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SPATIAL AND TEMPORAL PATTERNS OF *PINUS NIGRA* (AUSTRIAN PINE) SPREAD IN FOUR LAKE MICHIGAN SAND DUNE HABITATS

presented by

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By

Khara D. Grieger

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ABSTRACT

SPATIAL AND TEMPORAL PATTERNS OF *PINUS NIGRA* (AUSTRIAN PINE) SPREAD IN FOUR LAKE MICHIGAN SAND DUNE HABITATS

By

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Planted *Pinus nigra* is reproducing and spreading in Saugatuck Dunes State Park Natural Area, significantly altering natural dune conditions and impacting native species. Ten randomly located sites were selected in each of the four main dune habitats for estimating the rates and patterns of *P. nigra* spread and for comparing the selected parameters of the regeneration niches of *P. nigra* and native *P. banksiana*. The spatial occurrence of threatened *Cirsium pitcheri* and populations most threatened by the spread of *P. nigra* were also documented using GPS and GIS techniques. Currently stands of *P. nigra* are spreading to the north in the foredunes and northeast in the inland blowouts, attributed to prevailing southwesterly winds. Foredune stands have increased on average by 37% in area since original plantings in 1963, while inland blowout stands have increased 25% since 1966. The average rates of spread per plant ranged from 0.04 m yr^{-1} to 0.20 m yr^{-1}, but were as high as 15 m yr^{-1}. The wetpannes were considered the most threatened dune habitat, due to high densities of *P. nigra* progeny and the presence of a unique dune flora and fauna. The measured parameters of regeneration niches of *P. nigra* and *P. banksiana* co-occurring in the vicinity of planted *P. nigra* were similar, and no habitat partitioning was apparent. Eleven populations and 29 individuals of *C. pitcheri* were documented in the foredunes and inland blowouts, including five critical areas that contained both *P. nigra* progeny and *C. pitcheri*.

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CHAPTER 1

GENERAL INTRODUCTION

Pinus nigra (European black pine or Austrian pine) has been documented as an invasive species on the dunes of Lake Michigan, reproducing and spreading in Saugatuck Dunes State Park (SDSP), Michigan and ultimately impacting the native vegetation and various dune habitats (Leege 1997, Leege and Murphy 2000, 2001). It has been shown previously to accelerate dune succession, reduce biodiversity, and potentially change ground water levels (Leege 1997, Leege and Murphy 2000, Sherfinski 2000). Furthermore, it can shade out native plant species and ultimately jeopardize the welfare of threatened and/or endangered species such as *Cirsium pitcheri* (Pitcher's thistle) (Leege and Murphy 2001). The presence, reproduction, and spread of Austrian pine in SDSP is just one example of the increasing problem of biological invaders drastically altering native ecosystems.

Biological invaders are species that spread beyond their native range, thriving, dispersing, and reproducing in their new environment, often causing irreversible damage to native communities and ecosystems (Mack et al. 2000). Due to increased global trade, an unprecedented number of organisms are exposed to new habitat areas as human transportation improves, and species are thereby introduced both deliberately and accidentally to new environments (Lodge 1993). Both economically and ecologically, the negative consequences of invasive species can be seen throughout the world. It was estimated in 2000 that the U.S. Department of Agriculture spent $122 billion annually on the control of invasive species in agrarian systems, including associated property damage and resource losses (Delfosse 2000).

Ecologically, biological invasions have not only caused an unprecedented rate of species extinction, but are the second major cause of extinctions after habitat destruction (D'Antonio and Vitousek 1992). Labeled as 'biological pollutants,' and sometimes regarded as a greater threat to native communities than conventional pollution (Drake 1989, Cronk and Fuller 1995), invasive species can have long-term effects on ecosystems by altering fundamental processes such as trophic structure and disturbance regime of an invaded area (Vitousek 1990, Colton and Alpert 1998). In fact, many of these biological invasions are considered irreversible (Coblentz 1990). Native populations and communities are especially impacted when invasives outcompete native species by consuming precious resources or by changing pre-existing environmental conditions (Crawley 1986, D'Antonio and Vitousek 1992, Williamson 1996). Furthermore, it is estimated that approximately 10% of all introduced species will become established and 10% of those established will become invasive (Williamson and Fitter 1996). Plant invaders can alter fire patterns, nutrient cycling, hydrology, and energy budgets of native ecosystems (Mack et al. 2000). Many exotic trees, for example, have been planted in place of native species due to greater resistance to pests and disease, tree hardiness, adaptability to unfavorable conditions, and higher growth rates (Zobel et al. 1987).

Invasions by the genus *Pinus* have been documented worldwide, and at least 16 species have been listed as invasive in the Southern Hemisphere alone (Richardson et al. 1994). The widespread planting of this genus has led to the increased invasions (Richardson 1998a), and in many cases introduced pines have become a vigorous and dominant part of the local flora (Richardson and Bond 1991). A wide variety of problems attributed to pine introductions exists, especially for watersheds, protected areas, and managers of grazing lands (Richardson et al. 1994). Because they tend to grow in large, dense stands that may dominate natural ecosystems, invasive pines can alter ecosystem functions and processes, decrease native biodiversity, alter fire regimes, reduce water yields, change nutrient cycling processes, and alter biomass accumulation processes (Richardson and Bond 1991, Richardson et al. 1994, Richardson 1994). Commonly found on stressed sites, such as nutrient-deficient soils and sand dunes, invasive pines can also provide microhabitat space for native species not usually present under natural conditions (Richardson et al. 1994).

The presence of Austrian pine on the Lake Michigan sand dunes is just one example of an introduced pine dominating and altering a fragile native ecosystem. Originally planted as a sand stabilizer between 1956 and 1972 in the area now known as Saugatuck Dunes State Park Natural Area (SDSPNA), Austrian pine is changing the natural dune ecosystem (Leege 1997, Leege and Murphy 2000, 2001, Sherfinski 2000). Although Austrian pine is native to southern Europe, northern Africa, and Asia Minor, it has been planted worldwide due to its broad environmental tolerance (Dalimore and Jackson 1966, Burns and Honkala 1990). For example, it was one of the earliest tree introductions in the United States, and was planted in the Sandhills of Nebraska in 1891 as well as on the Great Plains in the early 1900's as a windbreak. In the northeast areas of the U.S., Austrian pine has been especially successful on acidic soils, and in the Great Lakes it has been successful on a broad range of soils including sandy loam, silty clay, and calcareous soils (Parfitt and Wade 2000). It has been widely planted as an ornamental and along roadsides throughout Michigan and surrounding regions (Barnes and Wagner 1981). Austrian pine also has been widely planted in the Southern hemisphere and has been documented as a naturalized invasive in Australia and New Zealand, invading large tracts of land (Richardson et al. 1994). The invasion of Austrian pine has affected Eucalypt forests, grasslands, scrublands, and montane shrublands in these areas. In New Zealand, Austrian pine established most frequently beneath tussock canopy and in sparse, low-growing vegetation between tussocks. It was documented to be the most influential, widespread invasive pine on the island and less affected by pests and disease than other pine species. Austrian pine seedlings are also considered less palatable to herbivores than other pine species at these sites in New Zealand (Crozier 1990). Although Austrian pine is found in smaller populations and is more limited in distribution in Australia than in New Zealand, it is still regarded as one of the most influential invasive pines. In North America, it is reported to have become naturalized in areas of New England and parts of the Great Lakes region of the U.S., where it is successfully reproducing and surviving without human intervention (Burns and Honkala 1990, Parfitt and Wade 2000).

Mature Austrian pine individuals produce a dense, pyramidal crown with two leaves per fascicle (Ouden and Boom 1965). Under favorable conditions, Austrian pine can grow to 30 m in height and reach 300 years of age (Van Haverbeke 1986). Its reproductive maturity usually occurs at 15-20 years of age, similar to most other pines, and maximum cone production occurs between 60-90 years. The window of time for successful pollination, similar to most pines, is short, around three days (Barnes and Wagner 1981). Under most conditions trees produce cones every year, but every 3-4 years the cone production is abundant. One pinecone will usually produce about 30-40 seeds, approximately 50% of which are viable (Leege 1997). Austrian pine seeds are wind-dispersed, although some animal dispersal is also thought to occur (Burns and Honkala 1990).

Leege and Murphy (2000, 2001) showed the extent to which introduced Austrian pine has become dominant on the dunes, and documented certain aspects of its reproduction, germination, seedling establishment, and invasive potential. They demonstrated that Austrian pine survivorship varied across dune habitats, being greatest in the wetpannes and lowest in the foredunes (for a description of the dune habitats see Chapter 2). Foredune seedlings had the lowest survivorship because of greater canopy cover, lower light intensity, and a deeper needle-litter layer (Leege and Murphy 2000, 2001). Leege (1997) and Leege and Murphy (2000, 2001) also documented that the wetpannes contained the highest growth rates of Austrian pine populations, compared to other dune habitats.

Leege and Murphy (2000, 2001) examined some microsite conditions that could influence seedling establishment and success. They investigated the role of soil moisture, light levels, litter layer depth, canopy openness, and soil pH on Austrian pine seedling establishment. Soil moisture was found to be the most important abiotic factor affecting germination and survivorship of Austrian pine, while light intensity and litter layer were found to be important in establishment and growth.

Some aspects of Austrian pine dispersal were also studied by Leege and Murphy (2000). Seed cones and seeds were collected and counted, and mean seed production per reproductive tree was calculated. They found average seed production per tree in the foredunes to be 10 times higher than in the wetpanne and inland blowouts, and 20-40 times higher than along the surrounding deciduous forest.

Sherfinski (2000) and Benefiel (unpublished report) examined the effects of Austrian pine on wetpanne ecology by comparing wetpanne characteristics in the presence and absence of Austrian pine. They studied the transpiration rates of Austrian pine and the native *Pinus banksiana* (Jack pine), and the potential long-term effects of their transpiration rates on wetpanne hydrology. Sherfinski (2000) concluded that Austrian pine has the potential to transpire more than Jack pine, due to a greater total leaf surface area, ultimately affecting ground water levels for wetpannes and thus, changing surrounding wetpanne flora and fauna.

Currently, the presence of invasive Austrian pine on the Lake Michigan sand dunes is of great concern. Austrian pine has the potential to rapidly alter native sand dune conditions and ultimately threaten endemic species, such as Pitcher's thistle. This study focuses primarily on the rates and spatial patterns of Austrian pine spread immediately surrounding planted Austrian pine stands on the dunes of Lake Michigan, and compares the regeneration niches of Austrian pine and Jack pine in the dune habitats. Chapter 2 documents the rates and spatial patterns of Austrian pine spread in the study site. The rate of spread is of particular interest because it suggests how quickly the dune environment may be altered by further Austrian pine establishment. The spatial patterns of spread in four habitats were examined to identify the specific habitats most impacted by the spread of Austrian pine and to pinpoint the areas most likely to be affected by Austrian pine. Chapter 3 compares some aspects of the regeneration niches of Austrian pine and Jack pine near Austrian pine stands in each dune habitat. The pattern of occurrence of both species in and around planted Austrian pine stands were compared, and microsite conditions favorable for the establishment of seedlings and saplings of both species were determined. Finally, Chapter 4 documents the spatial occurrence of Pitcher's thistle, an endemic plant on the Federal list of threatened species, and identifies areas where Pitcher's thistle populations are in close proximity to areas of Austrian pine spread in the study site.

CHAPTER 2

RATES AND SPATIAL PATTERNS OF INTRODUCED *PINUS NIGRA* (AUSTRIAN PINE) SPREAD ON THE DUNES OF LAKE MICHIGAN

INTRODUCTION

Invasion theory

Successful invasions are usually dependent upon characteristics of both the invader and the recipient environment. Habitats characterized by low levels of vegetation cover can easily be invaded by exotic plants, where competition with native species is limited (Crawley 1987). Areas with low levels of vegetation cover are often found on unstable substrates, nutrient-poor soils, or where there is high competition for ground water. In fact, most invasive pine trees are found in marginal habitats (Richardson and Bond 1991). It has also been well-documented that sites subject to some form of alteration in level of disturbance are especially vulnerable to invasive plants (Baker 1974). For example, changes in grazing and browsing, fire frequency, deforestation, and shifting cultivation have been cited to precede pine invasions (Richardson and Bond 1991). In addition, Richardson et al. (1994) listed four vegetation types most vulnerable to pine invasion: sparse vegetation on coastal dunes (most vulnerable), grassland, shrubland, and forest (least vulnerable).

It has been documented that invasive plants usually have a short juvenile period, small seed mass, and rapid population growth (Rejmanek and Richardson 1996). Also, longer flowering periods and vegetative reproduction are characteristics commonly associated with invasive plants. There are also some characteristics of pine trees that make them excellent invaders, such as small seed mass, short juvenile periods, and short intervals between large seed crops (Strauss and Ledig 1985, Richardson and et al. 1994). Richardson and Bond (1991) claimed that pines are successful colonizers, and in some cases invaders, due to drought-tolerance, subsistence in nutrient-poor sites, well-dispersed seeds and pollen, lack of required co-adapted agent, and ability of new colonies to form from isolated pioneers.

Pine spread is a dynamic process that is influenced by climatic factors, grazing pressure, species ecophysiology, seed source size and location, duration of delayed germination, seed dissemination duration, and site requirements (Ledgard 1988, Belton and Ledgard 1991, Richardson and Bond 1991, Richardson et al. 1994). Initial pine dispersal and spread occur in a negative exponential curve from the edge of the parental stands (Yocum, 1968, McCaughley et al. 1986, Richardson 1998a). Dispersal distances of pine seeds usually range up to 100 m from the parental source, but distances up to 8 km are common and 25 km was observed in one study (Richardson et al. 1994). At one location in New Zealand, Austrian pine seedlings were found up to 250 m from the parental source and most were found downwind (Ledgard 1988). Dispersal distances of pine seeds, and consequently tree spread, are also influenced by seed mass: larger seeds, such as those of Austrian pine (mean seed weight 0.0175 grams) (Burns and Honkala 1990), tend to land closer to the parental tree than smaller pine seeds. Most long distance seed dispersal originates from "take-off" sites, such as a ridge, hilltop, slopes exposed to prevailing winds, or via animal transport (Ledgard 1988).

Populations of spreading pine generally occur as masses of even-aged seedlings (Ledgard 1988). It also has been documented that pine seedlings sometime do not appear until several years after the parents first produce cones. In one study, *Pinus mugo* (Dwarf mountain pine) seedlings were not found until the parents were age 15, although cones are usually produced before age 8. Pine trees have also been documented to produce cones earlier in harsher environments (i.e., water-stressed sites) (Ledgard 1988).

Directions of spread seem to be primarily controlled by the location and timing of the first arrival, topography, and climate, including prevailing wind speed and direction. Rates of pine spread, on a per tree basis, typically range from 81-400 m yr^{-1} in North America to as much as 1500 m yr^{-1} in Europe on favorable sites (Richardson et al. 1994). At least one study examined pine spread around plantations in Australia and defined "light tree spread" as 1 individual/ 200 m^2 and "very low density spread" as ranging from 1 individual/ 10,000 m^2 to 1 individual/100,000 m^2 (Belton and Ledgard 1991).

Pines are usually wind-dispersed, but birds and mammals are also known to influence the rates and spatial patterns of population spread (Ledgard 1988, Richardson 1998a). Especially *Sciurus carolinensis* (Grey squirrel), species of *Calyptorhynchus* (Cockatoos), *Peromyscus leucopus* (white-footed mouse), and various species of rabbits have been known to disperse pine seeds (Buchanan 1989, Belton and Ledgard 1991, Richardson 1998a). In fact, stands of invasive *Pinus pinea* (Italian stone pine) increased in size in at least one site due to seed dispersers that were attracted to the pine stands (Richardson and Cowling 1995). In fact, Richardson (1998b) cited rodents as an integral part of pine dispersal and establishment. Conversely, rabbits, hares, and grazing livestock have been known to control populations of Austrian pine and other pines in

New Zealand by browsing seedlings (Richardson and Bond 1991, Richardson et al. 1994), and *Didelphis virginiana* (opossums) have been cited to severely browse developing Austrian pine seedlings (Wills and Begg 1986). However, Richardson et al. (1994) found no evidence that seed predation has prevented spread in any region.

Lake Michigan sand dunes

Due to the shifting sand, the Lake Michigan sand dune ecosystem is an environment subject to disturbance, characterized by dry conditions caused by porous sand and minimal shading (Peterson and Dersch 1982). A strong prevailing southwesterly wind from Lake Michigan is influential in creating distinct habitats, including foredunes, inland blowouts, wetpannes, and forested dunes (Olson 1958) (Figure 2-1). Although it is recognized that there are more than four main dune habitats in this system, these are the primary habitats recognized and used in previous studies (Leege 1997, Leege and Murphy 2000, 2001, Sherfinski 2000) and throughout this paper. The foredunes are the youngest dunes near the beach and run parallel to adjacent Lake Michigan. Dune formation is initiated when foredune vegetation, such as stands of *Ammophila breviligulata* (Marram grass), establish and anchor the sand with their roots and rhizomes. These open areas are characterized by especially high light and dry surface conditions, and are subjected to high levels of sand burial or removal. The wetpannes (also known as interdunal ponds) are low-lying areas that can become saturated and contain standing water when the water table is high, but may be completely dry at other times. Wetpannes have a unique dune flora and fauna that exploit the moister conditions. The oldest and most stable dunes, known as the backdunes or forested dunes, are found furthest from the beach. The forested dunes are characterized by deciduous forest vegetation growing on dune sand. Occasionally disturbance events will create blowout regions, characterized by open areas of shifting sand, referred to as inland blowouts.

Research questions

This chapter addresses the following questions:

1. What is the rate and spatial pattern of Austrian pine spread in the study site?
2. What are the primary directions of spread?
3. Which habitats are most invaded by Austrian pine and which areas contain the most Austrian pine regeneration?

To answer these questions, data were collected during the summers of 2001 and 2002 in each of the four dune habitats in the study site: foredunes, forest edge, inland blowouts, and wetpannes.

METHODS

Study site

This study was conducted in SDSPNA near the city of Saugatuck and located in Allegan County, MI (42° 41'N, 86° 12'W) (Figure 2-2). The Natural Area lies north of the Kalamazoo River and is in the southern portion of the park.

The average annual rainfall for the study site is between 76 and 81 cm (Seeley 1917). The mean annual temperature is approximately 8.3°C, while the mean January and July temperatures are -3.8°C and 21.1°C, respectively. The lowest temperature can reach -23°C, while the highest temperatures range from 34°C to 36°C (Seeley 1917). The winds primarily prevail from the southwest (Eichmeier 1971), and average wind speed is 16.4 km hr^{-1}, average gust speed is 36.8 km hr^{-1}, and high wind speed is 28.8 km hr^{1} (Andresen 2003). During storm events, high winds range from 40.3 km hr^{-1} to 53.1 km hr^{-1} (Andresen 2003).

Approximately 26,000 Austrian pine trees were planted as small seedlings in the study site between 1956 and 1972 by private landowners as part of a sand stabilization measure. The seedlings were planted in each of the four previously defined dune habitats throughout the study site (foredune, forest edge, inland blowout, and wetpanne). In the last decade, many of the original trees became reproductively mature and Leege (1997) was the first to fully document the successful establishment and growth of Austrian pine on the Lake Michigan sand dune.

Sampling sites

To sample Austrian pine rates of spread (m yr^{-1}), spatial patterns of spread, and seedling and sapling densities (# individuals/m^2), 10 sites were randomly selected in each of the four habitats using a stratified random sample design. The sample size of 10 sites per habitat was considered to be adequate, based on a power statistical analysis for each habitat (Z-test). A stratified random sample was used in each habitat to ensure representative sampling of the entire study site (Figure 2-3). In the foredune, inland blowout, and wetpanne habitats, study sites were comprised of stands of mature (planted) Austrian pine trees. In the forest edge, a habitat site was defined as a 50 m x 15 m area along the edge of the forest, adjacent to the planted Austrian pine trees (Figure 2-3). Fifteen meters was chosen as the greatest distance to randomly sample Austrian pine spread into the forest due to poor visibility for seedlings and saplings in the dense forest vegetation (Figure 2-3).

The study site contains two large inland blowouts, formed by strong southwesterly winds eroding the dune surface following post-logging disturbances. In the study site, wetpannes are usually found on the eastern (i.e., inland) side of the foredunes. Austrian pine was originally planted in the foredunes, inland blowouts, and areas surrounding the wetpannes of the Natural Area. It was not planted within the deciduous forest, but sampling was performed in this habitat to document any Austrian pine intrusion. The forested dunes comprise the oldest, most stable dunes, and are found on the eastern edge of the study site.

