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THE ECOLOGICAL IMPACT OF AUSTRIAN PINE (*PINUS NIGRA*) ON THE SAND DUNES OF LAKE MICHIGAN: AN INTRODUCED SPECIES BECOMES AN INVADER

By

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ABSTRACT

THE ECOLOGICAL IMPACT OF AUSTRIAN PINE (*PINUS NIGRA*) ON THE SAND DUNES OF LAKE MICHIGAN: AN INTRODUCED SPECIES BECOMES AN INVADER

By

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The sand dunes of the Great Lakes are exposed to continuous natural disturbance and may be vulnerable to invasion by exotic species. In this study, the effects of an introduction of more than 25,000 Austrian pines (*Pinus nigra*), planted in 1956-1972 as a stabilization measure, were investigated on the Lake Michigan sand dunes in Allegan County, Michigan. The post-planting establishment success of viable trees, their biotic and abiotic effects on the dune system, and their reproductive capacity, and recruitment success were examined in four seral stages: foredunes, forest edges, wetpannes (ephemeral dune ponds), and inland blowouts.

Measures of establishment success (height, dbh, and stem volume) indicate that *P. nigra* grows as well or better on the dunes than in its native range. Tree size differs more within seral stages than among them, indicating that the coarse-scale differences in environmental factors among stages, such as soil moisture and wind exposure, account for only some of the variation in growth. The broad ecological tolerance of *P. nigra* appears to be a major attribute in its successful establishment in a variety of dune conditions.

Pinus nigra inhibits the growth of native dune vegetation in all four seral stages, and depresses species richness by up to 80% relative to sites lacking *P. nigra* in all stages but foredunes. It provides colonization sites for forest species absent from the adjacent dune communities, however, and a higher density of woody seedlings and saplings such as *Sassafras albidum* occur under pine canopy at the edge of native forest than in comparable sites lacking *P. nigra*. Additionally, wetpannes surrounded by *P. nigra* were drier than the native *Pinus banksiana* wetpannes and were characterized by a higher density of shrubs.

Pinus nigra foredune seed production per tree is 10-40 times that of other seral stages, but survivorship of seedlings is five times higher in blowouts and wetpannes. Light availability is positively correlated with survivorship in all stages (Spearman Rho = 0.52) and is postulated to regulate recruitment of seedlings after initial germination. Demographic projection models indicate that population growth rates are highest in wetpannes (lambda = 0.998 to 1.201), despite the higher understory cover and species richness of this seral stage. These findings suggest that *P. nigra* has made the transition from introduction to invasion on the sand dunes of Lake Michigan.

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CHAPTER 1

GENERAL INTRODUCTION

Biological invasions are among the most pressing ecological issues of our day. The rate of non-native species introductions has dramatically accelerated with the improvement of human transportation systems, and the biota of the world is rapidly being homogenized (Lodge 1992). Sometimes termed "biological pollution," invaders present a more persistent and pervasive threat than other types of pollution, because they are alive and reproducing and do not disappear when the inputs cease (Cronk and Fuller 1995).

Defined from a biogeographical perspective (Rejmanek 1995), biological invaders are species which occur outside their native range and are capable of forming self-sustaining populations and persisting in a novel, receptor community. It is well known that not all non-native species become problematic invaders; in fact, only a small subset of introduced species goes on to reproduce and persist, transitioning from introduction to invasion (Loope 1989, Williamson 1996). Williamson and Fitter (1996) quantified this pattern of invasion success in describing the "tens rule." Of all introduced species, only about 10% escape and are found in the wild; of escaped species, only approximately one in ten form self-sustaining populations and persist or become naturalized, and only about 10% of naturalized species go on to become economically damaging "pests." Though this rule represents a rough estimate, it holds true for both angiosperms and Pinaceae in Britain, and for insects, fishes, mollusks and plant pathogens in the U.S. (Williamson 1996).

Of plant species that do become invaders, most have negligible effects upon the systems into which they have been introduced (Loope 1992, Williamson 1996). Others, however, can dramatically alter their receptor communities by depressing growth rates or causing local extirpation of native plant populations (Walker and Vitousek 1991).

