et al. 2002). Tree recruitment in savannas occurs in occasional favorable climate spells (Higgins et al. 2000, Jeltsch et al. 2000) that maintain tree populations in environments generally unfavorable for juveniles, but favorable for adults (such as dry, sandy soil for white pine, Wendel and Smith 1990). In species with long life-spans and high fecundity, such as white pine, population growth during such favorable periods is “stored” in the adult population (Warner and Ches-

TABLE 3. Sapling spatial patterns within and between post-drought and pre-drought sapling size classes within the field center.

Spatial structure	Sapling height (m)	SND by distance class (m)	
		0–4	4–8
Post-drought	0.2–1	1.97	1.35
Pre-drought	>2	3.91*	1.67
Post-drought vs. pre-drought		–2.53*	–1.58

Notes: Spatial patterns are expressed as standard normal deviates (SND) for distance classes 0–4 and 4–8 m. SND values ≥ 2 (marked with asterisks) indicate statistically significant positive association or clumping (aggregation) of individual saplings at the given distance class (at $P < 0.05$ significance level) and SND values ≤ -2 indicate statistically significant negative association (overdispersion) at a given distance class.

son 1985). At low adult population density, typical for white pine in the Anoka Sand Plain (Marschner 1974), a storage effect can cause high population growth (Warner and Chesson 1985) within specific spatiotemporal windows (demographic bottlenecks) related to spatial patterns of adults and climatic fluctuations in time (Myster 1993, Sankaran et al. 2004).

Sapling arrivals and climate

At Boot Lake, there were two distinct temporal opportunity windows coinciding with two white pine invasion waves, separated from each other by a severe 1988 drought. The pre-drought invasion occurred during a period with approximately average climate (including a minor drought in 1980), but the post-drought invasion occurred during a moister and cooler than normal period. These climatic fluctuations also influenced the grassland communities of other nearby old fields; the 1988 drought reduced their species richness by 37% and their aboveground biomass by 47% (Tilman and El Haddi 1992), but they recovered to or exceeded pre-drought levels during the subsequent moist period (Tilman 1996). Although the herbaceous species richness and aboveground biomass at Boot Lake may have followed a similar trajectory, high species richness and aboveground biomass did not preclude white pine invasion and recruitment to taller size classes during the moist period. The post-drought white pine invasion at Boot Lake appears to be related to moister and cooler climate rather than to intensifying competition from herbaceous vegetation, which would have decelerated succession and inhibited further tree invasions (Gleeson and Tilman 1990, Foster and Tilman 2000). Moisture influences tree recruitment in exposed old-field environments (De Steven 1991a, b, Davis et al. 1999, Mitchell et al. 1999) and savannas (Higgins et al. 2000, Jeltsch et al. 2000), and white pine seedlings were positively related to moist seedbeds, even within the sheltered environment under forest canopies (Dovčiak et al. 2003).

Distance to forest edge, seed rain, and shade

The invasion at Boot Lake occurred within two types of spatial opportunity window, proximity to forest edge and proximity to seed source. Saplings from both invasion waves were most abundant near the forest edge. However, while the pre-drought saplings were absent from the field center, the post-drought saplings, which invaded during a period of wetter climate, successfully colonized it and recruited to taller size classes there. Tree seedling mortality in old fields tends to be low in wet years and to decrease dramatically over time (De Steven 1991b), and thus the post-drought invasion (recruitment pulse) may be able to speed up succession within the Boot Lake field center (cf. Warner and Chesson 1985, Higgins et al. 2000). In contrast, during average climatic conditions, the forest edge at Boot Lake provided a sheltered habitat that facilitated white pine recruitment (cf. Connell and Slatyer 1977, Finegan 1984). Forest edge additionally served as a heterogeneous seed source. The density of pre-drought saplings was influenced positively by seed rain and negatively by the interaction of seed rain and shade, likely due to higher competition and mortality in the dense sapling clumps in high shade. Seed rain influenced the density of post-drought saplings less obviously, since many suitable sapling establishment sites in high seed rain areas were already occupied, while new suitable sites became available in low seed rain areas in the field center during the moist period. Seed rain appears to limit tree recruitment more than time since abandonment or nitrogen content do in nearby old fields on the

TABLE 4. Spatial regression models for the density of saplings from the post-drought white pine invasion into the Boot Lake old field.