Sample sites in the foredunes, inland blowouts, forest edge, and wetpannes contained planted Austrian pine stands that varied in size, density, and individual tree characteristics. In the foredunes, the average stand size ranged from 9 m^2 (consisting of 2 trees) to 7,500 m^2 and averaged 1,853 m^2. Density of foredune stands varied from 1.6 trees $100m^{-2}$ to 21 trees $100m^{-2}$ and averaged 9.1 trees $100m^{-2}$. Stand age ranged from 32-39 years and averaged 38 years. Average tree height was estimated as 6.9 m and average stem diameter at breast height (DBH) (1.25 m above ground level) was 20.3 cm (Leege 1997). Stands in the inland blowouts ranged in size from 576 m^2 to 7,740 m^2, and averaged 2,276 m^2. Stand density ranged from 1 tree $100m^{-2}$ to 28 trees $100m^{-2}$, and averaged 9.3 trees $100m^{-2}$, while stand age ranged from 33 years to 39 years and averaged 35 years. Average tree height was estimated as 7.1 m and DBH as 15.6 cm (Leege 1997).

Austrian pine stands adjacent to the native forest ranged in age from 34 to 41 years and averaged 38 years. Although forest-edge stand size was not estimated, since sample sites were along a 50 m transect and 15 m into the native forest, Leege (1997) documented that forest edge stands averaged 11.8 trees $100m^{-2}$. Average tree height was estimated as 8.9 m and DBH as 14.8 cm (Leege 1997). Wetpannes ranged in size from 37.4 m^2 to 1680 m^2 and averaged 307.5 m^2. Adjacent Austrian pine trees ranged in age from 31-41 years and averaged 36 years, and average stand density was 11.7 trees $100m^{-2}$ (Leege 1997). Tree height was estimated as 9.6 m and DBH as 17.2 cm (Leege 1997).

Rates and spatial patterns of Austrian pine spread

To determine the rates and spatial patterns of Austrian pine spread, sampling occurred in each of the 40 previously described habitat sites. Seedlings were defined as individuals less than 20 cm in height (Wenny and Dumroese 1991). Saplings were individuals greater than 20 cm but less than 30 years of age, thereby including all Austrian pine regeneration. Seedlings and saplings that have established through natural reproductive processes are termed regeneration, and collectively referred to as progeny. Because this study was designed to determine the rates and spatial patterns of Austrian pine spread from the original plantations, all individuals that had established through natural processes (i.e., were not planted) were included. Since Austrian pine plantations in the park were first established in 1956, and the species typically starts reproduction after 15 years of age (Burns and Honkala 1990), all Austrian pine progeny in the study site were assumed to be less than 30 years of age. For comparative purposes, Jack pine seedling and sapling densities were also estimated in each habitat and will be discussed in Chapter 3.

Tree age determination

Austrian pine age determination was based on DBH measurements and whorl counts. Relationships between age and DBH were determined for each dune habitat with the assistance of Mr. Joseph Harsh. See Appendix A1 for methodology and relationships of age and DBH for all four dune habitats.

Rate estimation

Estimates of the rates at which Austrian pine trees are spreading from planted trees were based on analysis of the ages of seedlings and saplings and their distances from presumed seed-source trees, which were assumed to be the closest mature individual. The following equation was used:

$$\text{Rate (m yr}^{-1}\text{)} = \frac{\text{distance from seed source (m)}}{\text{(age of seed source trees in years -15) - age of seedling and sapling (yrs)}}$$

The rate of spread (m yr^{-1}) reflects the rate at which an individual Austrian pine tree has become established in the dune habitat, based on its distance from the assumed parental source and the ages of both the progeny and parental tree stand, and it is acknowledged that some seeds may have been dispersed to greater distances than recognized in this work. A factor of 15 years was subtracted from the age of seed source trees to account for the fact that Austrian pine does not generally reproduce before age 15 (Burns and Honkala 1990). Age of parental trees and larger sapling trees was estimated from DBH, as described in Appendix A1. Age of seedlings and smaller saplings were based on the number of branch whorls (Wenny and Dumroese 1991), and since most non-serotinous pine seeds do not persist long in the soil bank (i.e., due to high predation rates), it was assumed that seedlings established in the same year as seeds were dispersed (Richardson 1998a).

At each habitat site, random and targeted (i.e., non-random) 1m^2 plots were sampled for Austrian pine regeneration. Targeted 1m^2 plots were used to record the occurrence of above-average densities of seedlings and saplings not included within the random samples for the purpose of documenting all regeneration, but these data were not included in any of the estimates of average values unless specified. It was acknowledged that targeted plots were indeed selected non-randomly, and they were therefore data additional to the random samples. Targeted plots included 1 m^2 plots that contained five or more seedlings (based upon average seedling densities estimated using random samples) or any saplings (since saplings represent established individuals). In each 1m^2 plot, seedling height, sapling stem diameters (cm), and whorl counts were measured for age estimations. Distance (m) and direction of progeny relative to the parental source were also recorded. Parental stand age was estimated from average tree DBH (see Appendix A1).

In the foredune and inland blowout sites, randomly placed belt transects containing 1m^2 plots were run from the parental stands to 5 m or to the furthest extent of regeneration in each cardinal direction (N, S, E, W). Transects extended to 5 m because most regeneration occurred at the stand edge or in the immediate areas surrounding the parental stands (see Results). Transects that were closer than 5 m to another stand in foredune and inland blowout sites were omitted. Consequently, in three inland blowout sites in close proximity to the other sites, transects were run in NE, NW, SE, and SW directions.

Sampling along the forest edge was designed to document any Austrian pine spread into the native deciduous forest at each of the 10 random sites. Along a 50 m tape placed at the edge of the deciduous forest, five random $1m^2$ plots were located at the edge of the forest, 5 m, 10 m, and 15 m into the forest. Fifteen meters, rather than 5 m as in the other habitats, was chosen as the farthest distance to sample into the native forest because of the poor visibility of Austrian pine progeny among the dense deciduous forest trees.

Because the sampled wetpannes were typically surrounded by Austrian pine trees, it was the spread of Austrian pine into the interior of the wetpanne that was measured. Austrian pine seedling and sapling densities in the wetpannes were determined by inventorying the entire wetpanne for regeneration and recording whether regeneration was found in the wetpanne interior or at the edge (defined as the outermost 2 m of the wetpanne). The total number of seedlings and saplings was divided by the total wetpanne area (m^2) to estimate density. Nine wetpannes were completely inventoried for regeneration. One wetpanne site, too large to be completely inventoried, was sampled using 10 x $1m^2$ plots in both the edge and interior. Seedling and sapling densities found at the edge and interior of the wetpannes were then compared.

Statistical tests were run on the regeneration densities at given distances (and directions, used in determining spatial pattern) from the parental source. Using the SAS statistical program, two-way analysis of variance (ANOVA) tests were performed to detect differences between different distances and directions of Austrian pine regeneration both between and within each habitat. Tukey-Kramer multiple comparison tests were also performed, with direction and distance as two factors, to indicate at what distances and directions from the Austrian pine stands most regeneration occurred. A significance criterion of α=0.05 was used for all statistical tests.

Spatial pattern

Austrian pine seedling and sapling densities were estimated both underneath and at the edge of planted Austrian pine stands. Sampling under and around the stands was designed to determine if Austrian pine is reproducing underneath its canopy, and therefore replacing itself, and/or if it is successfully reproducing at or beyond the edge of its canopy, and therefore spreading. Within each habitat site in the foredunes, inland blowouts, and wetpannes, five $1m^2$ plots were randomly placed underneath the Austrian pine canopy and five $1m^2$ plots at the edge. Refer to Figure 2-4 for more detail on the sampling procedure used in the 10 foredune and inland blowout sites.

In the forest edge sites, the previously described $1m^2$ plots extending from the forest edge to 15 m into the forest were used to estimate rate and spatial pattern of Austrian pine spread. Directions and distances from the parental source were measured and recorded for all regeneration found in these sites.

Using SAS as the statistical program and $\alpha=0.05$, one-way ANOVA's were performed with location (underneath or at the edge of the canopy) as the factor to determine differences between regeneration densities found in each location both between and within each habitat. Tukey-Kramer multiple comparison tests were run to indicate which location had the highest regeneration. To detect directional aspects of spread, densities extending away from the parental stands were pooled for their direction (N, S, E, W). Tukey-Kramer multiple comparison tests were used to identify the direction(s) most correlated with regeneration for each habitat.

RESULTS

Rates and spatial patterns of Austrian pine spread

Rates of spread

The mean rate of spread for Austrian pine, on a per-tree basis, across all foredune sites was 0.06 m yr^{-1}, while the mean rate across inland blowout sites was 0.20 m yr^{-1} (Table 2-1, Table 2-3). These values were based upon random sampling of seedlings and saplings. However, rates of spread obtained through targeted plots were higher because of the inclusion of all regenerating seedlings and saplings: 0.18 m yr^{-1} in the foredunes and 0.67 m yr^{-1} in the inland blowouts (Table 2-2, Table 2-4). Based on random sampling across the foredune and inland blowout sites, mean rates of spread ranged from 0.00 in two sites to 0.28 m yr^{-1} in the foredunes, and 0.00 in five sites to 1.61 m yr^{-1} in the inland blowouts. The maximum rate of spread observed for an individual, based on random sampling, was 0.54 m yr^{-1} in the foredunes, and 0.73 m yr^{-1} in the inland blowouts (Table 2-1, Table 2-3).

For the above stated reasons, targeted plots showed higher rates than randomly selected plots in the foredune and inland blowout habitats (Table 2-2, Table 2-4). Rates of spread obtained through targeted plots ranged from 0.01 to 1.88 m yr^{-1} in the foredunes and 0.06 to 15 m yr^{-1} in the inland blowouts. The maximum rate of spread for an individual found in the entire study site, located in the inland blowout, was 15 m yr^{-1} (inland blowout site #4), compared to 1.88 m yr^{-1} in the foredunes (foredune site #10).

Although the forest edge sites had very little regeneration compared to the other dune habitats (Table A2-1, Figure 2-5), the mean rate of spread in the forest edge was 0.04 m yr^{-1} (Table 2-5). Based on random sampling, rates of spread ranged from 0.00 m yr^{-1} in two sites to 0.12 m yr^{-1}. However, rates as high as 2.11 m yr^{-1} were seen in one forest edge site (forest edge site #1) (Table 2-6).

In the wetpannes, although Austrian pine regeneration was found both underneath and at the edge of planted Austrian pine stands, seedling densities were highest at the canopy edge. Sapling densities were the highest in the wetpannes compared to the other habitats, averaging 0.42 saplings m^{-2} underneath the canopy and 0.33 m^{-2} at the edge (Table 2-7, Figure 2-5). However, there were no differences between the amount of regeneration at the edge or underneath Austrian pine canopy (P=0.1707). There was site-to-site variation of seedling and sapling densities in the interiors and edges of the wetpannes, and there were no differences between densities found at the edge and interior of the wetpannes (P=0.1689) (Figure 2-9).

Spatial pattern

Mean seedling densities found at the edge of Austrian pine stands were greater than those found underneath the canopy in all habitats except the forest edge (Table 2-7, Figure 2-5). In the foredunes, mean seedling density at the edge of Austrian pine canopy was 2.19 m^{-2} compared to 1.34 m^{-2} underneath the canopy. In the inland blowout habitat, mean seedling density was 1.48 m^{-2} at the edge of the canopy and 0.42 m^{-2} underneath. In the wetpannes, mean seedling density was 1.10 m^{-2} at the edge of the canopy and 0.36

m^{-2} underneath. However, in the forest edge habitat, the mean seedling density was 0.06 m^{-2} at the canopy's edge compared to 0.12 m^{-2} underneath the canopy.

Mean sapling densities found at the edge of Austrian pine canopy were also higher than underneath the canopy in the foredunes, 0.04 m^{-2} and 0.00 m^{-2} respectively (Table 2-7, Figure 2-5) In the inland blowout and forest edge, mean sapling densities were the same at both locations (0.12 m^{-2} and 0.08 m^{-2} respectively). However, in the wetpannes, the mean sapling density was higher underneath Austrian pine canopy than at the edge of the canopy (0.42 m^{-2} and 0.33 m^{-2} respectively).

Only in the inland blowout habitat were there differences between regeneration densities underneath and at the edge of the canopy (P=0.0004) (Table 2-8). However, when comparing habitats, the foredunes had the greatest amount of regeneration underneath the canopy (Lsmeans=0.8083), followed by the wetpannes (Lsmeans=0.2760) and inland blowouts (Lsmeans=0.2013) (SAS. Inst. 2001, Tukey-Kramer Tests, α=0.05). The forest edge had the least amount of regeneration underneath the canopy (Lsmeans=0.1665). Similarly, the foredunes had the greatest amount of regeneration at the edge of the canopy (Lsmeans=0.6265), followed by the wetpannes (Lsmeans=0.6119) and inland blowouts (Lsmeans=0.4200) when compared to the other dune habitats. The forest edge also had the least amount of regeneration at the edge of Austrian pine canopy (Lsmeans=0.0400).

Based on random and non-random sampling, the average number of progeny was greatest at the edge of the Austrian pine canopy and decreased as distance increased from the stand edge in the foredune, inland blowout, and forest edge habitat (Figures 2-6 to 2-8, Table A2-1). There was a trend in all three habitats, although there were no strong correlations between the average number of progeny and distance from parental stand. The strongest relationship between the average number of progeny as a function of the distance from the parental stand was found in the inland blowout (R^2=0.557). In the foredunes, there was a weaker relationship between the average number of progeny and distance from the parental stand (R^2=0.4526). The forest edge had the weakest correlation (R^2=0.3488).

In the foredunes and inland blowouts, the highest mean number of Austrian pine progeny was found at the edge of the stands and decreased with distance from the stand edge (Figure 2-6, Figure 2-7, Table A2-1). The mean number of progeny was based on the total number of progeny found at a given distance from the stand edge or underneath the stand divided across all 10 sites per habitat. In the foredunes, the mean number of Austrian pine progeny found at the stand edge was 29.6 individuals which decreased by 68% at 1 m from the stand to 9.5 individuals. The mean number of progeny continued to decrease with distance from the stand. The mean number of progeny found underneath the stand was also 51% less than the mean number found at the edge of foredune stands (14.5 individuals), and at least one individual was 22 m from the parental stand in this habitat (Figure 2-6, Figure 2-10). In the inland blowouts, the mean number of Austrian pine progeny found at the edge, 13.6, decreased by 52% to 6.5 at 1m from the stand edge, and continued to decrease with distance from the stand. The mean number of progeny found underneath the stand was also 55% less than the mean number found at the edge of inland blowout stands, and progeny were found out to 19 m from the parental stand in this habitat (Figure 2-7, Figure 2-13).

In the forest edge habitat, similar to the foredunes and inland blowouts, the highest mean number of Austrian pine progeny was found at the edge of the forest (1.3 individuals) (Figure 2-8). Progeny decreased by 54% to 0.6 individuals at 1 m into the forest, and increased to 1.2 individuals at 5 m into the forest and decreased again with distance into the forest. However, one Austrian pine tree, located through non-random sampling, was found 28 m into the forest under dense forest canopy (Table A2-1, Figure 2-8, Figure 2-16). This suggests that although the forest edge generally is not conducive to Austrian pine regeneration, there are cases of substantial penetration (e.g., 28 m) into the forest.

The patterns of Austrian pine spread in the foredunes showed high variability across years of progeny establishment (Figure 2-10). Most spread occurred within a few meters from the planted stands in the north and west directions. However, progeny that were established in 1993, 1994, 1996, and 1997 all showed a southwesterly direction of spread. The 10 year sapling found 22 m from the stand edge may be an outlier in these data.

The average size of the original planted Austrian pine stands located in the foredunes was estimated as 1,853 m^2. Based on age analysis using tree DBH, the average age of foredune stands was 38 years (Table 2-1). As of 2001, the maximum percent increase in area of Austrian pine spread in the foredunes was 153% estimated by the maximum frontier of Austrian pine spread, defined as the greatest distances that Austrian pine progeny were found from a stand edge in each direction in the foredunes (Figure 2-11). However, the average percent increase in area of Austrian pine spread in the foredunes was found to be 37%, estimated by the average frontier of spread across all ten foredune sites (Figure 2-12). Therefore, 38 years after the foredune trees were originally planted in 1963, the average stand size increased in area by 37% to 2,529 m^2.

Although Austrian pine spread in the inland blowouts varied annually, spread was mainly to the northeast (Figure 2-13). Spread was also seen more frequent to the north and east, but visible in all cardinal directions from the planted stands. In the early years of pine spread (i.e., 1983-1989), most regeneration was found within 5 m from the parental stands. In years 1983, 1987, 1991, 1993, and 1994, there was only 1 remaining individual from the frontier of spread of those years and could potentially be an outlier. Using established DBH to tree age relationships in the inland blowout, the average Austrian pine stand in the inland blowouts was estimated as 35 years (planted in 1966) with a size of 2,276 m^2. As of 2001, the maximum percent increase in area of Austrian pine spread in the inland blowouts was 132%, estimated by the maximum frontier of Austrian pine spread (Figure 2-14). However, the average percent increase in area of Austrian pine spread in the inland blowouts was found to be 25% (Figure 2-15). Therefore, 35 years after the original Austrian pine plantings in the inland blowouts, these stands have increased in area on average by 25% to 2855 m^2 (Figure 2-15).

Although spread into the native forest was limited, there was a general pattern of northern spread into the forest edge (Figure 2-16). Similar to the foredunes and inland blowouts, the pattern of Austrian pine spread was variable across years. In many cases, there is only one individual from certain age classes (i.e., individuals established in 1981, 1983, 1984, 1988, 1989, 1990, 1997, and 1999) and could potentially be outliers, exhibiting rare spread events into the native forest. As previously mentioned, there was one individual found 28 m (northeast) from the presumed parental source, as well as an individual of age 4 years found 20 m north from the parental trees. These indicate that long distance seedling establishment events are possible, even within the dense native forest or via animal transport. Average stand increases in the forest edge and wetpannes were not estimated since spread was measured into the native forest (with little regeneration found) and into the wetpannes from planted adjacent stands.

Although the average number of Austrian pine seedlings and saplings were higher in the wetpanne interior than at the wetpanne edge (25.2 and 13.7, respectively), there were no differences between the number of seedlings and saplings found at either wetpanne location (P=0.1689) (Figure 2-17).

Primary directions of spread

In the foredunes, the majority of Austrian pine spread is within two meters from the parental stands in the northern and western directions, shown statistically and also through observation (Table 2-9, Table 2-10, Table A2-1, Figure 2-10). Although the majority of spread was to the north and west of the planted stands, spread in the eastern and southwestern directions was also observed (Figure 2-10). The pattern of spread in the inland blowouts is primarily in the northern and eastern directions, with the majority of progeny in the northeastern direction (Table A2-1, Figure 2-13). Statistically, the primary directions of spread were between 1 and 3 m from the parental stand to the north (Table 2-9, Table 2-10).

Austrian pine spread into the forest edge is mainly between the edge and 5 m into the forest, but there were no statistical differences among regeneration densities found at different locations in this habitat (P=0.2751) (Figure 2-8). Although spread in the forest edge habitat is limited and Austrian pine does not appear to be significantly spreading into the forest, patterns of spread display a northern direction (Figure 2-16).

DISCUSSION

Overview

Rates of Austrian pine spread across the study site were highest in the inland blowouts, averaging 0.20 m yr^{-1}, and lowest in the forest edge, averaging 0.04 m yr^{-1} (Table 2-3, Table 2-5). The foredunes exhibited intermediate rates of spread, averaging 0.06 m yr^{-1}(Table 2-1). Furthermore, rates as high as 15 m yr^{-1} were seen in the study site and at least some penetration (i.e., up to 28 m) into the native deciduous forest was observed (Table 2-4, Figure 2-16). Austrian pine spread is primarily in the northern directions, due to the prevailing southwesterly winds of Lake Michigan. On average, foredune stands have increased in area by 37% since original plantings in 1963, while inland blowout stands have increased 25% since 1966. While regeneration was found in all dune habitats, most regeneration occurred at the edge of the Austrian pine stands in the foredune and inland blowout habitats and in the wetpannes. In the foredunes, forest edge, and inland blowouts, average number of progeny was related to distance from the parental source, although the square of correlation values were not significant (ranged from R^2=0.3488 to R^2=0.557). The wetpannes contained the highest sapling densities (0.42 m^{-2} underneath Austrian pine canopy and 0.33 m^{-2} at canopy edge), due to greater densities of seed source trees and favorable soil moisture conditions compared to the other dune habitats. Although the wetpannes contained high levels of Austrian pine regeneration, there were no differences between regeneration found at the wetpanne interior and edge, suggesting no differential spread into the wetpannes (P=0.1689).