Biological invasions may significantly alter species composition (Woods 1993), and may even have consequences at the ecosystem level (Vitousek 1990). Tamarisk (*Tamarix ramosissima*) lowers water table in river systems of the American West (Brock 1994); the fire tree (*Myrica faya*) fixes nitrogen in volcanic soils of Hawaii, altering the trajectory of succession in these nitrogen poor communities (Vitousek and Walker 1989); and ice bush (*Mesembryanthenum crystallinum*) concentrates salt which inhibits germination of native species in coastal California (Williamson 1996). The impact of an invader is not simply a function of its attributes, however, but is mediated by the characteristics of the receptor community.

Plant communities tend to differ in their susceptibility to invasion (Fox and Fox 1986, Williamson 1996). Ecosystems that experience some sort of regular disturbance (e.g. grazing or fire) seem to be particularly vulnerable to exotic species invasions (Ewel 1986, Fox and Fox 1986, Orians 1986, Hobbs 1989, Hobbs and Huenneke 1992). The sand dunes of the Great Lakes are an ideal system for the study of invasions because they are continually disturbed by the natural process of sand movement which may open up space for an invader gain a foothold. In addition, sand dune systems comprise an array of habitats within a small space, and simultaneous invasions in more than one dune community type can be compared to gain insight into the differential invasibility of communities.

Great Lakes sand dune systems are partitioned into distinct community types which are termed "dune habitats" or "seral stages" (Figure 1-1, Olson 1958). Foredunes are defined as the youngest dunes just behind the beach, usually vegetated by grasses, forbs and small shrubs, and regulated almost entirely by geomorphological processes (Peterson and Dersch 1981). Wetpannes, or interdunal swales (ephemeral dune ponds), are low-lying slack areas located behind the foredunes, which are inundated with standing water during a portion of the growing season. They include wetland vegetation, and represent an unusual assemblage of species in this ecosystem otherwise characterized by water deficit (Ranwell 1972). Inland blowouts are areas of shifting sand which form as a result of natural or human-related disturbance and are located inland from foredunes and wetpannes. A diverse community of bunch grasses and forbs provide sparse vegetation cover in this seral stage (Peterson and Dersch 1981). Forest edges, defined as areas of open dunes adjacent to mature oak-beech-maple forest vegetation, normally occur inland from the wetpannes and along the edges of large blowouts. They are vegetated by the blowout grasses as well as by small trees and shrubs.

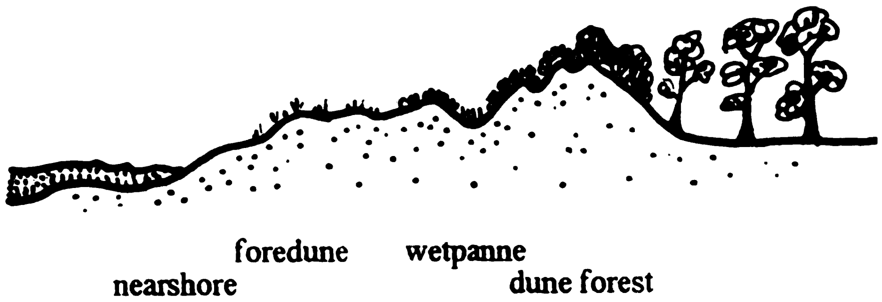


Figure 1-1. Cross section through a typical dune system. Inland blowouts (not shown) are formed when vegetation is removed as a response to natural or human-caused disturbance.

A great deal of research has been directed towards aquatic invaders of the Great Lakes; for example, the dynamics and effects of zebra mussels (*Dreissena sp.*), alewives (*Alosa pseudoharengus*), and lamprey (*Petromyzon marinus*) are well known (Mills et al. 1993), but very little work has focussed on the invasion threats to the terrestrial component of the Great Lakes Basin. The sand dunes of the Great Lakes represent the most extensive freshwater dune system in the world (EPA 1995), and are under tremendous pressure from development and destructive recreational interests. These pressures translate into an even more critical need to determine other potentially threatening impacts to the dune system. This dissertation begins to fill the gap in our understanding of the impact of biological invasions on the dune system of the Great Lakes.