Best predictors	Coefficient	SE
Seed and Shade Model, SSM ($\chi^2_6 = 159.8045^{***}$)		
Seeds	0.0687	0.0449
Shade	0.1814*	0.0721
(Shade) ² †	0.4028***	0.0600
Seeds \times shade	–0.1141**	0.0408
PreDD	0.0995*	0.0438
(PreDD) ² †	–0.0823***	0.0166
Distance-Based Model, DBM ($\chi^2_4 = 13.6897^{***}$)		
minDist	–0.0108***	0.0017
(minDist) ² ‡	0.0003***	0.0001
PreDD	0.1163**	0.0439
(PreDD) ² ‡	–0.0830***	0.0167

Notes: The best fits were determined by forward stepwise procedure for two alternative models, the Seed and Shade Model (SSM) and the Distance-Based Model (DBM). Full models were the same as in Table 2, but they also included pre-drought sapling density (PreDD) and related interaction terms. The error structure was modeled by conditional spatial autoregression (CAR). The models were tested by the likelihood-ratio tests (χ^2_{df}) due to Cressie (1993:562).

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

† Quadratic terms in the full SSM were (Seeds)², (Shade)², and (PreDD)².

‡ Quadratic terms in the full DBM were (minDist)² and (PreDD)².

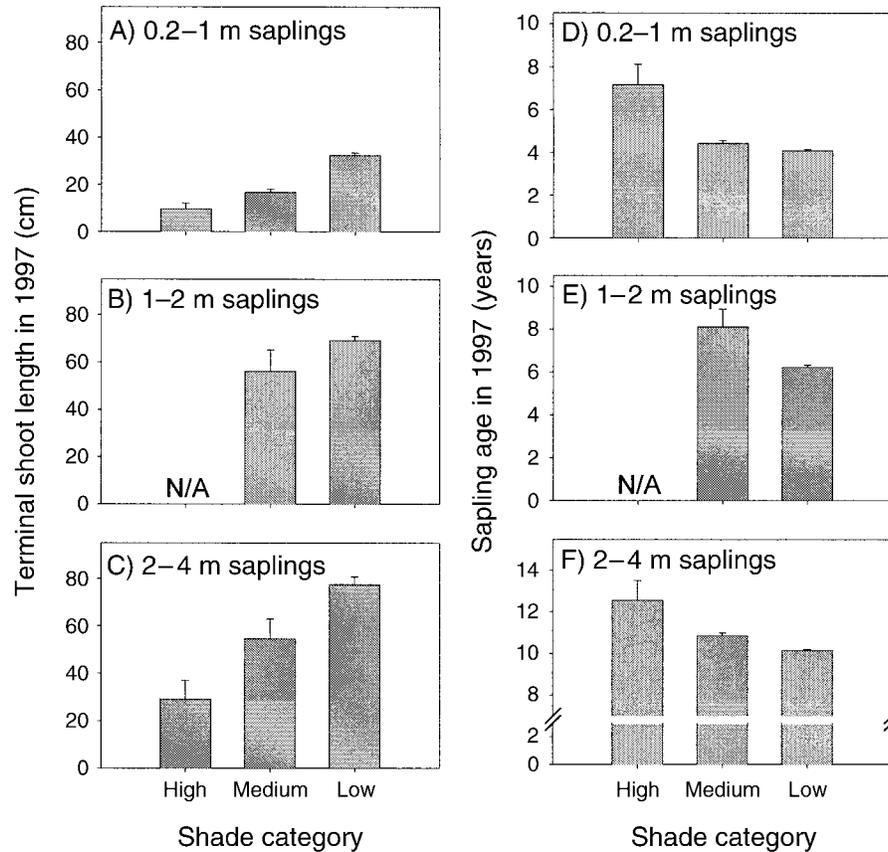


FIG. 7. Annual and long-term growth of saplings of different height classes in different shade categories as expressed by (A–C) their terminal shoot length in 1997 and (D–F) sapling age (number of branch whorls). Shade categories are the same as in Fig. 5. The terminal shoot length and the number of branch whorls was not evaluated for saplings 1–2 m tall in the highest shade because there were too few plots that conformed to the maximum density requirement that we imposed for this height class to control for competition among saplings. Error bars show +SE.

Anoka Sand Plain (Lawson et al. 1999), and more than germination, microclimate, or soil characteristics do in some abandoned tropical pastures (Holl 1999). Complex interactions between seed rain and suitable establishment sites were also documented in forest gaps and clearings in cedar–hemlock forests of British Columbia (LePage et al. 2000) and in simulated Scots pine invasions into French grasslands (Prévost et al. 2003).