Rates and spatial patterns of Austrian pine spread

Mean rates of Austrian pine spread in the inland blowouts ranged from 0.00 m yr^{-1} in some sample stands to 1.61 m yr^{-1} in others, with an average of 0.20 m yr^{-1} across the ten sites (Table 2-3, Table 2-4). However, maximum rates of spread in this habitat and for the study site were as high as 15 m yr^{-1}, and progeny were found up to 19 m from the parental source (Table 2-4, Figure 2-13). Rates of spread in the foredunes ranged between 0.00 and 0.28 m yr^{-1}, with an average of 0.06 m yr^{-1} across the ten sites (Table 2-1, 2-2). Rates in the foredunes were as high as 1.88 m yr^{-1}, and progeny were found up to 22 m from the parental stand (Table 2-2, Figure 2-10). Consistent with Leege (1997) and Leege and Murphy (2001), the forest edge had the least amount of Austrian pine regeneration. Although regeneration densities in this habitat were relatively low, it is notable that at least one Austrian pine individual was found 28 m into the forest under dense forest canopy. This also suggests that similar relatively long-distance dispersal events may have occurred in the other habitats as well, and perhaps the wrong parental source may have been assumed. It is also recognized that pine dispersal via animal transport may be possible and account for long-distance dispersal events, such as individuals found deep into the native forest. Rates of spread ranged from 0.00 to 0.12 m

yr^{-1}, averaging 0.04 m yr^{-1}, and reached as high as 2.11 m yr^{-1} in one site (Tables 2-5, Table 2-6).

Although the foredune and inland blowout habitats had the highest seedling densities, the highest sapling densities were found in the wetpannes (Figure 2-9). This may be a result of greater seed production but lower survivorship in the foredunes and inland blowouts, as well as greater soil moisture levels in the wetpannes, consistent with Leege (1997) and Leege and Murphy (2000). In the foredune, forest edge, and inland blowout habitats, regeneration occurred both underneath and at the edge of the Austrian pine canopy, but the greatest densities and average numbers of progeny occurred at the stand edge, consistent with previous studies on pine seed fall (Yocum 1968, Richardson 1998a) (Figure 2-6 to 2-8). This suggests that the planted stands are both replacing themselves and expanding in area of coverage. All three habitats had a similar trend of decreasing average numbers of progeny as distance increased from stand edge, consistent with McCaughey et al. (1986) who documented that the pattern of pine seed dispersal was exhibited by a negative exponential curve with a peak frequency at the edge of the parental tree stands. However, the foredunes and inland blowouts had a stronger correlation between the average number of progeny and distance from the parental stand than the forest edge. The most significant correlation was in the inland blowouts (R^2=0.557) (Figure 2-7).

Austrian pine spread is mainly towards the north in the foredunes and northeast in the inland blowouts, resulting from the prevailing southwesterly winds (Figures 2-10 to 2-15). Pine spread was also observed to the west of the foredune stands (Figure 2-10), unexpected from the direction of the prevailing winds. However, this may be caused by the more open dune areas to the west of the foredunes stands or due to complicated eddies not found in other habitats. Although spread was limited in the native forest, a general pattern of spread to the north was shown in the forest edge habitat. Austrian pine stands in the foredunes have increased, in area, on average by 37%, while the stands in the inland blowouts have increased on average by 25% (Figure 2-12, Figure 2-15). However, based on the maximum distances Austrian pine progeny were found from a stand edge across all foredune and inland blowout sites, foredune stands increased up to 153% and inland blowout stands increased up to 132% (Figure 2-11, Figure 2-14). This shows the potential for Austrian pine spread in these habitats. Inland blowout sites had the greatest amount of local dispersal events around Austrian pine stands in the study site, consistent with the literature on the spread of pines, due to 'take off sites' where seeds may be dispersed at farther directions from the original Austrian pine stands (Richardson and Bond 1991). Although the wetpannes contained high regeneration densities (especially sapling densities), there were no statistically significant differences between densities found at the edge and interior of the wetpannes (P=0.1689) (Figure 2-17). This indicates that seedlings and saplings established equally as well in both locations. Because most wetpannes were surrounded by mature Austrian pine trees, it was spread into the wetpannes that was documented whereas possible spread away from the wetpannes was not determined.

Although there are few documented examples of the spatial patterns of pine spread over a large area extending from planted pine stands, the spatial pattern and densities of Austrian pine spread in the study site were higher than those found by Belton and Ledgard (1991). Belton and Ledgard (1991) documented pine spread in Australia that ranged from 1 individual/ 200 m^2 to as low as 1 individual/100,000 m^2. In the study area, the spread of Austrian pine is remarkably greater in density than those found by Belton and Ledgard (1991), which may suggest that Austrian pine spread is quite vigorous and aggressive compared to other examples of the spread of invasive pines. However, rates of Austrian pine spread in the study site are lower than average rates of native pine spread in North America and Europe (Richardson et al.1994), which range from 81-400 m yr^{-1}. Richardson et al. (1994) cited rates of pine spread based on pines spreading in their native habitats, and not those for exotic or invasive pines in novel (especially harsh) conditions. Finally, more examples of local patterns of pine spread in and around planted stands in non-native regions is needed to fully characterize and compare Austrian pine spread on the dunes of Lake Michigan.

Habitats most invaded by Austrian pine

The wetpannes are considered the most invaded and thus the most endangered dune habitat in the study site, due to high Austrian pine seedling and sapling densities and the high concentration of seed-source trees, consistent with previous dune research (Leege 1997, Leege and Murphy 2000, 2001, Sherfinski 2000). Stands in the wetpannes contained high densities of seed-source trees relative to the other dune habitats and have contributed to the successful regeneration of Austrian pine (Leege 1997). Austrian pine may also reduce ground water levels in these areas, as supported by Sherfinski (2000), and also may affect other dune areas by producing large numbers of progeny due to the high concentrations of parental trees. The wetpannes possess unique dune flora and fauna, resulting from higher soil moisture, and therefore are at an even greater risk from Austrian pine alteration than the other dune habitats. Although stand densities in the inland blowout were significantly lower than in the wetpanne, the inland blowouts contained the highest rates of spread and may harbor take-off sites to aid in further Austrian pine spread. The inland blowouts, therefore, should also be closely monitored for future impacts of Austrian pine.

Conclusions

All dune habitats within the study site contained Austrian pine regeneration. Regeneration occurred both underneath and at the edge of the Austrian pine canopy, but the greatest densities occurred at the edge. This suggests that the planted stands are both replacing themselves and expanding in area of coverage. On average, the foredune stands have increased 37% since 1963, while the inland blowout stands have increased 25% since 1966.

Austrian pine spread is mainly towards the north in the foredunes and forest edge and northeast in the inland blowouts, resulting from the prevailing southwesterly winds. Mean rates of Austrian pine spread in the inland blowouts ranged from 0.00 m yr^{-1} in some sample stands to 1.61 m yr^{-1} in others, with an average of 0.20 m yr^{-1} across the 10 inland blowout sites. However, maximum rates in this habitat were as high as 15 m yr^{-1}. Rates of spread in the foredunes ranged between 0.00 and 0.28 m yr^{-1}, with an average of 0.06 m yr^{-1} across the 10 foredune sites. Maximum rates in the foredunes were as high as 1.88 m yr^{-1}. The forest edge had the least amount of Austrian pine regeneration.

However, at least some penetration into the native forest was observed (i.e., up to 28 m). Rates of spread ranged from 0.00 to 0.12 m yr^{-1}, averaging 0.04 m yr^{-1}, and reached as high as 2.11 m yr^{-1} in one site. The wetpannes contained high regeneration densities relative to the other dune habitats (0.42 and 0.33 saplings m^{-2}, underneath and at the edge of Austrian pine canopy, respectively), most likely attributed to high soil moisture levels and proximity to seed-source trees. However, there were no clear differences between regeneration found at the edge and interior of the wetpannes (P=0.1689), suggesting that regeneration occurs equally as well at both locations.

Table 2-1. Mean Austrian pine rates of spread (m yr^{-1}) per plant across 10 foredune sites, based upon randomly selected 1 m^2 plots extending from the edge of parental stands to 5 m or until regeneration was no longer observed.

Site#	**Mean Rate**	**SE**	**Min Rate**	**Max Rate**	**N (# m^2 plots)**	**Parental age (yrs)**
1	0.000	0.000	0	0	20	32.1
2	0.002	0.002	0	0.04	20	38.9
3	0.002	0.002	0	0.05	32	37.9
4	0.283	0.017	0	0.51	20	37.4
5	0.045	0.015	0	0.20	20	37.4
6	0.008	0.005	0	0.06	20	37.2
7	0.048	0.012	0	0.18	20	38.4
8	0.043	0.013	0	0.13	20	38.4
9	0.000	0.000	0	0.00	20	38.9
10	0.118	0.033	0	0.54	28	39.1
Mean	**0.06**					37.6
SE	**0.03**					0.61
Total N	10				220	10

Table 2-2. Mean Austrian pine rates of spread (m yr^{-1}) per plant across 10 foredune sites, based upon non-random 1m^2 plots extending from the edge of parental stands to varying distances.

Site#	**Mean rate**	**SE**	**Min Rate**	**Max Rate**	**N (# m^2 plots)**	**Parental age (yrs)**
1					0	32.1
2	0.117	0.001	0.11	0.12	5	38.9
3					0	37.9
4	0.078	0.006	0.03	0.17	60	37.4
5					0	37.4
6	0.056	0.043	0.01	0.12	6	37.2
7	0.081	0.008	0.05	0.14	28	38.4
8	0.159	0.069	0.05	0.56	7	38.4
9	0.318	0.130	0.04	0.45	3	38.9
10	0.437	0.077	0.05	1.88	23	39.1
Mean	**0.18**					37.6
SE	**0.01**					0.61
Total N	7				132	10

Table 2-3. Mean Austrian pine rates of spread (m yr^{-1}) per plant across 10 inland blowout sites based upon randomly selected $1m^2$ plots extending from the edge of parental stands to 5 m or until regeneration was no longer observed.

Site#	Mean Rate	SE	Min Rate	Max Rate	N (# m^2 plots)	Parental age (yrs)
1	1.612	0.032	0	0.40	20	33.5
2	0.003	0.003	0	0.006	20	33.6
3	0.000	0.000	0	0.00	20	34.7
4	0.000	0.000	0	0.00	20	33.2
5	0.000	0.000	0	0.00	20	33.4
6	0.000	0.000	0	0.00	20	36.8
7	0.109	0.014	0	0.27	20	34.9
8	0.169	0.032	0	0.48	20	37.6
9	0.055	0.034	0	0.73	20	36.5
10	0.000	0.000	0	0.00	20	38.7
Mean	**0.20**					35.3
SE	**0.16**					1.1
Total N	10				200	10

Table 2-4. Mean Austrian pine rates of spread (m yr^{-1}) per plant across 10 inland blowout sites based upon non-random $1m^2$ plots extending from the edge of parental stands to varying distances.

Site#	Mean rate	SE	Min Rate	Max Rate	N (# m^2 plots)	Parental age (yrs)
1	0.298	0.149	0.15	0.46	4	33.5
2					0	33.6
3	0.874	0.357	0.08	2.08	6	34.7
4	1.866	1.265	0.06	15.00	11	33.2
5	0.143	0.338	0.06	0.35	14	33.4
6					0	36.8
7	0.067	0.001	0.07	0.070	3	34.9
8	0.559	0.121	0.09	1.38	12	37.6
9	0.727	0.000	0.73	0.73	1	36.5
10	0.865	0.045	0.82	0.91	2	38.7
Mean	**0.67**					35.3
SE	**0.20**					1.1
Total N	8				53	10

Table 2-5. Mean Austrian pine rates of spread (m yr^{-1}) per plant across 10 forest edge sites based upon randomly selected $1m^2$ plots at the forest edge, 5 m, 10 m, and 15 m into the forest.

Site#	Mean rate	SE	Min Rate	Max Rate	N (# m^2 plots)	Parental age (yrs)
1	0.116	0.092	0	1.82	20	38.5
2	0.069	0.022	0	0.27	20	39
3	0.061	0.045	0	0.66	20	38.7
4	0.039	0.034	0	0.67	20	33.9
5	0.002	0.002	0	0.04	20	39.8
6	0.000	0.000	0	0	20	41.3
7	0.025	0.025	0	0.50	20	39.1
8	0.009	0.009	0	0.176	20	38.7
9	0.000	0.000	0	0	20	36.5
10	0.092	0.072	0	1.43	20	38.9
Mean	**0.04**	0.013				38.5
SE	**0.14**					1.0
Total N	10				200	10

Table 2-6. Mean Austrian pine rates of spread (m yr^{-1}) per plant across 10 forest edge sites based upon non-randomly selected $1m^2$ plots at varying distances into the forest. This table shows only sites that had non-random plots included.

Site#	Mean rate	SE	Min Rate	Max Rate	N (# m^2 plots)	Parental age (yrs)
1	1.118	0.054	0.05	2.11	5	38.5
2	0.134	0.062	0.04	0.44	6	39
3					0	38.7
4	0.908	0.573	0.34	1.48	2	33.9
5	0.042	0.000	0.04	0.04	1	39.8
6	0.106	0.026	0.08	0.16	3	41.3
7					0	39.1
8	0.416	0.086	0.16	0.417	9	38.7
9					0	36.5
10	0.98	0.289	0.05	1.82	5	38.9
Mean	**0.53**				31	38.5
SE	**0.19**					1.0
Total N	7				200	10

Table 2-7. Mean Austrian pine regeneration densities (#ind/m^2) underneath and at the edge of Austrian pine stand in each dune habitat. Densities were taken from five randomly placed 1m^2 plots both underneath and at the edge of Austrian pine canopy in each habitat site. Ten sites were randomly selected in each dune habitat.

	Underneath canopy				**At edge of canopy**			
Habitat	Seedling	SE	Sapling	SE	Seedling	SE	Sapling	SE
Foredune	1.34	0.17	0.00	0.00	2.19	0.41	0.04	0.01
Forest edge	0.12	0.04	0.08	0.01	0.06	0.01	0.08	0.01
Inland blowout	0.42	0.07	0.12	0.02	1.48	0.23	0.12	0.03
Wetpanne	0.36	0.08	0.42	0.13	1.10	0.14	0.33	0.06

Table 2-8. Statistical comparison of mean Austrian pine regeneration densities underneath and at the edge of Austrian pine canopy within each dune habitat (SAS Inst. 2001, one-way ANOVA α=0.05). Densities were taken from five randomly placed 1m^2 plots both underneath and at the edge of Austrian pine canopy in each habitat site. Ten sites were randomly selected in each dune habitat.

Habitat	**Differences between Austrian pine regeneration densities underneath and at the edge of Austrian pine canopy?**	**Significance value (P)**
Foredune	No	0.2014
Forest edge	No	0.2052
Inland blowout	Yes	0.0004
Wetpanne	No	0.1707

Table 2-9. Directions of Austrian pine spread in the foredunes and inland blowouts, based on pooled random and non-random sampling. Random sampling included transects extending in all four cardinal directions from edge of parental stand to 5 m or to farthest extent of Austrian pine regeneration, while non-random sampling included regeneration observed not previously in random samples

Habitat	Direction	Significance value (LSMEANS)
Foredune	North*	0.1543
	West	0.1212
	East	0.0396
	South	0.0050
Inland blowout	North*	0.093
	East	0.035
	South	0.0106
	West	0.0050

* indicates the cardinal direction most statistically significant in locating Austrian pine regeneration in each dune habitat

Table 2-10. Austrian pine regeneration occurring away from edge of parental stands in all four cardinal directions in each dune habitat. The following is a list of the distances and corresponding directions most statistically significant in locating Austrian pine progeny away from the parental stands (SAS Inst. 2001, ANOVA and Tukey-Kramer tests, $\alpha=0.05$). Random and non-random data were pooled for this analysis in each dune habitat.

Habitat	Distance (m)	Direction	Significance value (Lsmeans)
Foredune	1	W	0.650
	1	N	0.639
	2	N	0.444
	2	W	0.300
	10	E	0.250
	11	E	0.250
Inland Blowout	1	N	0.325
	2	N	0.200
	3	N	0.125
Forest Edge	**	**	**
Wetpanne	**	**	**

** indicates no statistically significant directions in locating Austrian pine progeny

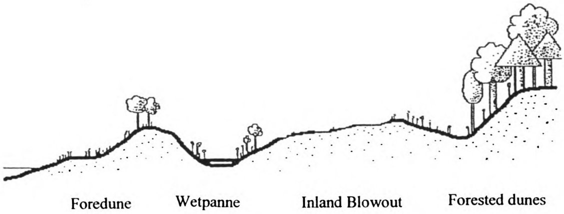

Figure 2-1. Various dune habitats in the Lake Michigan sand dune ecosystem.

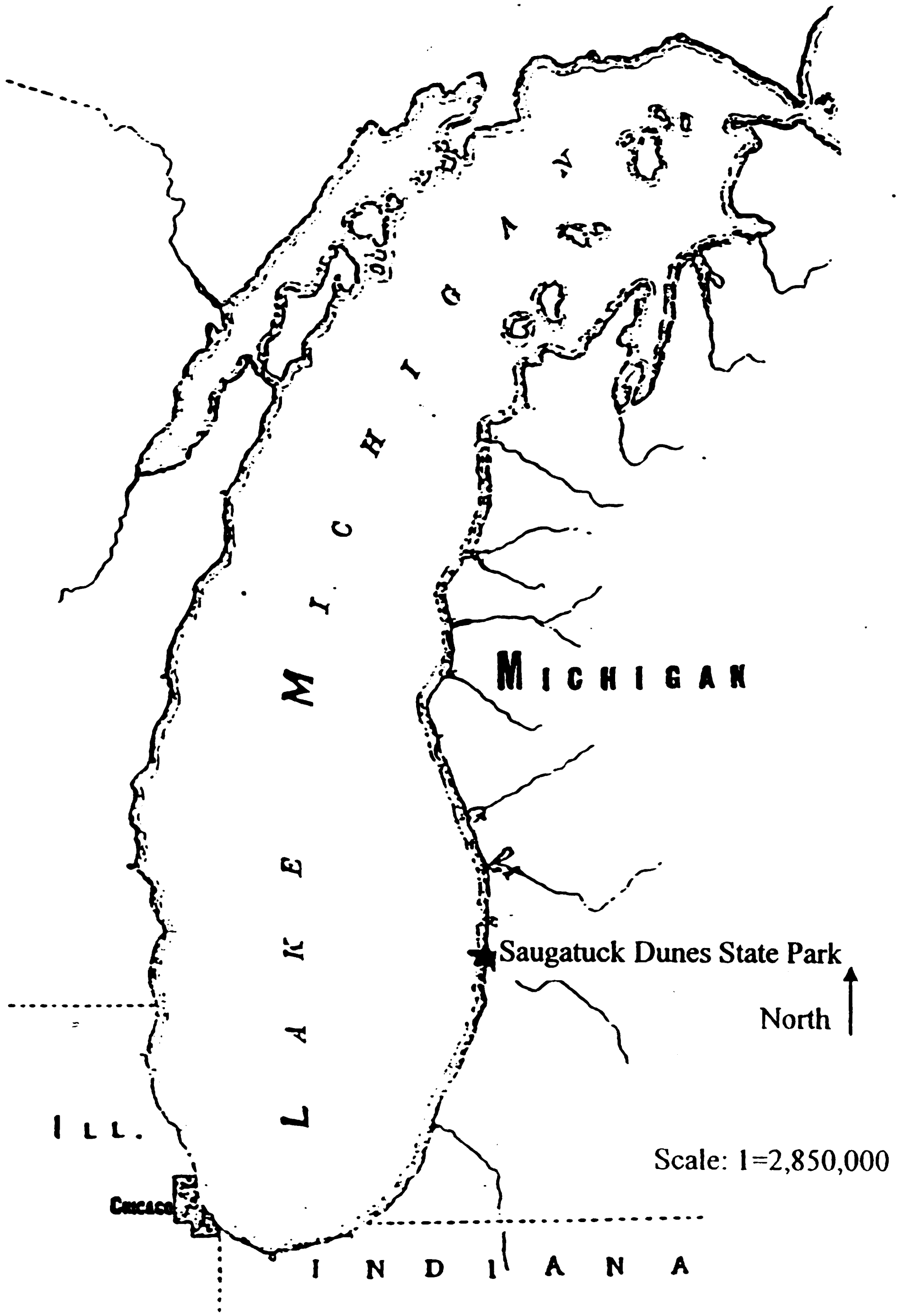

Figure 2-2. Location of study site (Saugatuck Dunes State Park), in Allegan County, MI (from Cowles 1899). The Natural Area lies within the park.