This study focusses on the impact of *Pinus nigra* Arnold (Austrian pine), a non-native pine introduced into a dune system of Lake Michigan, at what is now Saugatuck Dunes State Park, Allegan County, MI. Between 1956 and 1972, more than 25,000 *P. nigra* individuals were planted into the dunes as a sand stabilization measure. *Pinus nigra* is a long-lived pine which reaches reproductive maturity within 15-20 years. Because the trees planted in the dunes had just begun to reproduce within the previous 15 years, this investigation presented a unique opportunity to focus on the earliest stages of invasion while they were occurring. Chapter 2 documents the primary establishment phase (i.e. post-planting survivorship and growth) of the pine on the dunes and investigates the differential success of *P. nigra* among four seral stages, as evidenced by growth in height, dbh, and stem volume. Chapter 3 examines the effects of the pine on community composition and structure in four seral stages and relates these biotic effects to alterations in abiotic characteristics brought about by the invader. The effects of *P. nigra* stands on community structure are compared with those of native cottonwood and jack pine stands. To determine *P. nigra*'s potential to persist in the dune system, Chapter 4 examines reproduction and recruitment of *P. nigra* in foredune, wetpanne, and inland blowout seral stages. A demographic projection matrix model is developed to predict population growth rates, and both invader and community attributes are examined to explain invasion success. Overall conclusions of this study and suggestions for future research are summarized in Chapter 5. The terms Austrian pine and *P. nigra* will be used interchangeably throughout this dissertation.

CHAPTER 2

GROWTH AND PRIMARY ESTABLISHMENT OF THE INTRODUCED *PINUS NIGRA* ON THE SAND DUNES OF LAKE MICHIGAN

INTRODUCTION

Invasion theory

Among the most serious threats to natural ecosystem conservation is the introduction of exogenous species capable of forming self-sustaining populations and dispersing among sites. Species introductions can affect all levels of ecological organization, from the dynamics of native populations (Walker and Vitousek 1991, Equihua and Usher 1993, Paton 1993) and community interactions (Witkowski 1991, Tyser and Worley 1992, Woods 1993, Pysek and Pysek 1995) to the alteration of ecosystem function (Singer et al. 1984, Ramakrishnan and Vitousek 1989, Vitousek 1990, Musil and Midgley 1990, D'Antonio and Vitousek 1992). Though attributes of successful invaders and characteristics of invasible communities have been described repeatedly (e.g. Bazzaz 1986, Orians 1986, Noble 1989), only recently has there been some success in predicting the potential for invasions by exotic species (Rejmanek 1995, Pysek and Smilauer 1995, Rejmanek and Richardson 1996). The present study seeks to determine the invasive potential of *Pinus nigra* (Austrian pine) on the sand dunes of Lake Michigan, where it was introduced for dune stabilization purposes.

Vermeij (1996) separates the invasion process into three phases: arrival, establishment, and integration. The arrival phase is primarily concerned with dispersal and transport routes, while establishment involves the persistence of the immigrant population through local reproduction and recruitment. Integration is the final phase in which the exotic species, once established, influences the dynamics of the recipient community and in turn is influenced by the community of which it has become a part. This outline of the invasion process may be appropriate over long time-scales or for species with rapid life cycles, but it de-emphasizes the critical survival and growth phase that must occur after arrival and prior to reproduction if the invader is to be successful in its new environment. I suggest a five-part framework more appropriate for the study of long-lived woody species in which the establishment phase is split into three separate phases: primary establishment, reproduction, and recruitment. Primary establishment is defined here as the period of survival and growth that must occur following the introduction and is treated separately from regeneration. Primary establishment is followed by a reproduction phase, and finally a recruitment (or secondary establishment) phase, during which the population must become self-sustaining prior to integration.

Knowledge of potential limitations within the arrival, primary establishment, reproduction, and recruitment phases of the invasion process will aid in making predictions regarding the potential success of the invader. The arrival phase is predominately controlled by human activities (Mack 1990), but primary establishment is regulated by the interaction between the invader and its environment; therefore, both genetic and environmental factors may limit this phase. The reproduction phase may be stimulated or inhibited by the environment, but is primarily under genetic control. Indeed, from an extensive list of pine species attributes, Rejmanek and Richardson (1996) found intrinsic reproductive characteristics to be of highest value in predicting their potential for invasion success. Recruitment represents the establishment phase of successive generations, and like the primary establishment phase, is regulated by interactions between invader and environment.

While some attention has been given to arrival (Mack 1990, Williamson 1996), reproduction (Rejmanek 1995, Rejmanek and Richardson 1996), and recruitment (D'Antonio 1993) phases of the invasion process, few ecologists have considered the primary establishment phase in detail. This is a critical step in the invasion process which may be of particular interest to managers assessing the invasion potential of long-lived woody species and is the focus of this paper.