Demographic interactions

Large saplings from the pre-drought invasion wave influenced new sapling arrivals in the Boot Lake old field by both facilitative and inhibitory mechanisms (Connell and Slatyer 1977). Large saplings generally inhibited new arrivals in high shade near the forest edge, but only very high densities of large saplings had the same inhibitory effect in medium or low shade. Thus additional shade from large saplings may add to forest-edge shade to inhibit recruitment of new saplings. On the other hand, medium density of large saplings facilitated the establishment of new saplings in medium and low forest-edge shade. Several mecha-

nisms for such facilitation could be at work, but amelioration of climatic extremes (Finegan 1984) and the decrease in competition from grass (Archer 1989) due to added shading appear to be most consistent with the patterns of post-drought invasion. Similar facilitative effects were attributed to nurse shrubs in northern Patagonia (Kitzberger et al. 2000) and to mesquite (*Prosopis glandulosa*) trees in southern Texas (Archer 1989). At Boot Lake, the individual large saplings in areas receiving very low shade (<2 h/d) did not have positive effects on new arrivals. Instead, pre-drought and post-drought saplings appear to be clustered within different environmental patches. Such small-scale heterogeneity promotes grass–tree coexistence in semiarid savannas, and the scale of environmental patchiness and intraspecific competition determine the scale of eventual tree clustering (Myster 1993, Jeltsch et al. 1998, Barot and Gignoux 2003).

Pathways of succession

In the Boot Lake old-field succession toward a white pine forest, spatial variation in white pine seed rain and

forest-edge shade are responsible for three alternative successional pathways, while the temporal variations in climate may accelerate or decelerate white pine invasion into the field and potentially mediate switches among these pathways.

The first pathway can be described as a gradual creeping invasion by white pine, and it may occur near forest edges under average climate conditions and low white pine seed rain. Saplings establish mostly in high shade next to the forest edge, where their growth is slow. When saplings reach >2 m height, they may inhibit newer arrivals in high shade, and their density in low and medium shade is too low to facilitate seedling establishment farther out in the field. Thus the invasion of white pine saplings into the field is slow, although its future rate will depend on the few saplings along the edge that reach reproductive maturity and provide additional shade and seed. Over time this pattern of invasion would result in a creeping advance of the forest edge, during which most of the field retains its grassland character. This pathway resembles slow, sparse tree invasions in other Anoka Sand Plain old fields where white pine forms only ~1% of species composition of old-field tree communities and surrounding forests (Lawson et al. 1999).

The second pathway can be described as a discrete-step invasion by white pine, and it may occur at short to medium distances from forest edges under average climatic conditions and high white pine seed rain. With high seed rain, the chance that seeds will land in suitable microsites is high, and a considerable number of saplings may establish, even in areas with medium and low shade where moisture is more limiting. High-density sapling establishment occurs near forest edges, but saplings recruit faster to taller size classes farther out in medium- and low-shade areas; these saplings facilitate more arrivals in less densely colonized areas until all gaps are filled, leading to a relatively broad, well-defined zone (a step out into the field), that is filled with saplings (i.e., a positive feedback switch, Wilson and Agnew 1992). As opposed to discrete clusters facilitated by individual mesquite trees in southern Texas (Archer 1989), single large saplings in extreme conditions closer to the center of the Boot Lake old field do not have the same facilitative effect, which limits the width of the step-like advance of the forest edge into the field. Unlike the creeping invasion, the discrete-step invasion involves a complex interaction between seed rain, forest-edge shade, and facilitation by earlier arrivals.

The third pathway can be described as a deferred invasion by white pine, and it may occur in a field center at medium to long distances from forest edges where white pine seed rain and forest-edge shade are low. Under average or droughty climate, white pine saplings cannot establish in the extreme environment of the field center, but if the climate becomes more favorable for a period of a few years, white pine sap-

lings may establish and recruit to taller size classes that are less susceptible to the extreme conditions of an open field. Unlike gradually creeping or discrete-step invasion, that rely on white pine seed rain and sheltering effects of forest edges, deferred invasion is less predictable, as it relies on recruitment pulses that correspond to incidences of favorable climate (cf. Higgins et al. 2000, Jeltsch et al. 2000).

The grassland stages documented in other Anoka old fields were attributed to competition for limiting nitrogen (Gleeson and Tilman 1990), but white pine seedling emergence, survival, and growth in forests were unrelated to nitrogen (Walters and Reich 2000, Catovsky and Bazzaz 2002), and white pine generally competes best on dry, sandy soils of low to medium site quality (Wendel and Smith 1990). At Boot Lake, the grassland stage in the field center prior to the post-drought invasion was due to the lack of a spatiotemporal window necessary for white pine invasion. After the drought, a temporal window opened in the field center due to climatic conditions that allowed white pine invasion even in very low shade and low white pine seed rain. Demographic-bottleneck mechanisms, such as the ones described in this paper, need to be considered in addition to more traditional, competition-based mechanisms in order to fully understand vegetation dynamics in tree-grass systems (Sankaran et al. 2004).

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