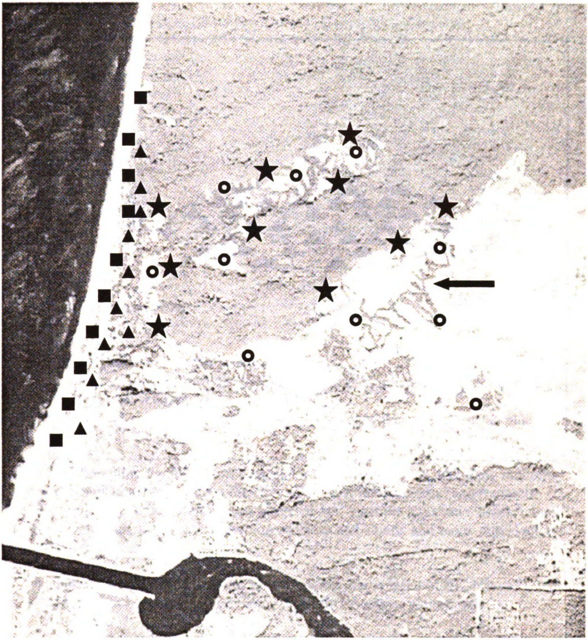

Figure 2-3. Study site: Saugatuck Dunes State Park Natural Area (SDSPNA). Austrian pine plantations can be seen as dark lines (see arrow for example) in the foredunes and inland blowout habitats. 1cm=120m.
Key:
■ = foredune site ○ = inland blowout site

▲ = wetpanne site ★ = forest edge site

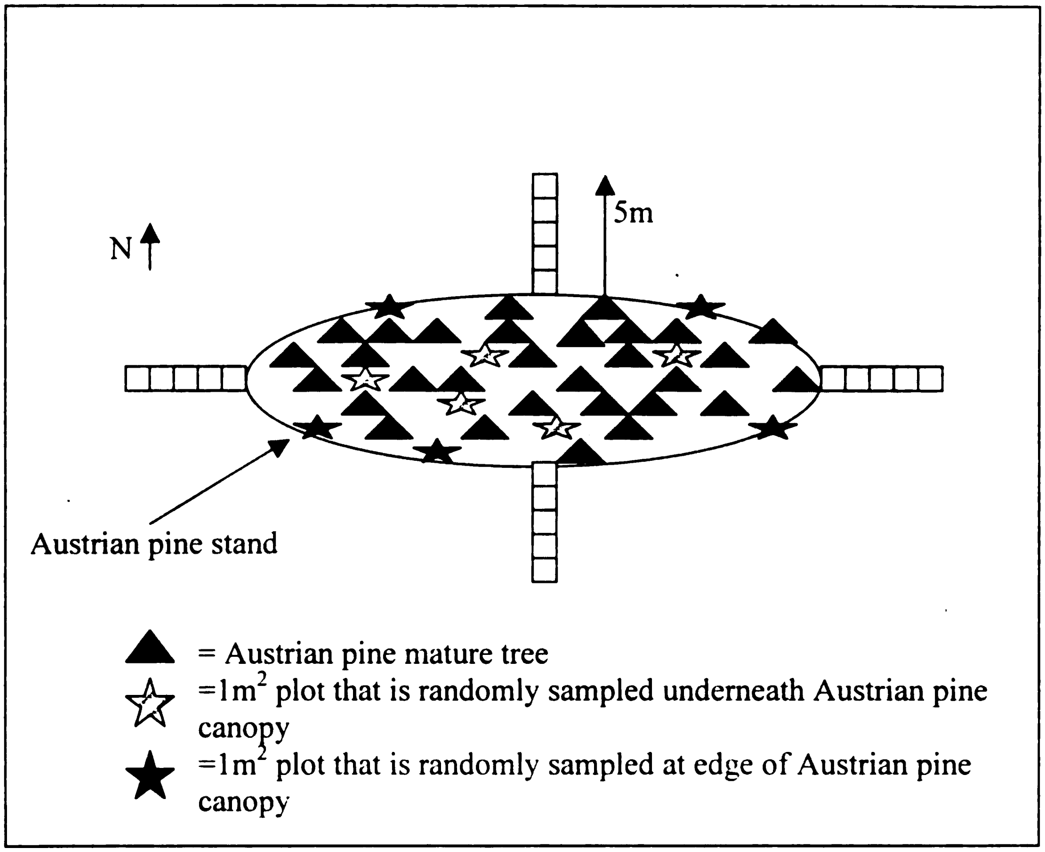

Figure 2-4. Sampling model for foredune and inland blowout sites, including randomly placed $1m^2$ plots underneath and at the edge of an Austrian pine stand and transects extending in all four cardinal directions (targeted $1m^2$ plots are not shown here).* In all $1m^2$ plots, both Austrian pine regeneration densities and abiotic and biotic dune factors were measured.

*Note: in three inland blowout sites, transects were placed in NE, NW, SE, and SW directions to avoid interference with other Austrian pine stands

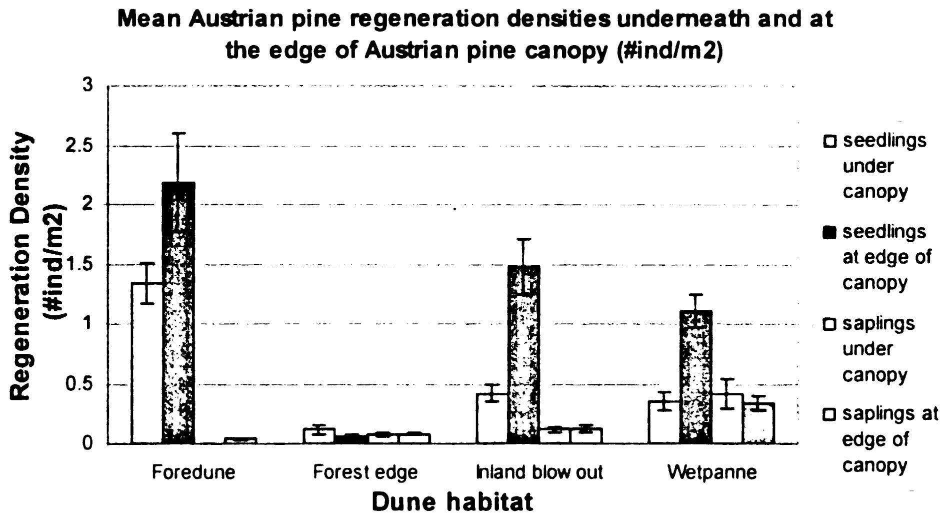

Figure 2-5. Mean Austrian pine regeneration densities (#ind/m^2) underneath and at the edge of Austrian pine canopy in each dune habitat. See Table 2-7 for exact values. Five randomly placed 1m^2 plots were sampled both underneath and at the edge of Austrian pine stands in each habitat site.

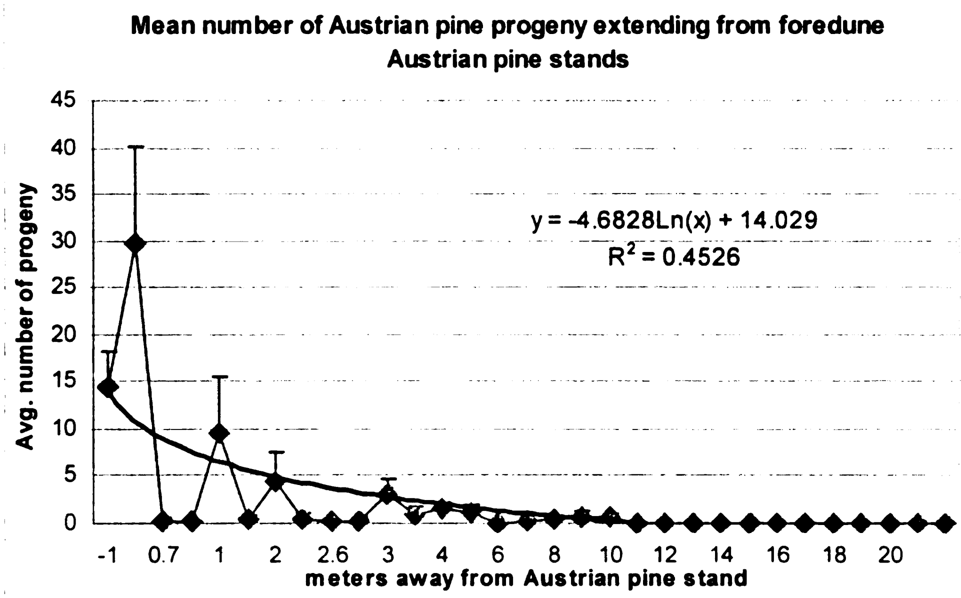

Figure 2-6. Mean number of Austrian pine progeny extending from the edge of mature Austrian pine stands across the ten foredune sites, based on random and non-random sampling. Locations underneath the canopy are designated as "-1." Random sampling was performed using randomly located 1m^2 plots underneath and at edge of canopy and along transects running N, S, E, W fromthe edge of the stand to 5 m or the furthest extent of Austrian pine regeneration. Non-random sampling occurred wherever regeneration was observed not previously captured in the random samples.

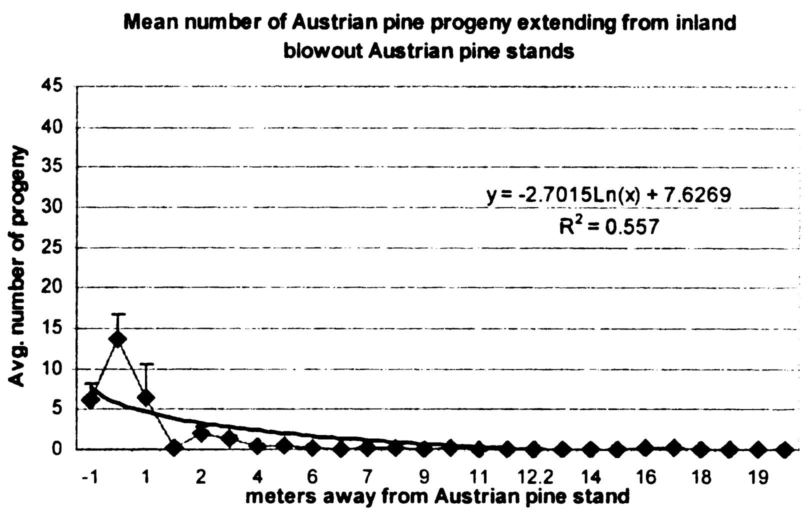

Figure 2-7. Mean number of Austrian pine progeny extending from the edge of mature Austrian pine stands across the ten inland blowout sites, based on random and non-random sampling. Locations underneath the canopy are designated as "-1." Random sampling was performed using randomly located 1m^2 plots underneath and at edge of canopy and along transects running N, S, E, W from the edge of the stand to 5 m or the furthest extent of Austrian pine regeneration. Non-random sampling occurred wherever regeneration was observed not previously captured in the random samples.

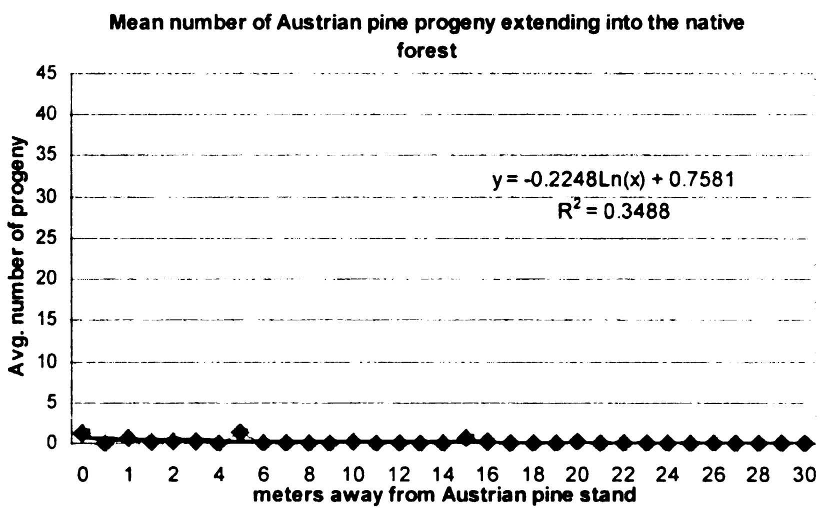

Figure 2-8. Mean number of Austrian pine progeny extending from the edge of mature Austrian pine stands into the native forest across ten forest edge sites, based on random and non-random sampling. Random sampling was performed using five random 1m^2 plots at forest edge, 5 m, 10 m, and 15 m into the forest at each of ten forest edge sites. Non-random sampling occurred wherever regeneration was observed not previously captured in the random samples of the ten forest edge sites. Note: there were no statistically significant differences between densities found at each location into the forest (SAS Inst. 2001, one-way ANOVA, α=0.05, P=0.2751).

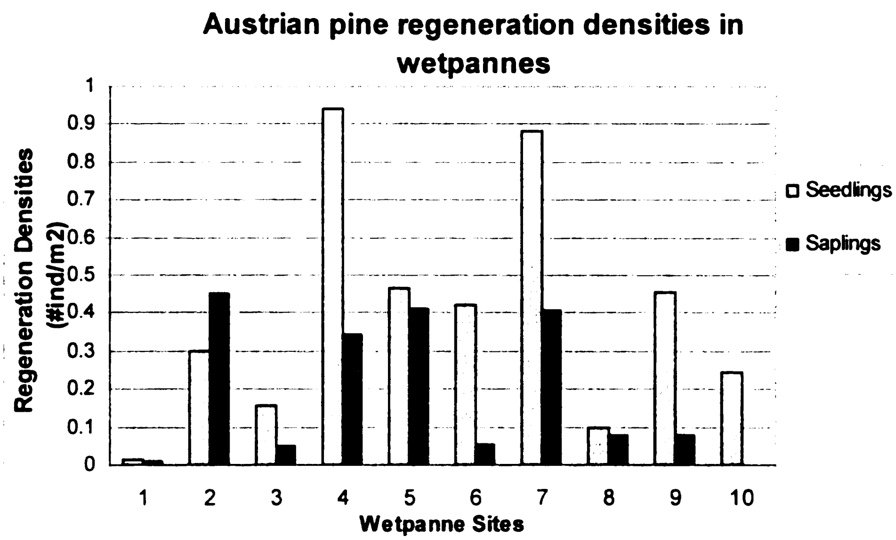

Figure 2-9. Mean Austrian pine regeneration densities (#ind/m^2) at edge and interior of the wetpannes. In nine wetpannes, densities were calculated by inventorying the wetpanne for regeneration and dividing by total area. One wetpanne site was sampled for regeneration using 10 random 1m^2 plots at the edge and interior of the wetpanne. Note: there were no statistically significant differences between densities occurring at the edge and interior of the wetpannes (SAS Inst. 2001, one-way ANOVA, α=0.05, P=0.1689).

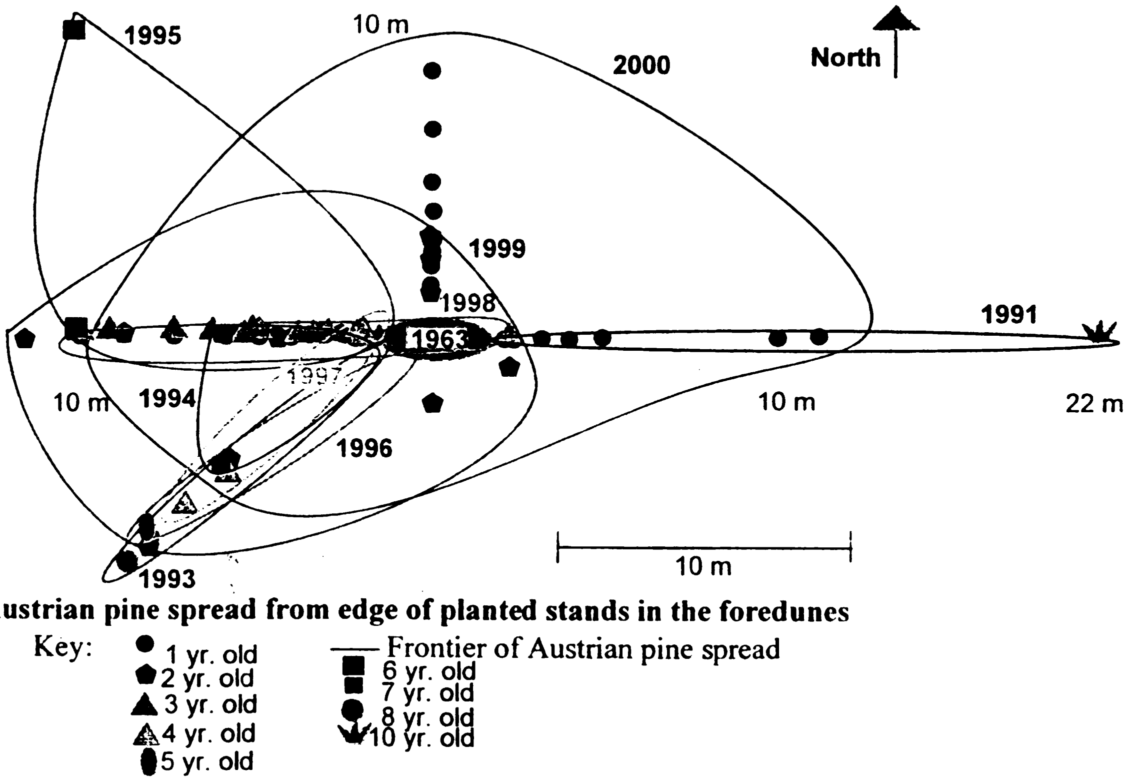

Figure 2-10. Austrian pine spread from edge of planted stands in the foredunes. Sampling was based on randomly and non-randomly located $1 m^2$ transect belts running N, S, E, W from the edge of the stand to 5 m or the furthest extent of Austrian pine regeneration in 10 sites. Non-random sampling occurred wherever regeneration was observed not previously captured in the random samples. Note: original Austrian pine foredune stands were planted in 1963, based on average tree age estimates and stand size is not drawn to scale.

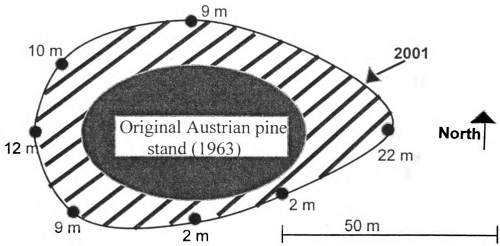

Figure 2-11. Maximum frontier of Austrian pine spread in the foredunes as of 2001. This figure shows the outermost distances that Austrian pine progeny were found from the stand edge in each direction and indicates the maximum area of spread across the ten foredune sites. According to this analysis, foredune stands have increased in area by a maximum of 153% since original plantings in 1963. Stand age was based on average tree age estimates.

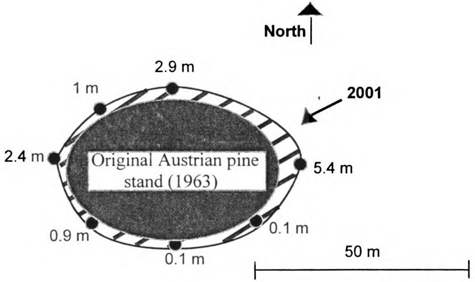

Figure 2-12. Average frontier of Austrian pine spread across 10 foredune sites as of 2001. This figure shows the average outermost distances that Austrian pine progeny were found from the stand edge in each direction. According to this analysis, the average Austrian pine foredune stand increased in area by 37% sine original plantings in 1963. Stand age was based on average tree age estimates.