Methods for assessing the primary establishment success of a potential invader in its novel habitat must include an analysis of survivorship as well as some measure of growth or productivity. A significant difference in survivorship or in size characteristics such as height, dbh (diameter at breast height), or stem volume among trees of similar age introduced into different habitats would suggest that extrinsic factors limit successful primary establishment. Information about species survivorship and growth in the home range might provide a baseline comparison with primary establishment in the novel habitat (Sukopp and Starfinger 1995). It is also useful to directly compare environmental characteristics such as latitude and climate in native and exogenous ranges in order to assess the similarity of environmental factors which may regulate the establishment of an invader.

Non-native species invasions on the sand dunes of the Great Lakes

The sand dunes of the Great Lakes comprise a dynamic, yet fragile ecological system maintained by continuous endogenous disturbance in the form of sand movement. As a result of their unstable substrates, available space (i.e. uncolonized ground), and small population sizes, dune systems may be particularly vulnerable to invasion by exotic species and may be severely impacted by new species which threaten to alter the natural disturbance regime. Despite the potential vulnerability of dunes to invasion, however, exotic tree species have been introduced repeatedly as potential dune stabilizers in the Great Lakes dune system (Lehotsky 1972).

For example, in one Lake Michigan sand dune system, private land owners planted more than 30,000 conifer seedlings, the majority of which were *P. nigra*, in an effort to stabilize the shifting sand and maintain property values. During a 16-year period beginning in 1956, the pines were introduced into four distinct seral stages: foredunes, forest edges, wetpannes, and inland blowouts. The present study concerns this group of over 25,000 *P. nigra* individuals in the dunes at Saugatuck Dunes State Park (SDSP), Michigan. Stands of *P. nigra* have thrived in all of these seral stages since planting 25-40 years prior to the study, and the species is becoming an increasingly prominent component of the dune vegetation at SDSP.

Distribution and characteristics of Pinus nigra

Pinus nigra Arnold is native to Southern Europe, Northern Africa, and Asia Minor and is distributed from 5° W to 40° E longitude and from 35° N to 48° N latitude (Figure 2-1, Burns and Honkala 1990). Its distribution is highly discontinuous within its native range, and it is quite genetically variable, hence, there has been some disagreement as to the most appropriate taxonomic treatment of the species (Vidakovic 1974). It is now generally recognized, however, that the species is composed of a number of interfertile subspecies, many of which were formerly of species rank (Vidakovic 1974). *Pinus nigra* ssp. *austriaca* (Hoss) Bid., the subspecies present at SDSP, occurs in Austria, Slovenia and western Croatia where it inhabits areas from 250m to 1000m above sea level (Vidakovic 1991).

In its native range, *P. nigra* often occurs in pure stands where it attains heights of 30-40m and may live 300 years (Vergos 1985, Vidakovic 1991). First reproduction typically occurs between 15 and 20 years of age, but under harsh conditions cones may not be produced until the pines are more than 40 years old (Vidakovic 1991, Burns and Honkala 1990). The species is known to be frost tolerant in the northern reaches of its native range; northern varieties can withstand temperatures as low as -30° C, and southern varieties, -7° C. Annual precipitation is between 610mm and 1020mm in its native range.

Forestry practices and cultivation of P. nigra

In North America, *P. nigra* is successfully planted from Nova Scotia to northern Missouri (Burns and Honkala 1990). Cultivated in the U.S. as early as 1759, *P. nigra* was grown both in National Forests for timber, and as a landscape and windbreak species in the Great Plains states by the early 1900s (Burns and Honkala 1990). It tolerates a wide variety of soil conditions and is planted extensively along highways because of its high tolerance to road salt runoff (Burns and Honkala 1990, Wheeler et al. 1976). It has become naturalized in parts of New England and the Great Lakes states, but is known only as a localized escape elsewhere in North America (Burns and Honkala 1990).

Insight into the success of *P. nigra* in North America may be gained by examining the rationale for its appeal as a reforestation species in Greece. Matziris (1989) lists four reasons for its extensive use. First, it tolerates a wide range of environmental conditions and has been shown to have three ecotypes in Greece. Second, it can grow in highly disturbed environments and has few special requirements. Third, it competes well with other plants at a young age and can establish with minimal management, and fourth, it grows rapidly and produces high quality wood. These characteristics make *P. nigra* an excellent reforestation species in its native habitat and attractive to managers. Its tolerance of a wide range of environmental conditions may also make it an excellent invader in novel environments.

The vigor of *P. nigra* and its ability to colonize many types of sites and soils (Hepting 1971) give it the potential to alter a variety of communities, including sand dunes. The dense canopy of *P. nigra* stands creates deep shade in which an understory is usually absent. Its tendency to stabilize shifting sand may also be detrimental to some native dune species which rely on open sand for colonization (McEachern 1992).

Research questions

This paper addresses the following questions:

1) which dune habitats are most conducive to primary establishment of *P. nigra* , and hence may be most impacted by its presence?
2) are weather patterns and site conditions such as slope and wind stress correlated with *P. nigra* growth in the dune ecosystem at SDSP, and
3) how does the ecology of *P. nigra* at SDSP compare with that of *P. nigra* growing in its native European range?

To answer these questions, growth and size measures of *P. nigra* trees and stands were made in foredune, forest edge, wetpanne, and inland blowout seral stages during the growing seasons of 1994 to 1996.

METHODS

Study site

This investigation took place between May 1994 and August 1996 in the state-designated Natural Area of SDSP, and on adjoining private property, in Allegan County, Michigan (42 41'N, 86 12'W, Figure 2-2 and 2-3). Interviews of previous land owners conducted by former MSU student, Debra Reynolds, revealed that approximately 26,000 Austrian pines were planted throughout the 120-ha site while the land was still in private ownership. The plantings, for which the seed source is not known, took place between 1956 and 1972 and were initiated to stabilize the dunes. Study plots were distributed throughout foredune, wetpanne, forest edge, and inland blowout seral stages.

Weather data from a Holland, Michigan weather station approximately 13 km north of SDSP, indicated that this site falls within the natural climatic variation for *P. nigra* in its native range. All weather data used in this study were derived from the Holland weather station. Average annual precipitation for 1955-1996 in Holland, MI was 911mm and mean growing season (May - August) temperature, 19^{o}C. In February 1978, six years after *P. nigra* plantings had ceased, a low temperature of -15^{o} C was recorded, 15^{o} higher than -30^{o}C temperatures in the northern native range of *P. nigra* .

Sampling sites

One goal of this study was to establish baseline data for long-term study of dispersal and invasion of *P. nigra* on the dunes. Consequently, 20 permanent sampling sites were randomly selected from a larger set of potential sites on a vegetation map of

SDSP, and five sampling sites were established in each of the four dune habitats where *P. nigra* had been planted. *Pinus nigra* occurred in small stands of 3-11 trees in foredunes, in large stands of hundreds of trees in wetpannes and at forest edges, and in stands of variable size (25 - hundreds of trees) in inland blowouts. Sampling sites selected for study in the large stands included only a portion of the trees, but included all the trees in small and moderately sized stands (up to 50 individuals).

Sampling sites were established in areas of *P. nigra* occurrence as follows: five in foredune sites, defined as small, discrete stands of trees covering areas of $150m^2$ - $420m^2$; five at the forest edge, all portions of larger stands ($576m^2$ - $1890m^2$); five in wetpanne sites, all portions of larger stands ($550m^2$ - $1225m^2$); and five in inland blowouts, two of which were discrete stands and three of which represented portions of larger stands ($312m^2$ - $916m^2$). Sampling sites extended only as far as did the canopy of *P. nigra* in these self-contained stands and individuals that were more than 15m from pines at the edge of discrete stands were not included. Because stand area differed among sites, all comparisons among sampling sites were made on a percent or unit-area basis. All sampling sites were established in May and June 1994, except for two wetpanne sites which were established in May 1995. Seral stages were defined by the type of characteristic native vegetation bordering the planted pines.

Characteristics of individual trees

Size measurements.--Ten mature, planted *P. nigra* individuals, hereafter termed "focal trees," were randomly selected for size measurements in each wetpanne, forest-edge and inland-blowout sampling site. Due to a limited number of trees in foredune sites, only three trees were sampled in each of these sites. Height was measured with a Haga altimeter and diameter at breast height (dbh) was measured at 1.25m above the soil surface for each sample tree in 18 sites in May and June 1994, and in the two remaining wetpanne sites in May 1995.