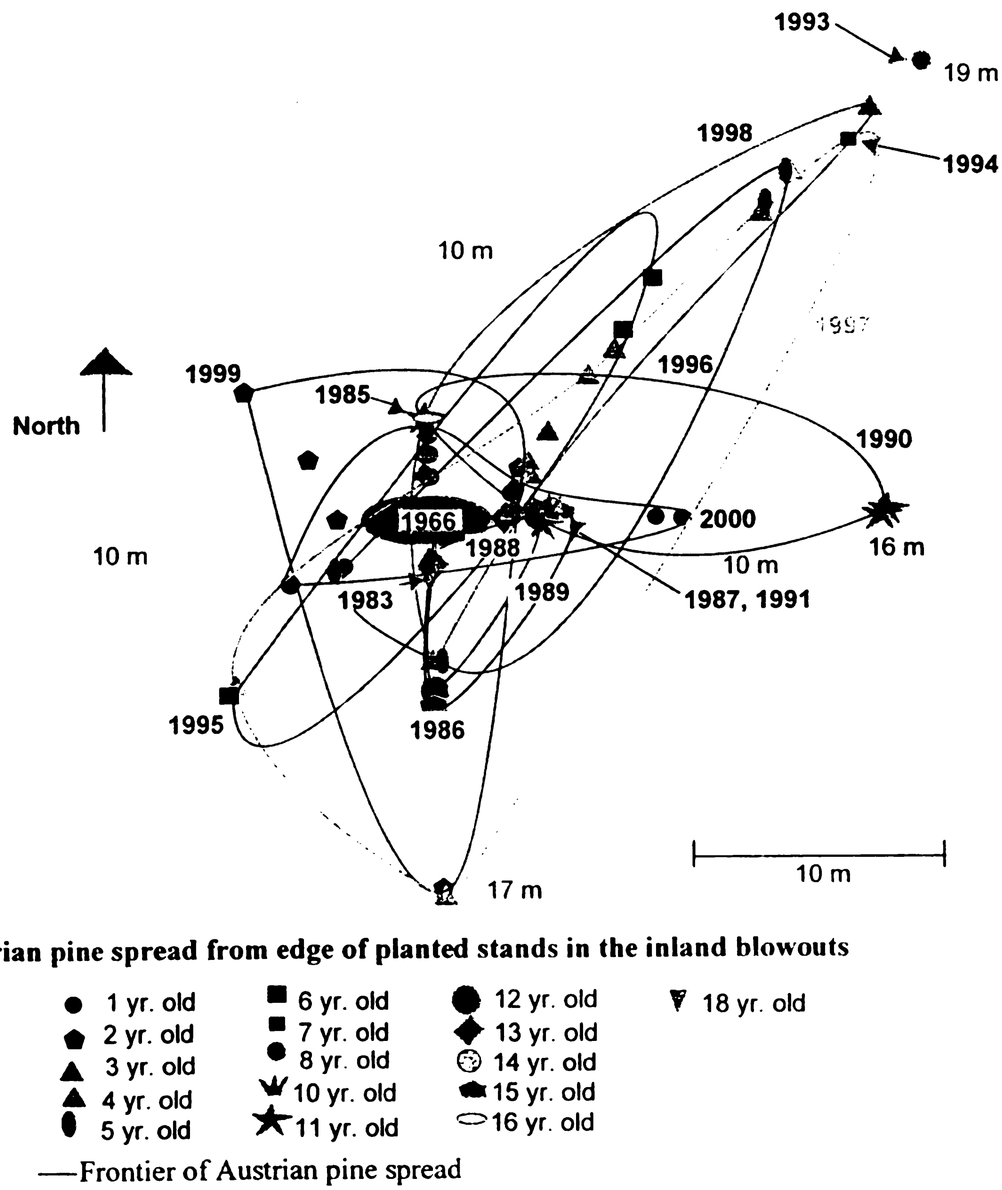

Figure 2-13. Austrian pine spread from edge of planted stands in the inland blowout habitats. Sampling was based on randomly and non-randomly located $1m^2$ transect belts running N, S, E, W in most sites and NE, NW, SE, SW in three sites from the edge of the stand to 5 m or the furthest extent of Austrian pine regeneration. Non-random sampling occurred wherever regeneration was observed not previously captured in the random samples. Note: original stands were planted in 1966, based on average tree age estimates and stand size is not drawn to scale.

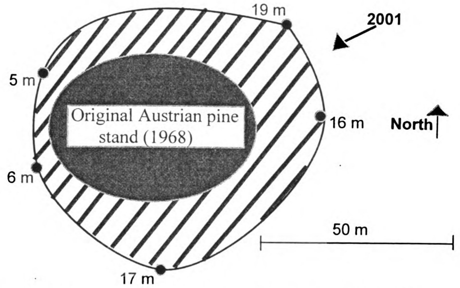

Figure 2-14. Maximum frontier of Austrian pine spread in the inland blowouts as of 2001. This figure shows the outermost distances that Austrian pine progeny were found from the stand edge in each direction and indicates the maximum area of spread across the ten inland blowout sites. According to this analysis, inland blowout stands have increased in area by a maximum of 132% since original plantings in 1966. Stand age was based on average tree age estimates.

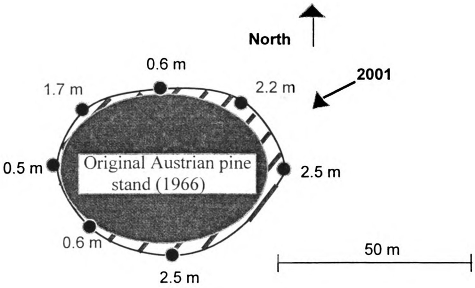

Figure 2-15. Average frontier of Austrian pine spread across 10 inland blowout sites as of 2001. This figure shows the average outermost distances that Austrian pine progeny were found from the stand edge in each direction. According to this analysis, the average Austrian pine inland blowout stand increased in area by 25% since original plantings in 1966. Stand age was based on average tree age estimates.

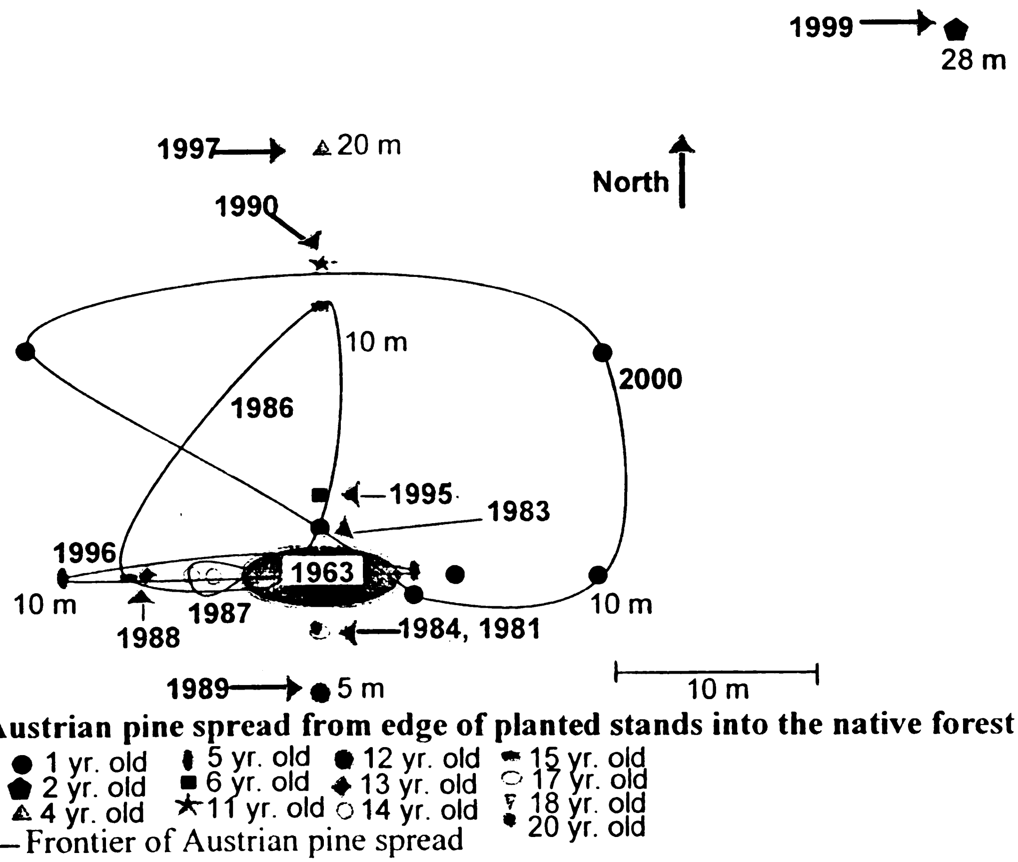

Figure 2-16. Austrian pine spread from edge of planted stands into the native forest, based on randomly and non-randomly $1 m^2$ plots at distances into the forest. Non-random sampling was used wherever regeneration was observed not previously captured in the random samples. Note: original stand were planted in 1963, based on average tree age estimates and stand size is not drawn to scale.

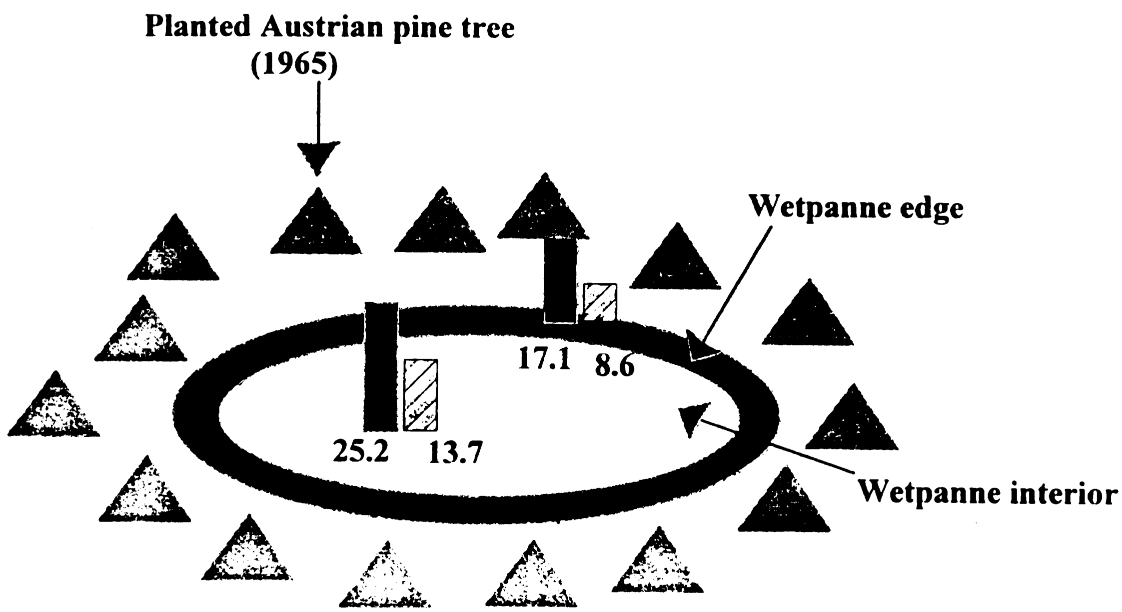

Figure 2-17. Mean number of Austrian pine seedlings and saplings found at wetpanne interior and edge. Nine wetpannes were surveyed for Austrian pine regeneration, and one wetpanne, too large to survey, was sampled using 10 1-m^2 plots at the wetpanne edge and interior. The wetpanne edge was defined as the outermost 2 m of the wetpanne. Although there was greater regeneration at the interior of the wetpannes, there were no significant differences between regeneration found in the interior and at the wetpanne edges (P=0.1689).

CHAPTER 3

REGENERATION NICHES OF INTRODUCED, INVASIVE *PINUS NIGRA* AND NATIVE *PINUS BANKSIANA* IN FOUR LAKE MICHIGAN SAND DUNE HABITATS

INTRODUCTION

Previous studies have documented the successful establishment and spread of introduced, exotic *Pinus nigra* (Austrian pine) on the dunes of Lake Michigan, near Saugatuck MI, and have shown its capacity to alter the native dune conditions (Leege 1997, Leege and Murphy 2000, 2001, Sherfinski 2000). These studies have shown that Austrian pine, originally planted as 26,000 seedlings between 1956 and 1972 in Saugatuck Dunes State Park Natural Area (SDSPNA), is impacting native vegetation and significantly changing the dune environment by accelerating succession, reducing biodiversity, and potentially changing ground water levels (Leege 1997, Leege and Murphy 2000, 2001, Sherfinski 2000). Austrian pine was originally planted throughout the dune system, and is now reproducing, replacing itself and increasing stand size (see Chapter 2). However, the patterns of occurrence of Austrian pine and the native *Pinus banksiana* (Jack pine) and microsite conditions favorable for the establishment of both pines, have not been determined in this dune area. The patterns of occurrence of Austrian pine and Jack pine regeneration (i.e., seedlings and saplings that established through natural reproductive processes) in and around stands of Austrian pine are important to study if fundamental similarities and/or differences between the regeneration characteristics of both species in the study site are to be determined. Additionally, information on microsite conditions favorable for Austrian pine and Jack pine regeneration will aid in making predictions of the dune sites and/or habitats most likely to be invaded in the future. Therefore, this study identifies the patterns of occurrence of Austrian pine and Jack pine regeneration in and around planted stands of Austrian pine in SDSPNA, and also documents the microsite conditions correlated with the distribution of both species.

Austrian pine invasion of Saugatuck Dunes State Park

Between 1956 and 1972, private landowners planted approximately 26,000 Austrian pine trees in the area now known as Saugatuck Dunes State Park (SDSP). To stabilize the shifting dunes, seedlings were planted in stands along the foredunes, in large erosional areas (inland blowouts), around the wetpannes, and adjacent to the native deciduous forest. For Austrian pine stand characteristics, see Chapter 2. Jack pine is found naturally in SDSP and although it can be found scattered throughout the dune habitats, the highest densities are found in and surrounding the wetpannes.

Jack pine: distribution and ecology

Jack pine is a small to medium-sized coniferous tree found throughout the North American boreal forests (Rudolph and Laidly 1990). It is one of the most widely distributed conifers in North America, and its native range extends from northern Canada to the northeastern and midwest states of the U.S. (Riemenschneider 1982). Mature trees reach 15-20 m in height and 20-30 cm in diameter (Kenkel 1988). While it is a relatively short-lived species (mature trees start to deteriorate after 80 years on the best sites and after 60 years on poor sites), some individuals have been known to survive to 230 years (Rudolph and Laidly 1990). Especially during the first 50 years of growth, Jack pine has a high growth rate, and growth usually stops after 80 years (Reimenschneider 1982). Under most conditions, the age of first reproduction is between 5 and 10 years, and reproduction is fairly regular and increases annually until crown competition becomes a limiting factor (Rudolph and Laidly 1990).

Jack pine is well adapted to pyric and semipyric (such as SDSP) ecosystems, and the spatial and temporal distribution (i.e., age classes) of this species is controlled mainly by fire (Gauthier et al. 1996). It primarily produces serotinous cones, however, especially in the southern portion of its range, nonserotinous cones are also produced. The cones open immediately after a fire or following high surface soil temperatures, releasing a large number of seeds (15-72 seeds/cone). While seed dispersal distances are usually up to two tree heights (30 m) from the parental tree, the majority of established seedlings are found within one tree height (15 m) (Xie and Knowles 1991). Seedling establishment is most successful when there is a high water table, some shade, and reduced competition from other vegetation (Kenkel 1986, Rudolph and Laidly 1990).

The natural distribution of Jack pine populations has been described as both random and non-random. According to Ohmann (1968), Jack pine found in Itsaca Park, Minnesota exhibited a random distribution. However, Kenkel (1988) concluded that only the combination of living and dead trees gave a random distribution. Kenkel stated further that live trees showed a regular distribution, while the dead trees showed a clumped distribution. Kenkel et al. (1989) concluded that local competition in naturally occurring Jack pine populations resulted in self-thinning and more even-sized stands.

Although Jack pine usually grows on sandy spodosols and entisols, it can also be found on loamy and rocky soils and performs best on well-drained loamy sands (Rudolph and Laidly 1990, Riemenschneider 1982).

Jack pine in the study site

Jack pine is a native species on the dunes of Lake Michigan and is distributed throughout the four dune habitats. It can be found in small stands or as individual trees scattered throughout the foredunes and occasionally in the deciduous forest. Larger stands are found in the inland blowouts, and especially high densities of Jack pine are commonly found in and around the wetpannes. This distribution pattern also occurs in other Great Lake dune ecosystems. For example, one Indiana dune ecosystem contained Jack pine within and surrounding wetpannes, on open slopes, in woodlands, on dune-complexes, or in mixed-hardwood stands (Menges and Armentano 1985). Jack pine reproduction was shown to be especially dense in and around the wetpannes, which is consistent with its reproduction in the study site, but it also occurred in more open areas with cottonwood, sand cherry, and red cedar (Menges and Armentano 1985).

Although Austrian pine has been documented as an invasive species in the study site, it is unclear how Jack pine compares to Austrian pine with respect to its site preferences, ability to spread on the dunes, and competitiveness with Austrian pine. Jack pine, similar to other pine species, has been cited as invasive in Australia and New Zealand. For example, it has invaded extensively managed grasslands, shrublands, and tussock grasslands in South Island, New Zealand (Sykes 1981, Richardson et al. 1994).

Furthermore, Grotkopp et al. (2002) described Jack pine as more invasive than Austrian pine, at least in certain habitats. They used the Z scores established by Rejmanek and Richardson (1996) that ranged from 11.41 for the most invasive to -13.58 for least invasive, to categorize 29 pine species based on their invasiveness. Their results show that Jack pine has a Z score of 8.85, while Austrian pine is rated as 1.33. The Z scores were based upon the species mean seed mass, minimum juvenile period, and mean interval between large seed crops and did not take into account specific site conditions.

Research objectives

This study compares some aspects of the regeneration niches of Austrian pine and Jack pine in SDSPNA, examining the spatial occurrence and distribution and microsite conditions favorable for successful germination and establishment of progeny. More specifically, the patterns of occurrence of Austrian pine and Jack pine seedlings and saplings are compared underneath and around Austrian pine stands in the study site. If the patterns of occurrence are similar for Austrian pine and Jack pine, then the two species may be able to regenerate under similar conditions and thus, little or no niche partitioning may occur in this system. Alternatively, if Austrian pine and Jack pine regenerate under different microsite conditions, there would be less reason to expect a severe impact from Austrian pine on Jack pine, such as competition for resources and/or space, and perhaps habitat or niche partitioning may occur.

This study also compares the microsite conditions favorable for the regeneration of the two pines. More specifically, abiotic and biotic dune features such as % coverage and depth of litter, slope, % coverage of overstory vegetation, % coverage of understory vegetation, associated dominant plant species, and height of understory vegetation were correlated with the occurrence of Austrian pine and Jack pine regeneration to determine site and/or habitat preferences for both species. A comparison of the distribution patterns of Austrian pine and Jack pine in and around Austrian pine stands will document fundamental similarities or differences in the regeneration niches of both species.

Therefore, the objectives of this study were to determine some aspects of the regeneration niches of Austrian pine and Jack pine in and around planted Austrian pine stands in SDSPNA. This includes determining the patterns of occurrence of seedlings and saplings of both species where they coexist as well as the dune microsite conditions for successful establishment of the two species in those areas.

The following research questions formed the basis for this study:

1) Are there fundamental similarities between the regeneration niches of Austrian pine and Jack pine regeneration in and around planted Austrian pine stands?
    a. Does the regeneration of both species occur in similar patterns in and around Austrian pine stands?
    b. Are both species found in similar microsites?
    c. Is there habitat partitioning between Austrian pine and Jack pine?
2) Does the spread of Austrian pine influence, either positively or negatively, where Jack pine may be able to occur in the dune system? If yes, where on the dunes does Jack pine face competition from Austrian pine?

METHODS

Study site

This investigation took place in the Natural Area of Saugatuck Dunes State Park (SDSPNA), as described in Chapter 2. Sampling occurred in each of the four dune habitats (foredunes, forest edge, inland blowouts, and wetpannes) during the summers of 2001 and 2002.

Patterns of occurrence of Austrian pine and Jack pine regeneration underneath and surrounding planted Austrian pine stands

Randomly and non-randomly located $1m^2$ plots were sampled for Austrian pine and Jack pine regeneration underneath and surrounding Austrian pine stands, as described in Chapter 2. The same $1m^2$ plots used to document the rates and spatial patterns of Austrian pine spread (Chapter 2), were used to document Jack pine regeneration. In each $1m^2$ plot sampled, the presence of both Austrian pine and Jack pine seedlings and saplings were recorded and abiotic and biotic dune features were measured. Seedlings and saplings will be referred to collectively as progeny. Jack pine seedlings were defined as individuals less than 20 cm tall, while saplings were individuals greater than 20 cm but not yet reproductively mature (i.e., no cones visible) (Rudolph and Laidly 1990). Austrian pine seedlings were defined as individuals less than 20 cm in height (Wenny and Dumroese 1991). Austrian pine saplings were individuals greater than 20 cm in height and less than 30 years in age, thereby encompassing all trees that had established through natural processes (i.e., were not planted). Because Austrian pine plantations in the park were first established in 1956, and the species typically starts reproduction after 15 years of age (Burns and Honkala 1990), all Austrian pine progeny in the study site were assumed to be less than 30 years of age. Age determination was based on stem diameter measurements and whorl counts (see Appendix A1). For the purposes of displaying patterns of occurrence of Austrian pine and Jack pine regeneration, progeny were pooled, by species, in the analysis.