Because formulae specific to *P. nigra* were unavailable, cubic volume of the main stem was calculated for each focal tree using the formula for a parabaloid:

$y^3 = 1/2A_bh$;

where $A_b = \pi r^2$ = basal area, r= 1/2 tree dbh at 1.25m above the soil surface, and h=height.

Actual stemwood volume for conifers typically falls between that of a cone and a parabaloid (Husch 1982), so this formula may slightly overestimate actual stem volume. Height, dbh, and cubic volume of Austrian pines were compared within and among seral stages using a nested ANOVA in which stage was treated as a fixed effect and site(stage) as random. Transformations did not improve non-normal distributions of height, so site data were pooled by stage and compared among stages using a non-parametric Kruskal Wallis ANOVA.

Size correlations.--To investigate specific environmental factors that might be correlated with tree size, slope measurements were taken with a clinometer from the edge of the Austrian pine canopy to 10m into the pine stand, and "wind exposure" category was determined for each site. Category 1 included sampling sites which were completely isolated from any other trees which might buffer them from the wind, previously described as "discrete stands." Category 2 included sites which were bordered on one side by a stand of trees, and Category 3 sampling sites were surrounded by trees on all sides. Mean height, dbh and stem volume for each site were analyzed relative to percent slope and degree of slope using a non-parametric Spearman's rho. Mean size variables for each site were also analyzed by wind exposure category with a Kruskal Wallis ANOVA.

Kellogg Forest comparison.-- To compare *P. nigra* growth in the dunes with that of an established plantation, height and dbh were measured on a *P. nigra* provenance trial stand (plantation 61), established in 1961 by J. Wright of Michigan State University. The site is described as "rolling with slopes of 0-25%, with Oshtemo loamy sand," and is located at Kellogg Experimental Forest in Augusta, MI, approximately 75km east of SDSP (Wheeler et al. 1976). To demonstrate the range of potential *P. nigra* growth in this site, trees from Corsican (413), Austrian (423) and Greek (425) seed lots were selected for sampling from a pool of 29 types. In 1976, at 15 years of age, these seed lots represented the minimum, median, and maximum heights of trees in the plantation (Kellogg Forest, unpublished data). Height, dbh, and parabaloid volume were obtained as previously described for all surviving trees of each seed lot (Corsican: n=6, Austrian: n=19, Greek: n=15). Stand density was calculated by dividing the total number of surviving trees by the area occupied by the original plantings.

Stand characteristics at SDSP

Stand density.--Stand density was determined by counting every planted Austrian pine in the 20 sampling sites at SDSP and dividing by the appropriate area. Naturally regenerated individuals in these stands (<10 years old) were smaller than 1cm in dbh and 1m in height and were not included in calculations of stand density. Stand density of pines within and among seral stages was compared using a One-Way ANOVA with Tukey-Kramer HSD multiple comparisons.

To evaluate the association among tree and stand characteristics, Spearman's rank correlations were determined for height, dbh, parabaloid stem volume and stand density.

Tree growth

Height growth.-- Annual height growth of *P. nigra* on the dunes was determined by measuring the distance between branch whorls (representing one year of growth) with a meter tape for the first 2m of the tree and with an altimeter for the portion of the tree above 2m. Growth in years 1-10 may be under-represented in the whorls present. Annual height increment of 10 trees was measured in foredune sites, and 11 trees were measured in each of the other seral stages. To further examine the growth pattern, cumulative height was regressed against tree age (total number of whorls).

A five-year growth rate was calculated by summing height growth across five-year increments and plotting the value against age. Transformation to normality was not possible, so separate nonparametric Kruskal Wallis One-Way ANOVA was used to test for differences in height growth rate across seral stage and in growth rate across five-year intervals. Spearman's rank correlations were used to determine the relationship between five-year growth interval and height growth rate.