Dune features correlated with Austrian pine and Jack pine regeneration

Several abiotic and biotic dune features were sampled along with the presence of pine regeneration to identify habitat and/or site characteristics conducive for successful pine establishment and survival. Similarities and differences of the habitat and/or site characteristics were compared between Austrian pine and Jack pine progeny. In each $1m^2$ plot sampled for pine regeneration, the following measurements were also taken: % coverage and depth (cm) of litter, slope (%), % coverage of overstory vegetation, % coverage of understory vegetation, dominant plant species, and height of understory vegetation (cm). Slope was measured with a clinometer. Percent coverage of overstory vegetation, understory vegetation, and litter were measured once per site to calibrate the researcher's eye and were estimated in subsequent $1m^2$ plots. The % coverage of understory vegetation and litter was measured using a $1m^2$ frame divided into 100 100-cm^2 sections, while % coverage of overstory vegetation was measured with a densiometer. Individual plant species were recorded and later categorized as tree, shrub, grass, or forb for statistical analysis.

Using SAS (2001) as the statistical program (α=0.05), the correlations between the occurrence of seedlings and saplings and the previously described dune features were determined. These correlations help determine if Austrian pine progeny and Jack pine progeny are found in similar habitats and/or sites. A binary system was used for density, where "0" indicated absence and "1" indicated presence of seedlings or saplings. Because of the non-normal distribution of the data, a forward stepwise regression was used as the regression model. This model chose the dune feature(s) most correlated with the presence of seedlings and/or saplings and produced corresponding significance values. Any dune feature with a P-value less than 0.05 was considered significant, and less than 0.01 highly significant, in contributing to Austrian pine or Jack pine regeneration success.

RESULTS

Patterns of occurrence of Austrian pine and Jack pine regeneration underneath and surrounding planted Austrian pine stands

Although the mean number of Jack pine progeny found underneath and extending from an Austrian pine stand in the foredunes were lower than those of Austrian pine, as expected, the relative distribution of both species were nearly identical (Figure 3-1, Figure 3-2). Compared to the total number of progeny found in the foredunes, the relative distributions of both species were extremely similar. Thirty percent of both

Austrian pine and Jack pine progeny were found underneath the canopy, and doubled at the edge of the canopy to 62.3% for Austrian pine and 63.2% for Jack pine. Both species decreased in abundance extending away from the canopy edge and thereafter.

In the inland blowouts, similar to the pattern observed in the foredunes, the mean number of Jack pine progeny was lower than those of Austrian pine underneath and extending away from the canopy edge (Figure 3-3). However, the relative distribution of Austrian pine and Jack pine progeny underneath and extending from the edge of the Austrian pine stand were extremely similar (Figure 3-4). Underneath the canopy, 26.6% of the total Austrian pine progeny and 18.2% for Jack pine progeny were found, and increased to 59.3% for Austrian pine and 72.7% for Jack pine at the canopy edge. At a distance of 0.1 m to 3 m away from the canopy edge, the percent of Austrian pine and Jack pine progeny decreased to 11.1% for Austrian pine and 9.1% for Jack pine and continued to decrease in abundance extending away from the canopy edge.

In the forest edge, similar to the foredunes and inland blowouts, the pattern of the relative distribution of Austrian pine and Jack pine progeny underneath and around Austrian pine stands was similar (Figure 3-5, Figure 3-6). Both species showed a similar pattern of the greatest abundance at the edge of the native forest (Figure 3-5). Based on the total number of progeny found in this habitat, 53.7% of Austrian pine progeny and 64.5% of Jack pine progeny were found at the edge of the forest. Extending into the native forest, both Austrian pine and Jack pine progeny decreased in abundance.

Due to the greater concentration of Jack pine parental trees and favorable conditions found in the wetpannes (i.e., higher soil moisture levels), Jack pine progeny were more abundant in the wetpannes than in the other dune habitats. The pattern of occurrence of Austrian pine and Jack pine progeny found at the wetpanne edges and interior were similar (Figure 3-7 and Figure 3-8). Both Austrian pine and Jack pine progeny were found in greater abundance in the interior of the wetpanne than at the edge, although the differences were not statistically different. Based on total number of progeny found at the wetpanne interior and edge, 55% of Austrian pine progeny were found at the wetpanne interior (an average of 38.9 individuals), compared to 67.9% for Jack pine progeny (an average of 32.8 individuals). Forty-five percent of Austrian pine progeny were found at the wetpanne edge (an average of 31.6 individuals), compared to 32.1% for Jack pine (an average of 15.5 individuals). The average size of the 10 wetpanne sites was 307 m^2 (see Chapter 2).

Dune features correlated with Austrian pine and Jack pine regeneration

In the foredunes, the percent of litter cover was negatively correlated with Jack pine seedlings and Austrian pine saplings and highly negatively correlated with Austrian pine seedlings (Table 3-1a, Table 3-1b). Jack pine seedlings were highly positively correlated with the percent of understory vegetation and positively correlated with the percent of overstory vegetation. Austrian pine saplings were negatively correlated with the percent of understory vegetation, and positively correlated with the percent of overstory vegetation. Austrian pine and Jack pine seedlings were positively correlated with the depth of litter layer. Austrian pine seedlings and saplings and Jack pine saplings were highly negatively correlated with the presence of dominant grasses and forbs.

In the forest edge, Austrian pine seedlings and Jack pine seedlings and saplings were positively correlated with the percent of litter cover, while Austrian pine saplings were negatively correlated with the percent of litter coverage (Table 3-1a). Austrian pine seedlings and Jack pine saplings were positively correlated with the percent of overstory cover, while Jack pine seedlings were negatively correlated with the percent of overstory cover. The depth of litter layer was correlated only with Austrian pine saplings (negatively). Austrian pine and Jack pine seedlings were negatively correlated with the presence of dominant grasses, while Austrian pine saplings were highly positively correlated. Jack pine seedlings were negatively correlated with the dominant shrubs. Both Austrian pine and Jack pine seedlings were positively correlated with the dominant trees, while Austrian pine saplings were highly negatively correlated.

In the inland blowout habitat, Austrian pine seedlings were highly positively correlated with the percent of understory and overstory vegetation, and highly negatively correlated with the percent of litter cover (Table 3-1a). Austrian pine saplings were positively correlated with the percent of overstory vegetation, the height of understory vegetation, and the slope. Jack pine seedlings were negatively correlated with the percent of understory and overstory vegetation, and positively correlated with the slope and the height of understory vegetation. Austrian pine seedlings were negatively correlated with the dominant shrubs and trees, while Austrian pine saplings were highly negatively correlated with the dominant shrubs and trees.

Finally, in the wetpannes, Austrian pine seedlings were positively correlated with the percent of overstory vegetation, the height of understory vegetation, and highly positively correlated with the depth of the litter layer (Table 3-1a). Jack pine seedlings were negatively correlated with the percent of understory vegetation. Austrian pine and Jack pine saplings were also positively correlated with the height of the understory vegetation, and Jack pine saplings were positively correlated with the depth of the litter layer. Austrian pine seedlings were positively correlated with the presence of the dominant forbs and grasses, while Jack pine seedlings were highly positively correlated. Austrian pine and Jack pine saplings were highly positively correlated with the presence of the dominant forbs. Austrian pine saplings were highly positively correlated with the presence of the dominant grasses, while Jack pine saplings were highly negatively correlated.

DISCUSSION

Patterns of occurrence of Austrian pine and Jack pine regeneration underneath and surrounding Austrian pine stands

Because sampling occurred in and around stands of Austrian pine in each dune habitat, the low numbers of Jack pine progeny compared to Austrian pine were expected, and are not indicative of fundamental differences in population characteristics of the two species. Of significance is the fact that despite the lower abundance of Jack pine progeny in the foredunes, forest edge, and inland blowouts, both species have similar patterns of occurrence underneath and extending from the Austrian pine stands (Figures 3-1 through 3-6). The wetpannes showed similar patterns of occurrence of both Austrian pine and Jack pine on a percentage basis and on a total number of progeny basis (Figure 3-7,

Figure 3-8). Therefore, the patterns of occurrence of both Austrian pine and Jack pine progeny were extremely similar underneath and extending from the edge of Austrian pine stands and in the wetpannes, and habitat partitioning is not apparent under these conditions.

Dune features correlated with Austrian pine and Jack pine regeneration

Based on the literature, pine seedlings, including Austrian pine and Jack pine, require high light and low-litter conditions for successful establishment (Steven and Carlisle 1959, Fowles 1965, Huntley and Birks 1983, Delcourt and Delcourt 1987, Rudolph and Laidly 1990, and Richardson 1998a). Furthermore, most pine seeds will readily germinate given adequate soil moisture and temperatures (Richardson 1998a). These results are consistent with those found in the study site. Lower percent litter cover, greater overstory vegetation, taller understory vegetation with fewer forbs, grasses, and shrubs are the most important dune features correlated with successful establishment of Austrian pine and Jack pine establishment.

In all dune habitats but the forest edge, there was a negative correlation between the percent litter cover and pine regeneration, indicating more regeneration in sites with low percent litter cover. The forest edge innately had more percent litter cover, due to dense forest vegetation in this habitat. Percent of litter cover is usually related to the amount of overstory and understory vegetation (i.e., fallen leaves and twigs, senescent grass blades, dead/decaying plant tissue), and a low percent litter cover would indicate less shading for the developing seedlings. Leege (1997) verified the importance of sufficient light for Austrian pine regeneration in the study site, and it is well-documented that Jack pine, similar to most pines, also requires sufficient light for developing seedlings (Harrington and Kelsey 1979, Rudolph and Laidly 1990).

The height of understory vegetation and percent overstory cover of vegetation are both positively correlated with Austrian pine and Jack pine regeneration. Progeny of Austrian pine and Jack pine were positively correlated with the height of understory vegetation, which implies more regeneration in sites with taller understory vegetation (i.e., less direct shading), consistent with results of Wills and Begg (1986). Although the percent of overstory vegetation was negatively correlated with Jack pine seedlings in the forest edge and inland blowouts, the majority of correlations were positive. A greater percent of overstory vegetation would indicate greater canopy cover, consistent with the general pattern of greater regeneration at the edge of the canopy of either Austrian pine stands or the native forest.

The presence of dominant shrubs was negatively correlated with both Austrian pine and Jack pine regeneration, except for Austrian pine saplings. This negative correlation is most likely attributed to the dense, shorter structure of most dune shrubs, blocking light needed for developing seedlings. Austrian pine saplings were highly positively correlated with the presence of the dominant shrubs, however, attributed to their greater height and less susceptibility to light blocked from shrubs. While the majority of correlations between grasses and pine regeneration were negative, except in the wetpannes with naturally greater densities of wetpanne flora, the majority of correlations between trees and pine regeneration were positive. Grasses have been known to outcompete pine seedlings, especially for soil moisture (Richardson and Bond 1991), while trees may provide a deeper litter depth, and consequently higher soil moisture, although they may also partially shade pine progeny. The correlations between forbs and pine progeny were negative in the foredunes and positive in the wetpannes. Forbs, similar to grass species, may outcompete pine seedlings for light, soil moisture, and/or soil nutrients. However, in the wetpannes with greater soil moisture and soil nutrients, pine progeny were able to survive and co-exist with other wetpanne flora.

Overall, Austrian pine and Jack pine seedlings and saplings seem to regenerate under similar conditions in each dune habitat in the study site. The relative distribution of both Austrian pine and Jack pine progeny underneath and around Austrian pine stands were extremely similar in all dune habitats. Microsite conditions favorable for the regeneration of the two species were also similar, indicating that habitat partitioning does not seem to occur between the two species. Finally, it is acknowledged and recognized that while all Austrian pine individuals that arose through natural processes (i.e., were not planted) were included, to fully document the invasive potential of exotic Austrian pine in the study site, only reproductively immature Jack pine individuals were included. This project was designed to document some aspects of Jack pine regeneration in the study site, and therefore immature individuals were only included, which may present at least some inequalities in sampling Austrian pine and Jack pine progeny.

Conclusions

Austrian pine and Jack pine appear to have similar regeneration niches in and around the planted Austrian pine stands in each dune habitat throughout SDSPNA. The relative distribution of both species seems to occur in similar spatial patterns, where most regeneration occurs at the edge of the Austrian pine stands or at the edge of the native forest. Both species were found in similar microsites and were favored by similar environmental factors. Austrian pine and Jack pine progeny were correlated with a low percent of litter cover, greater overstory vegetation, taller understory vegetation with few forbs, grasses, and shrubs. Therefore, habitat partitioning is not apparent between Austrian pine and Jack pine regeneration in the vicinity of Austrian pine stands, since both species seem to occur in similar patterns and microsite conditions. The spread of Austrian pine may affect the present and perhaps future distribution of Jack pine. Sites that are currently occupied by Austrian pine may be conducive to Jack pine regeneration, since both species require similar habitat and/or environmental conditions. For future management purposes, Jack pine may potentially be planted in areas currently occupied by Austrian pine with the intent of eventually replacing Austrian pine and converting the Lake Michigan sand dunes into a more natural state. However, continued research is needed to determine the specific interactions of Austrian pine and Jack pine seedlings and saplings and the role of interspecific competition between the two species.

Table 3-1a. Forward stepwise correlation between the presence of Austrian pine and Jack pine progeny and selected abiotic and biotic dune features (SAS Inst. 2001, $\alpha=0.05$). In each m^2 plot sampled, the presence of Austrian pine and Jack pine progeny was recorded and dune features measured in each habitat. A "1" indicates seedlings, and "2" indicates saplings. A significant correlation ($P\leq 0.005$) is indicated by a "*" for Austrian pine and "o" for Jack pine, while a highly significant correlation ($P<0.0001$) is indicated by "**" for Austrian pine and "oo" for Jack pine. Positive correlations are indicated by a "+", while a negative correlation is indicated by a "-." The total number of seedlings and saplings observed and analyzed are shown in Table 3-1b.

Dune feature	Foredune		Forest edge		Inland blowout		Wetpanne	
	1	2	1	2	1	2	1	2
% litter cover	**, - o,-	*,-	*,+ o,+	*,- o,+	**,-			
% understory vegetation	oo,+	*,-			**,+ o,-		o,-	
% overstory vegetation	o,+	*,+	*,+ o,-	o,+	**,+ o,-	*,+	*,+	
Height of understory vegetation					o,+	*,+	*,+ o,+	*,+ o,+
Depth of litter layer	*,+ o,+			*,-			**,+	o,+
Slope (%)					o,+	*,+		
Dominant Forbs	**,-	**,- oc,-					*,+ oo,+	**,+ oo,+
Dominant Grasses	**,-	**,- oo,-	*,- o,-	**,+			*,+ oo,+	**,+ oo,-
Dominant Shrubs			o,-		*, -	**,-		
Dominant Trees			*,+ o,+	**,-	*,-	**,-		

Table 3-1b. The total number of seedlings and saplings observed in each dune habitat and correlated with selected dune features. The dune features and their correlation(s) with Austrian pine seedlings and saplings are shown in Table 3-1a. AP=Austrian pine, JP=Jack pine. A "1" indicates seedlings and "2" indicates saplings.

Habitat	AP1	AP2	JP1	JP2
FD	694	50	76	13
FE	22	36	15	0
IB	248	97	37	1
WP	490	250	204	275

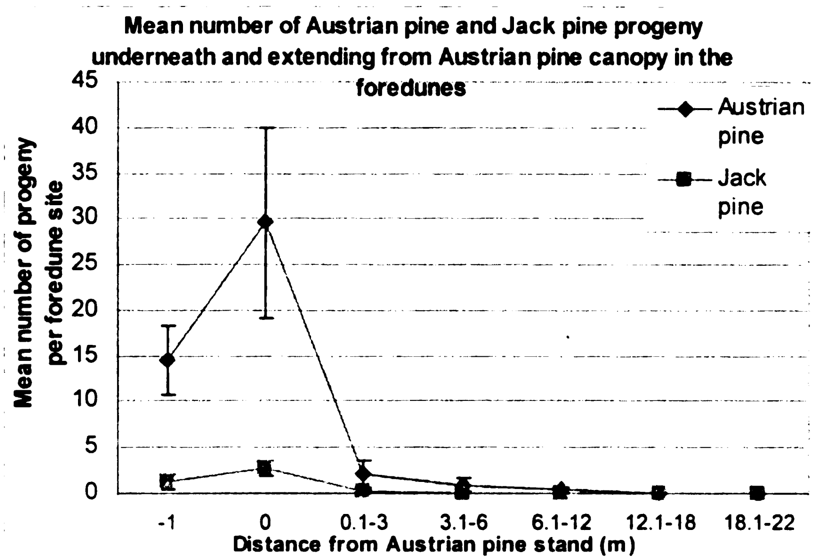

Figure 3-1. Mean number of Austrian pine and Jack pine progeny extending from the edge of mature Austrian pine stands across the ten foredune sites, based on random and non-random sampling. Locations underneath the canopy are designated as "-1." Random sampling was performed using randomly located 1m^2 plots underneath and at edge of canopy and along transects running N, S, E, W from the edge of the stand to 5 m or the furthest extent of Austrian pine regeneration. Non-random sampling occurred wherever regeneration was observed not previously captured in the random samples. These data are consistent with Table A2-2.

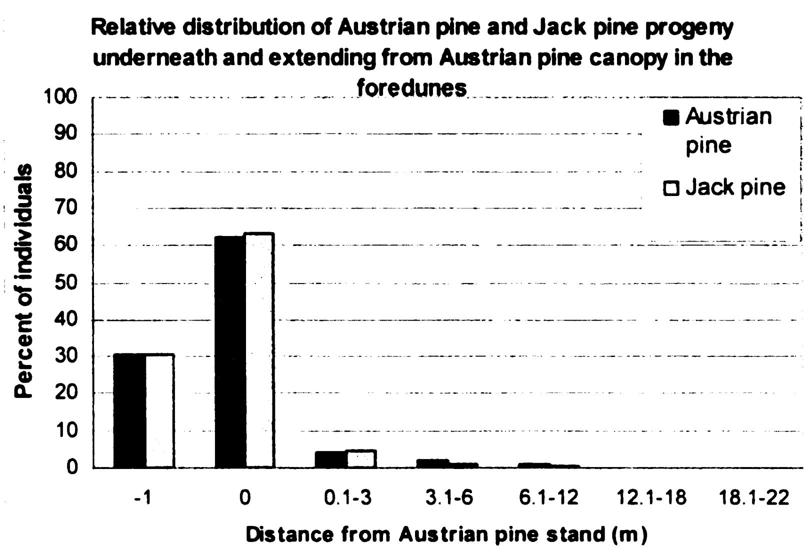

Figure 3-2. Relative distribution of Austrian pine and Jack pine progeny underneath and extending from Austrian pine canopy in the foredunes, based on the total number of progeny found in this habitat. These data are consistent with Figure 3-1, but are shown in percentages of total number of pine progeny.

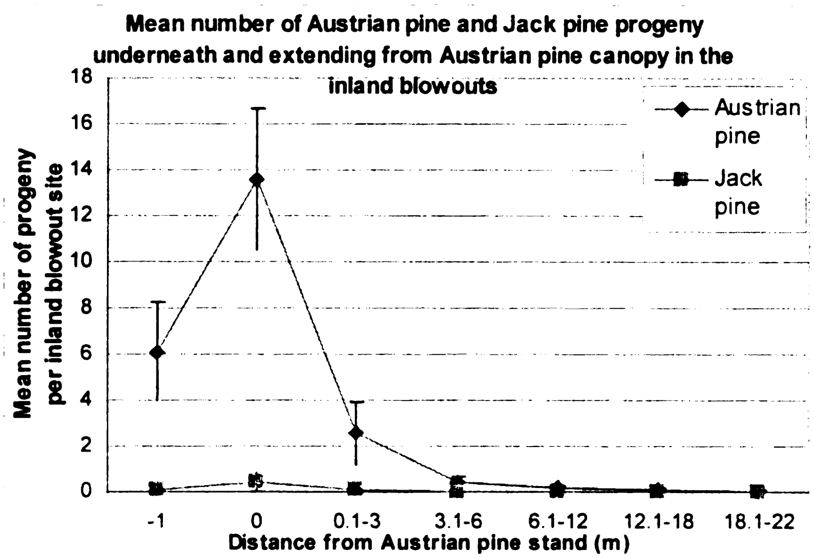

Figure 3-3. Mean number of Austrian pine and Jack pine progeny extending from the edge of mature Austrian pine stands across the ten inland blowout sites. Mean values were based upon random and non-random sampling. Locations underneath the canopy are designated as "-1." Random sampling was performed using randomly located $1m^2$ plots underneath and at edge of canopy and along transects running N, S, E, W from the edge of the stand, or NE, NW, SE, SW in three sites, to 5 m or the furthest extent of Austrian pine regeneration. Non-random sampling occurred wherever regeneration was observed not previously captured in the random samples. These data are consistent with Table A2-3.

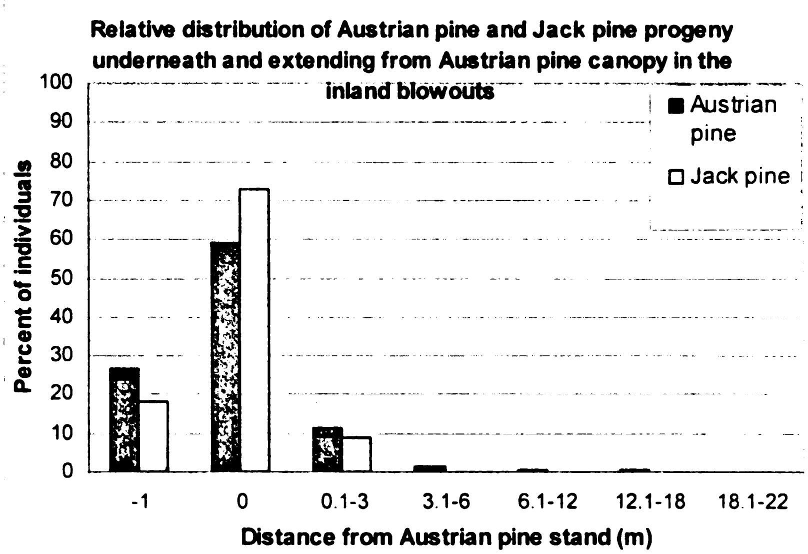

Figure 3-4. Relative distribution of Austrian pine and Jack pine progeny underneath and extending from Austrian pine canopy in the inland blowouts, based on the total number of progeny found in this habitat. These data are consistent with Figure 3-3, but are shown in percentages of total number of pine progeny.

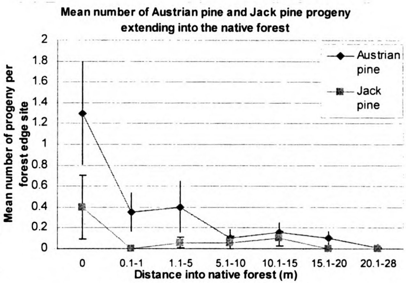

Figure 3-5. Mean number of Austrian pine and Jack pine progeny extending from the edge of mature Austrian pine stands across the ten forest edge sites, based on random and non-random sampling. Locations underneath the canopy are designated as "-1." Random sampling was performed using randomly located $1 m^2$ plots underneath and at edge of canopy and along transects running N, S, E, W from the edge of the stand to 5 m or the furthest extent of Austrian pine regeneration. Non-random sampling occurred wherever regeneration was observed not previously captured in the random samples. These data are consistent with Table A2-4.

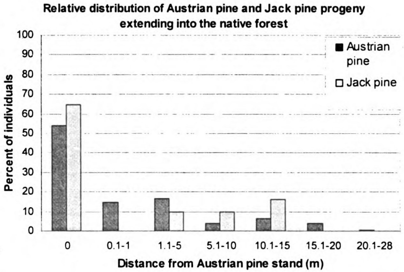

Figure 3-6. Relative distribution of Austrian pine and Jack pine progeny underneath and extending from Austrian pine canopy into the native forest, based on the total number of progeny found in this habitat. These data are consistent with Figure 3-5, but are shown in percentages of total number of pine progeny.

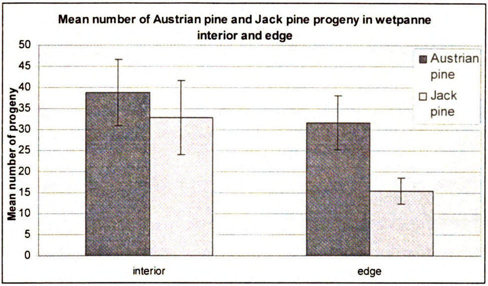

Figure 3-7. Mean number of Austrian pine and Jack pine progeny in wetpanne interior and edge, across ten wetpannes. Nine wetpannes were surveyed for regeneration, and one wetpanne, too large to survey, was sampled using 10 1-m^2 plots at the wetpanne edge and interior. Seedlings and saplings were pooled for both species.

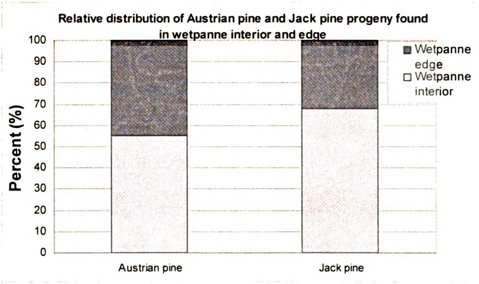

Figure 3-8. Relative distribution of Austrian pine and Jack pine progeny found in wetpanne interior and edge, based on the total number of progeny found in ten wetpanne sites.

CHAPTER 4

SPATIAL OCCURRENCE OF THREATENED *CIRSIUM PITCHERI* AND POTENTIAL EFFECTS OF INVASIVE *PINUS NIGRA*

INTRODUCTION

Cirsium pitcheri (Pitcher's thistle) is a species endemic to the Great Lakes sand dune ecosystem and is listed as threatened in both the U.S. and Canada (Congress of the United States 1988). Population numbers have continued to decline due to lakeshore development, artificial dune stabilization measures, and dune traffic caused by pedestrians and vehicles, resulting in its federal listing (Harrison 1988, Pavlovic et al. 1992). The most detrimental effects to Pitcher's thistle populations have occurred in the southern tip of Lake Michigan, where land use has been most intensive (MacEachern et al. 1994). Further threats from invasive plant species, such as the invasive *Pinus nigra* (Austrian pine), could jeopardize the survival of Pitcher's thistle on the eastern shores of Lake Michigan. Originally planted in the area now known as Saugatuck Dunes State Park (SDSP) by private landowners in a sand-stabilization effort between 1956 and 1972, Austrian pine has dramatically altered the native dune conditions. It has been documented to shade out native plant species, reduce sand movement, decrease species diversity, and possibly alter ground-water levels (Leege 1997, Leege and Murphy 2000, 2001, Sherfinski 2000). Although the specific effects of Austrian pine reproduction, dispersal, and local spread on rare dune species such as Pitcher's thistle are currently unknown, it is certain that Austrian pine will directly threaten the long-term persistence of rare species by altering native dune conditions.

Distribution and ecology of Cirsium pitcheri

Pitcher's thistle is a rare dune plant naturally occurring along the shoreline dunes of Lakes Huron, Michigan, and Superior. Although its range extends from southern Lake Michigan to northern Lake Superior, most Pitcher's thistle populations are found on the eastern shore of Lake Michigan (Beal 1870, Hamze and Jolls 2000). The largest populations in the U.S. occur only within protected parks of the Great Lakes, including Indiana Dunes, Sleeping Bear Dunes, and Pictured Rocks National Lakeshores (McEachern 1992). Pitcher's thistle usually colonizes open dunes and blowouts, but has also been found on more stabilized dunes (Loveless and Hamrick 1988).

Although most populations are relatively small, consisting of 20-30 flowering individuals per year, larger populations containing up to 100 individuals have been known to occur (Loveless and Hamrick 1988). Metapopulation dynamics play an important role in the survival of Pitcher's thistle, where a metapopulation is defined as a group of subpopulations inhabiting separate locations and actively exchanging individuals among subpopulations. It has been documented that the perpetuation of multiple populations comprised of smaller subpopulations are required to sustain this species (McEachern et al. 1994). As a monocarpic perennial with no vegetative reproduction, Pitcher's thistle usually persists as a rosette for 2-8 years before flowering, with light cream-colored inflorescences suited for bee, moth, and butterfly pollination (Loveless 1984, McEachern et al. 1994, Hamze and Jolls 2000). While plants are self-compatible, outcrossing is more common and rates of outcrossing range between 35-

88%. After fertilization, the mature fruits (achenes) are wind-dispersed. Pitcher's thistle seeds are the largest of any North American thistle (Gleason 1952), and therefore most dispersal is within five meters of the parent plant. Dispersal over longer distances is rare, attributed mostly to secondary dispersal and flower head detachments (Loveless and Hamrick 1988). Seedling emergence begins in late May, and the first true leaves are entire and densely tomentose. In later years, the leaves are pinnatifid and tomentose. Studies have shown that seeds require burial for successful germination and emergence (Hamze and Jolls 2000). Hamze and Jolls (2000) also concluded that long-term protection and propagation of Pitcher's thistle depends on the conservation of natural sand erosion and burial patterns necessary for maintaining open dune habitats.

Research objectives

The objectives of this study were to document the spatial occurrence of Pitcher's thistle and the populations most threatened by Austrian pine spread in Saugatuck Dunes State Park Natural Area (SDSPNA). In addition, Pitcher's thistle population densities were compared in the presence and absence of Austrian pine regeneration (i.e., seedlings and saplings that established through natural reproductive processes). Because Pitcher's thistle is a rare species, endemic to the Great Lake sand dunes, and also an endemic on the Federal list of threatened species, documentation of the spatial occurrence of this species is of the utmost importance to monitor present and future populations in this area. It is also important to identify populations that are most threatened by the spread of an invasive pine to provide information that may be useful in the overall assessment of the Austrian pine threat.

The following questions formed the basis for this study:

1) Where is Pitcher's thistle located in Saugatuck Dunes State Park Natural Area?

2) Where are the populations of Pitcher's thistle most threatened by the spread of invasive Austrian pine?

3) Does the presence of Austrian pine regeneration affect Pitcher's thistle population densities?

METHODS

Study site

This investigation took place in the Natural Area of Saugatuck Dunes State Park (SDSPNA), as described in Chapter 2.

Spatial occurrence of Cirsium pitcheri

The study site was surveyed for Pitcher's thistle populations and individuals. Since this species requires some disturbance and high light levels to complete its life cycle (Hamze and Jolls 2000), the foredune and inland blowout areas, with relatively low levels of vegetation cover, were the only areas surveyed for Pitcher's thistle. These areas were thoroughly surveyed, using transects spaced approximately 15 meters apart. Other dune areas, such as the wetpannes and forest edge (see Chapter 2 for description of dune habitats) were also briefly searched to ensure the absence of Pitcher's thistle in these habitats with dense vegetation cover. Locations of Pitcher's thistle populations were documented using a Trimble® GPS unit and were saved as polygon shapefiles. Most Pitcher's thistle populations were saved as polygon shapefiles, but individuals not found within a larger population were saved as individual (point) shapefiles. Because it is listed as a federally threatened species, areas that contained Pitcher's thistle populations within 10 m of a population of Austrian pine regeneration were also documented using a Trimble® GPS unit and labeled as critical. Ten meters was chosen due to the average dispersal distance of Pitcher's thistle (within 5 m of parental plant), and most Austrian pine regeneration occurred within 10 m of the parental source in the study site (see Chapter 2).

Austrian pine effects on Cirsium pitcheri density

To measure densities of Pitcher's thistle populations and investigate the potential effect of Austrian pine on these populations, the population densities (# ind/m^2) in five populations with, and five populations without, Austrian pine regeneration were compared using a one-way analysis of variance test (ANOVA) (SAS Inst., 2001, α=0.05).

RESULTS

Eleven Pitcher's thistle populations and 29 individual plants not found within a larger population were located in the foredunes and inland blowouts of the study site (Figure 4-1). Five critical areas were located that contained Pitcher's thistle populations within 10 m of Austrian pine regeneration (Figure 4-1). All five critical areas were found in the inland blowout habitat. The mean density of Pitcher's thistle populations in the absence of Austrian pine regeneration was 0.148 ind/ m^2, compared to 0.167 ind/ m^2 in the presence of Austrian pine regeneration (Figure 4-2). However, there were no differences between Pitcher's thistle population densities in the presence or absence of Austrian pine regeneration (P=0.8209). It should also be noted that although the wetpannes and forest edge were not sampled for Pitcher's thistle, no individuals or populations were found in these habitats.

DISCUSSION

Eleven populations and 29 individuals of Pitcher's thistle were located and documented in the open areas of the foredunes and inland blowouts. Consistent with the literature, most populations were found in open dune areas usually associated with high light conditions. Five areas were considered critical because they contained Pitcher's thistle populations in close proximity to Austrian pine regeneration. These critical areas should be monitored for future changes in Pitcher's thistle populations, such as changes in location, size, density, and flowering frequency, especially since it is known that smaller subpopulations are vital to the persistence of this species (McEachern 1992, McEachern et al. 1994). Although this study did not show any significant Austrian pine effect on Pitcher's thistle population densities (P=0.8209), it is believed that there will be negative long-term effects. Since it has already been documented that Austrian pine reduces sand movement and shades out understory plants (Leege 1997, Leege and Murphy 2000, 2001), the persistence of Pitcher's thistle may be jeopardized, since this species requires high light and moderate sand burial conditions. Additional threats from pedestrian traffic and tramping are recognized, as Pitcher's thistle is found near hiking trails located throughout the study site.

Summary and Conclusions

Eleven Pitcher's thistle populations and 29 individual plants were found in the open areas of the foredunes and inland blowouts of the study site. These populations should be monitored to ensure protection of this rare and threatened species. Although it is possible that some Pitcher's thistle populations have already been displaced by Austrian pine, our data showed no evidence that Pitcher's thistle density is presently affected by Austrian pine regeneration. However, as Austrian pine continues to spread, it will encroach upon Pitcher's thistle and other sensitive populations. These data may be useful for developing future management plans concerning rare, endangered, and threatened species in the presence of an invasive pine on freshwater dune systems.

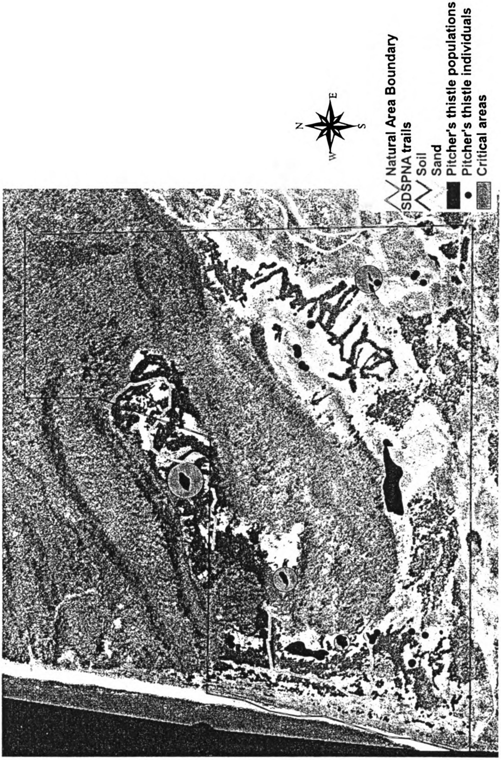

Figure 4-1. Spatial occurrence of Pitcher's thistle in SDSPNA and locations of critical areas. Critical areas were areas containing Austrian pine regeneration populations within 10 m of Pitcher's thistle.

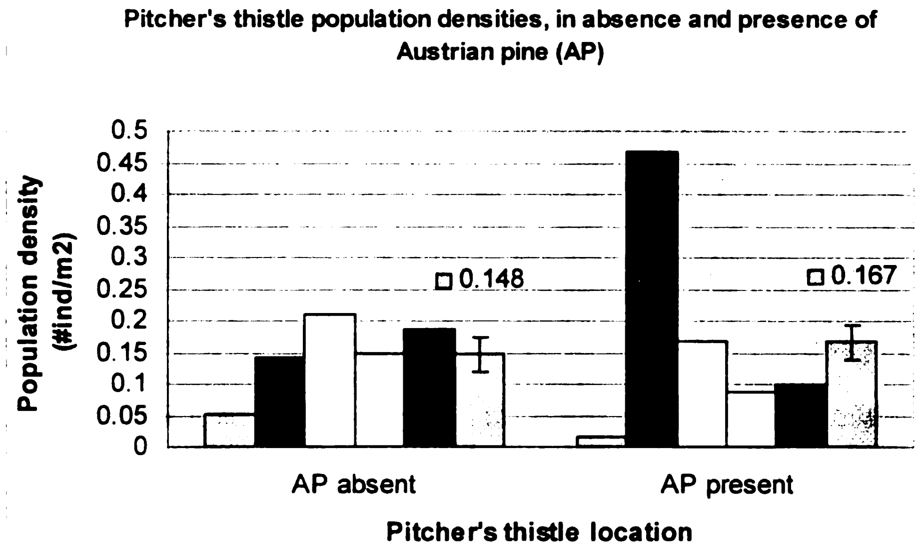

Figure 4-2. Pitcher's thistle population densities in the absence and presence of Austrian pine regeneration. There were no statistical differences between the densities of Pitcher's thistle populations in the presence and absence of Austrian pine regeneration (SAS 2001, one-way ANOVA, α=0.05, P=0.8209). The mean density in the absence and presence of Austrian pine progeny are shown numerically above.

CHAPTER 5

GENERAL SUMMARY AND CONCLUSIONS

This study provides information on the rates and spatial patterns of the spread of the invasive *Pinus nigra* (Austrian pine) immediately surrounding planted Austrian pine stands on the dunes of Lake Michigan, and compares regeneration niches of Austrian pine to the native *Pinus banksiana* (Jack pine). The spatial occurrence of the endemic and threatened *Cirsium pitcheri* (Pitcher's thistle) was also documented, and the potential effects of Austrian pine regeneration on Pitcher's thistle population densities were analyzed.

Originally planted between 1956 and 1972, Austrian pine is now reproducing in the four main dune habitats in the study site: foredunes, forest edge, inland blowouts, and wetpannes. In the foredunes and inland blowouts, although regeneration did occur underneath the stands, most regeneration occurred at the stand edge and decreased with increased distance from the stand edge. This suggests Austrian pine stand replacement and expansion. The wetpannes contained high regeneration densities of both seedlings and saplings, most likely due to close proximity to seed-source trees and higher soil moisture levels, and the highest sapling densities across all dune habitats were found in this habitat. However, the high densities of progeny at the edge and within the wetpannes were not significantly different from each other (P=0.1689), suggesting no spread into the wetpannes. There was limited regeneration in the forest edge compared to the other habitats, consistent with previous studies (Leege 1997, Leege and Murphy 2000, 2001).

However, there were some individuals found up to 28 m into the forest, suggesting the possibility of relatively long-distance dispersal events, perhaps via animal transport.

Rates of Austrian pine spread on a per-plant basis ranged from 0.00 m yr^{-1} in some stands to 15 m yr^{-1}. Rates in the inland blowouts ranged from 0.00 m yr^{-1} to 1.61 m yr^{-1}, averaging 0.20 m yr^{-1}, and were as high as 15 m yr^{-1}. Rates in the foredunes ranged from 0.00 to 0.28 m yr^{-1}, with an average of 0.06 m yr^{-1}. Maximal rate of spread found in this habitat was as high as 1.88 m yr^{-1}. Higher rates in the inland blowouts are most likely attributed to their open nature, where adjacent Lake Michigan winds can disperse seeds to greater distances. The forest edge had the least amount of spread, ranging from 0.00 to 0.12 m yr^{-1}, averaging 0.04 m yr^{-1}. The highest rate observed was 2.11 m yr^{-1} in one site, where an individual was found 28 m from the presumptive parental tree. Local patterns of spread were mainly towards the north in the foredunes and northeast in the inland blowouts, most likely attributed to the strong prevailing southwesterly winds. On average, foredune stands have increased in area by 37% since the original plantations were established in 1963, while inland blowout stands have increased by 25% since 1966. However based on the greatest distances that Austrian pine progeny were found from a stand edge in the foredunes and inland blowouts, the maximum increase in area was 153% for foredune stands and 132% for inland blowout stands. This represents the potential for Austrian pine to disperse in these directions and distances under favorable conditions in the study site.

Measured parameters of the regeneration niches of Austrian pine and Jack pine in the vicinity of Austrian pine stands were extremely similar in the study area. The relative distribution of Austrian pine and Jack pine progeny were strikingly similar in each of the four main dune habitats, where most regeneration occurred at the edge of Austrian pine stands or at the edge of the native forest. These results are consistent with the literature, stating that pine seedlings require high light and low-litter conditions and thus most seedlings successfully establish near the stand edge (Yocum 1968, McCaughey et al. 1986, Richardson 1998a). Austrian pine and Jack pine progeny were found under similar microsite conditions and were favored by similar environmental factors. A low percent of litter cover, greater overstory vegetation, and taller understory vegetation characterized by few forbs, grasses, and shrubs were correlated to pine regeneration. As both species have similar habitat requirements, habitat partitioning between Austrian pine and Jack pine is not apparent in or around Austrian pine stands in the study site. The spread of Austrian pine may influence the distribution of Jack pine, and sites currently occupied by Austrian pine may be open for future invasion from Jack pine. However, more research is needed to determine the specific interactions between Austrian pine and Jack pine regeneration, especially competition factors between the two species.

The spatial occurrence of Pitcher's thistle was documented in the study site. Eleven populations and 29 individuals were located within the foredunes and inland blowouts. Although our data did not show any significant effect of Austrian pine regeneration on the density of Pitcher's thistle populations, it is believed that future Austrian pine spread will affect Pitcher's thistle persistence. Pitcher's thistle populations should be routinely monitored for changes in population structure and location, especially in association with Austrian pine reproduction and local population spread. These data may be useful for managing federally threatened Pitcher's thistle or other rare species in the Lake Michigan sand dune ecosystem.

APPENDICES

APPENDIX A1: AGE DETERMINATION OF *PINUS NIGRA* IN SAUGATUCK DUNES STATE PARK

By

Joseph Harsh and Khara Grieger

INTRODUCTION

The primary objective of this study was to determine a tree age to stem-diameter relationship for introduced *Pinus nigra* (Austrian pine) in Saugatuck Dunes State Park Natural Area (SDSPNA), located near Saugatuck MI. This study expands on a previous study of Austrian pine tree age and radial growth (Leege 1997, Leege and Murphy 2000, 2001), and was designed to aid in the estimation of rates of Austrian pine spread in the study site.

Preliminary studies of Austrian pine in the study site established the viability of ring counting as an appropriate approach in the estimation of tree age, although cross-dating in young trees was difficult due to a few drought years (Leege 1997, Leege and Murphy 2000, 2001). Leege (1997) established: (1) the number of rings present corresponded well within the range of planting dates, and (2) broad annual growth increments were observed for most years except for narrow rings representative of two drought years (1987, 1988). These results led to the assumption that the tree cores exhibited no missing rings and therefore can be used in age estimation.

METHODS

Mature Austrian pine trees were selected for analysis in all four dune habitats: foredune, forest edge, inland blowout, and wetpanne. Using a stratified random sample design, adult trees were chosen from ten sites per habitat, using sites previously selected in the determination of the rates and spatial patterns of Austrian pine spread (Chapter 2).

Individuals were measured for stem diameter at breast height (DBH) and cored at 1.25 m above ground level, using standard coring, mounting, and analysis techniques of stem increment cores (Stokes and Smiley 1968) consistent with previous studies (Leege 1997). Austrian pine was classified into four stratified diameter classes for sampling: (1) small (S) 0 to 10.99 cm, (2) midrange-small (MS) 11.0 to 20.99 cm, (3) midrange-large (ML) 21.0 to 30.99 cm and (4) large (L) >31.0 cm. Seven individuals per diameter class were randomly selected for coring at DBH for each habitat, totaling 112 individuals cumulatively sampled in the dune system. Four individuals per habitat were cored or cut for disc analysis at ground level (i.e., root collar) and also at breast height for the determination of an age correction value for the period required to reach 1.25 m (breast height). In addition, seven woody juvenile individuals shorter than breast height were measured for diameter and cut for disc analysis at ground level in only the foredunes, inland blowout, and wetpannes. Forest edge juveniles below breast height were not collected due to sparse regeneration found in this habitat (Leege 1997, Leege and Murphy 2000, 2001, and Grieger 2003). All trees were measured, cored, and/or cut for disc analysis in 2001 and 2002.

Depending on stem diameter, increment cores were either taken entirely through the individual or from opposite sides to average asymmetric growth and allow analysis of samples exhibiting tree damage, branch growth, or the presence of incomplete rings. Age correction values, the observed age difference between ground and DBH level samples within each habitat, were applied to the age of trees sampled at DBH for a more accurate representation of individual tree age.

From the initial sampling of 128 individuals, only 119 individuals were analyzed due to structural damage or sampling error. The total number of individuals analyzed in each habitat is as follows: foredune (n=28), forest edge (n=31), inland blowout (n=29), and wetpanne (n=31). This deficit of individuals, however, is solely from the small size class (0-10.99 cm), having a nominal effect on the age to DBH relationship.

RESULTS AND DISCUSSION

Contrary to previous findings (Leege 1997, Leege and Murphy 2000), relationships of stem diameter to age exhibited low levels of variation within each habitat. Therefore these relationships are of value in estimating tree age based on stem diameter at breast height. Diameter of individuals <1.25 m tall, sampled at ground level, are not of value in age prediction due to variation levels which may be attributable to low sample size (n=7) and/or the sensitivity of juvenile individuals to intrinsic environmental factors. Therefore, ages of individuals <1.25m tall were estimated by whorl counts.

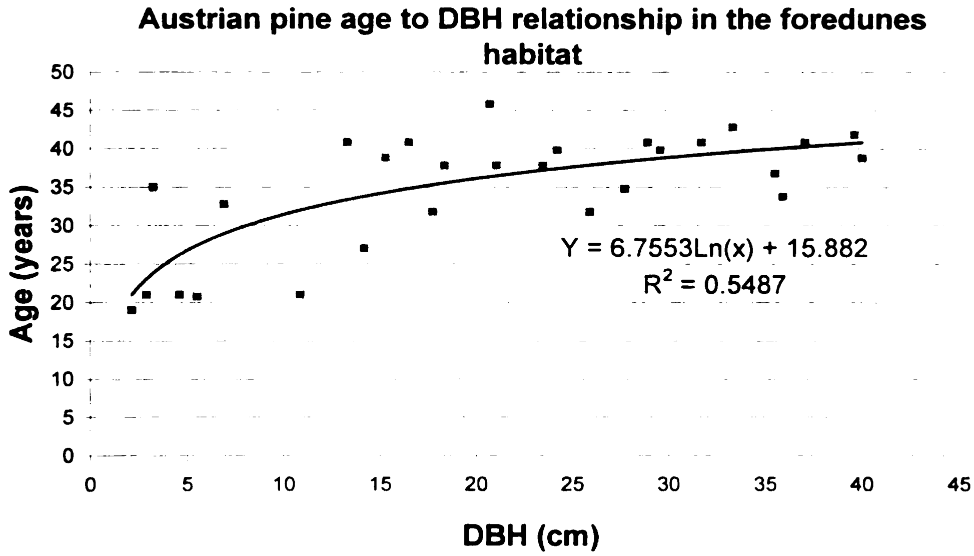

Figure A1-1. Relationship of Austrian pine tree age to stem diameter at breast height in the foredune habitat. Breast height measured at 1.25 m. Each point represents an individual.

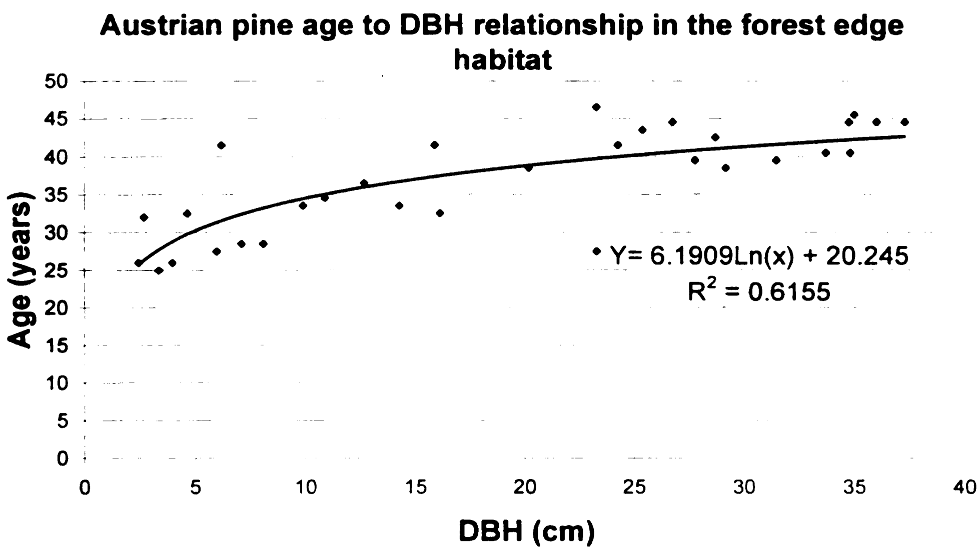

Figure A1-2. Relationship of Austrian pine tree age to stem diameter at breast height in the forest edge habitat. Breast height measured at 1.25 m. Each point represents an individual.

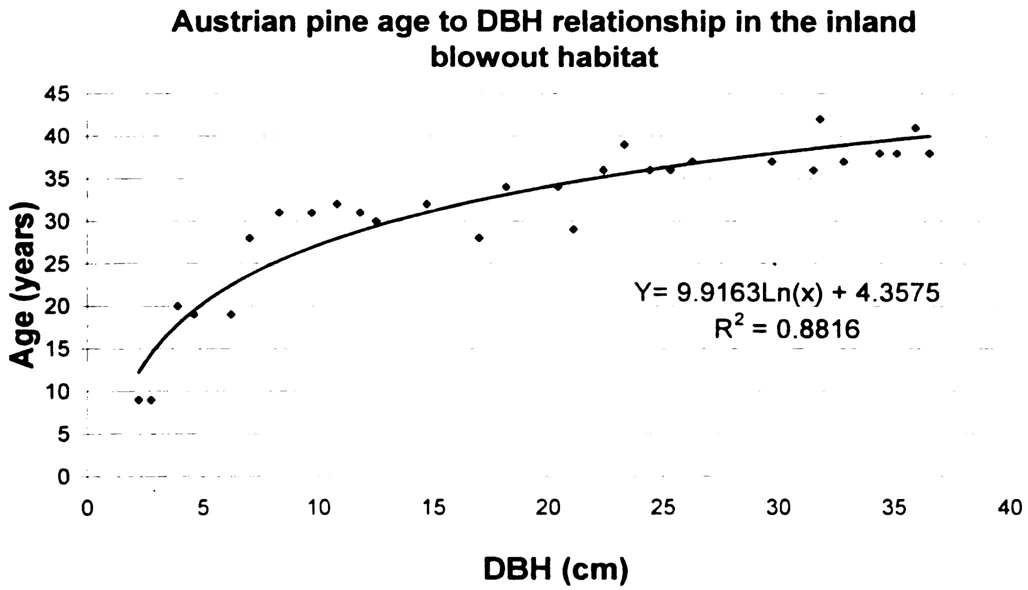

Figure A1-3. Relationship of Austrian pine tree age to stem diameter at breast height in the inland blowout habitat. Breast height measured at 1.25 m. Each point represents an individual.

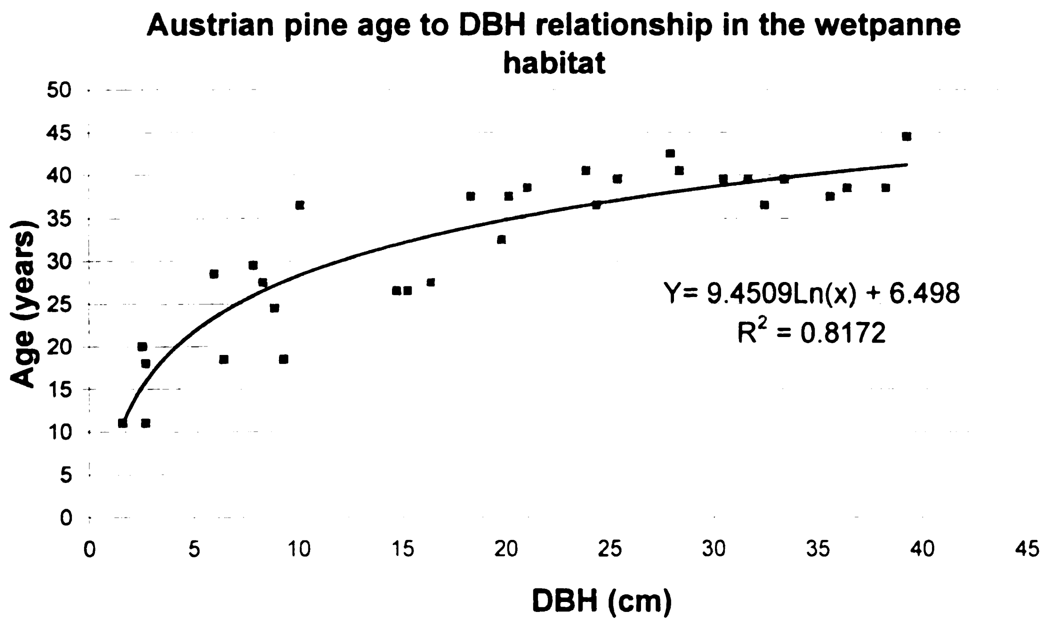

Figure A1-4. Relationship of Austrian pine tree age to stem diameter at breast height in the wetpanne habitat. Breast height measured at 1.25 m. Each point represents an individual.

APPENDIX A2: SUPPLEMENTAL DATA ON *PINUS NIGRA* AND *PINUS BANKSIANA* PROGENY UNDERNEATH AND EXTENDING FROM PLANTED *PINUS NIGRA* STANDS

Table A2-1. Mean number of *Pinus nigra* (Austrian pine) seedlings and saplings across 10 foredune, inland blowout, and forest edge sites, based upon randomly and non-randomly 1m^2 plots underneath and extending from canopy edge or into forest (for the forest edge). Locations underneath the canopy is designated as "-1."

Distance from Austrian pine stand edge (m)	Foredune	SE	Forest edge	SE	Inland blowout	SE
-1	14.5	3.69	0	0	6.1	2.14
0	29.6	10.4	1.3	0.5	13.6	3.08
0.7	0.3	0.3	0	0	0	0
0.5	0	0	0.1	0.1	0	0
0.91	0.2	0.2	0	0	0	0
1	9.5	5.91	0.6	0.27	6.5	4.09
1.1	0	0	0.2	0.2	0	0
1.2	0.4	0.4	0	0	0.3	0.21
2	4.4	3.04	0.3	0.3	2	0.83
2.5	0.5	0.5	0	0	0	0
2.6	0.2	0.2	0	0	0	0
2.7	0.3	0.3	0	0	0	0
3	3.2	1.55	0.3	0.21	1.4	0.45
3.5	0.9	0.9	0	0	0	0
4	1.5	0.79	0	0	0.4	0.27
5	1.2	0.85	1.2	0.51	0.5	0.22
6	0.1	0.1	0.1	0.1	0.3	0.21
6.3	0	0	0	0	0.1	0.1
7	0.3	0.21	0	0	0.3	0.21
8	0.4	0.4	0	0	0.2	0.13
9	0.7	0.6	0.1	0.1	0	0
10	0.7	0.5	0.3	0.21	0.2	0.2
11	0.1	0.1	0	0	0	0
12	0.1	0.1	0.1	0.1	0.1	0.1
12.2	0	0	0	0	0.1	0.1
13	0	0	0	0	0	0
14	0	0	0	0	0	0
15	0	0	0.7	0.33	0.1	0.1
16	0	0	0.3	0.21	0.3	0.21
17	0	0	0	0	0.2	0.2
18	0	0	0	0	0	0
18.7	0	0	0	0	0.1	0.1
19	0	0	0	0	0	0
20	0	0	0.2	0.13	0	0
21	0	0	0	0	0	0
22	0.1	0.1	0	0	0	0
23	00	0	0	0	0	0
24	0	0	0	0	0	0
25	0	0	0	0	0	0
26	0	0	0	0	0	0
27	0	0	0	0	0	0
28	0	0	0.1	0.1	0	0
29	0	0	0	0	0	0
30	0	0	0	0	0	0

Table A2-2. Mean number of *Pinus nigra* (Austrian pine) and *Pinus banksiana* (Jack pine) progeny extending from the edge of mature Austrian pine stands across the ten foredune sites, based on random and non-random sampling. Locations underneath the canopy are designated as "-1." Random sampling was performed using randomly located 1m^2 plots underneath and at edge of canopy and along transects running N, S, E, W from the edge of the stand to 5 m or the furthest extent of Austrian pine regeneration. Non-random sampling occurred wherever regeneration was observed not previously captured in the random samples.

Distance from stand edge (m)	Mean No. of Austrian pine progeny	SE	Mean No. of Jack pine progeny	SE
-1	14.5	3.69	1.3	0.87
0	29.6	10.4	2.7	0.88
0.7	0.3	0.3	0	0
0.91	0.2	0.2	0	0
1	9.5	5.91	0.9	0.5
1.21	0.4	0.4	0	0
2	4.4	3.04	0.5	0.31
2.5	0.5	0.5	0.1	0.1
2.6	0.2	0.2	0	0
2.7	0.3	0.3	0	0
3	3.2	1.55	0.3	0.15
3.5	0.9	0.9	0	0
4	1.5	0.79	0.1	0.1
5	1.2	0.85	0.1	0.1
6	0.1	0.1	0	0
7	0.3	0.21	0	0
8	0.4	0.4	0	0
9	0.7	0.6	0.1	0.1
10	0.7	0.5	0	0
11	0.1	0.1	0	0
12	0.1	0.1	0	0
13				
14				
15				
16				
17				
18				
19				
20				
21				
22	0.1	0.1	0	0

Table A2-3. Mean number of Austrian pine and Jack pine progeny extending from the edge of mature Austrian pine stands across the ten inland blowout sites, based on random and non-random sampling. Locations underneath the canopy are designated as "-1." Random sampling was performed using randomly located 1m^2 plots underneath and at edge of canopy and along transects running N, S, E, W from the edge of the stand to 5 m or the furthest extent of Austrian pine regeneration. Non-random sampling occurred wherever regeneration was observed not previously captured in the random samples.

Distance from stand edge (m)	Mean No. of Austrian pine progeny	SE	Mean No. of Jack pine progeny	SE
0	1.3	0.5	0.4	0.31
0.5	0.1	0.1	0	0
1	0.6	0.27	0	0
1.1	0.2	0.2	0.1	0.1
2	0.3	0.3	0	0
3	0.3	0.21	0	0
4	0	0	0	0
5	1.2	0.51	0.2	0.13
6	0.1	0.1	0	0
7				
8				
9	0.1	0.1		
10	0.3	0.21	0.3	0.3
11				
12	0.1	0.1		
13				
14				
15	0.7	0.33	0.5	0.34
16	0.3	0.21		
17				
18				
19				
20	0.2	0.13		
21				
22				
23				
24				
25				
26				
27				
28	0.1	0.1		
29				
30				

Table A2-4. Mean number of Austrian pine and Jack pine progeny extending from the edge of mature Austrian pine stands across the ten forest edge sites, based on random and non-random sampling. Locations underneath the canopy are designated as "-1." Random sampling was performed using randomly located 1m^2 plots at the canopy edge, 5 m, 10 m, and 15 m into the native forest. Non-random sampling occurred wherever regeneration was observed not previously captured in the random samples.

Distance from stand edge (m)	Mean No. of Austrian pine progeny	SE	Mean No. of Jack pine progeny	SE
-1	6.1	2.14	0.1	0.1
0	13.6	3.08	0.4	0.4
1	6.5	4.09	0.2	0.2
1.2	0.3	0.21	0	0
2	2	0.83	0	0
3	1.4	0.45	0	0
4	0.4	0.27	0	0
5	0.5	0.22	0	0
6	0.3	0.21		
6.3	0.1	0.1		
7	0.3	0.21		
8	0.2	0.13		
9				
10	0.2	0.2		
11				
12	0.1	0.1		
12.2	0.1	0.1		
13				
14				
15	0.1	0.1		
16	0.3	0.21		
17	0.2	0.2		
18				
18.7	0.1	0.1		
19				
20				

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