Radial growth and age estimation.--To estimate tree age and to determine radial growth rate, *P. nigra* trees were cored with an increment borer in the fall of 1994. Focal trees (see Methods: characteristics of individuals) were cored in three of the five established sampling sites in all seral stages. Rings were counted and measured on polished tree cores using a Henson measuring machine. The paucity of signature years in the relatively young trees (20 - 35 rings) made cross dating of the cores impossible (Stokes and Smiley 1968), but two factors indicated that ring counting was an appropriate approach to age estimation and dendroclimatological procedures (Telewski and Lynch 1991). First, the number of rings present corresponded well with the range of planting dates. Second, the presence of relatively wide annual increments for most years and two very narrow rings from the drought years of 1987 and 1988 gave good reason to believe that the cores had no missing rings. Average annual increment for five-year intervals was calculated for each tree core and averaged within sites and within seral stages. Data were square-root transformed to near-normality. Because the profile of annual radial growth across the life of the tree did not differ within seral stages, sites were pooled and seral stages were compared with a two-way ANOVA, with stage and growth interval as fixed effects.

To more directly compare growth across time, basal area increment (BAI) was also estimated for each year of growth from each core. Cumulative radial annual increment of the tree radius was used to calculate the basal area of the tree at each ring; the basal area of the tree in the previous year was subtracted from that of the year in question to determine the BAI of the tree for that ring alone. This method assumes that double the cumulative radius represents the true diameter of the tree. This may not always be an accurate assumption, however, if wind stress to the tree varies from one side to another, and results in unequal growth around the circumference of the tree. Patterns of growth, as measured by BAI, were compared within and among seral stages. The association between age and size (height and dbh) was determined using Spearman's rank correlations.

Tree growth and climate.--To determine the relationship between tree growth and annual climatic variation, Spearman's rank correlations were calculated between mean annual ring width within each seral stage and a variety of precipitation variables, including annual precipitation, growing-season precipitation (April-August), June, July, and August precipitation, as well as precipitation from the previous year in all the prior categories. Several monthly precipitation values were missing (August 1979, February 1985, and August 1987) and these years were eliminated from the analysis when the missing data affected the outcome of the correlation. The average ring widths for each seral stage used in the correlation analysis were determined by averaging ring widths of the same year for all trees within each site, and then averaging yearly site averages together for each seral stage.

All statistical analyses were performed using JMP software (SAS 1995).

RESULTS

Pinus nigra survivorship

Of the approximately 26,000 pines planted at SDSP, an estimated 21,366 were still present on the dunes in 1988: an 81% survival rate for trees which were 16-32 years of age (Reynolds, unpublished), although no data specific to seral stages were available. Survivorship on the dunes compared favorably with 35-year survivorship of the Austrian seed lot at Kellogg Forest plantations (79.2%, Table 2-1) but was much higher than that of the Greek seed lot (37.5%).

Table 2-1. Average 35-year survivorship of *P. nigra* from three different seed sources in a plantation at Kellogg Forest, Augusta MI, and at SDSP, Allegan Co., MI.

Seed Lot	Average Survivorship (%)	Standard Error (%)
Greek	37.5	7.2
Austrian	79.2	11.9
Corsican	62.5	10.7
SDSP*	81	

*Reynolds, unpublished data for survivorship from time of planting (1956-1972) to 1988.

Tree characteristics and stand density at SDSP

Tree age.-- Tree age, as measured by number of tree rings, was only moderately correlated with height of *P. nigra* planted on the dunes (rho=0.265; $p<.05$, n=86) and not at all correlated with dbh or stem volume (rho=0.007, p=0.95, n=86; and rho=0.051, p=0.64, n=86). Because of these negligible relationships between age and size within the age class of the trees planted on the dunes (25-40 years), it was not possible to directly compare height, dbh and volume of individuals trees based on age.

Tree size.-- Tree height, dbh, and stem volume were more variable within seral stage than among stages at SDSP (Table 2-2, Figures 2-4 to 2-6). When sites were pooled within stage, however, tree height was found to vary significantly among stages. Mean DBH was nearly different among stages (though this result was not statistically significant; p = 0.055), and mean stem volume did not differ among stages.

Table 2-2. ANOVA for DBH, height, and stem volume, where sites were nested within seral stage (foredune, forest edge, wetpanne, inland blowout); and Kruskal Wallis test, where data were pooled within seral stage. Measurements were taken in the growing seasons of 1994 and 1995, SDSP, Allegan Co., MI.

Tree characteristic	Source of Variation	df	ms	f (ANOVA)	p
DBH	Stage	3	139.392	0.709	0.560
(model r^2=0.448)	Site(Stage)	16	204.711	6.616	<0.0001
	Error	147	30.941		
Height	Stage	3	68.881	2.427	0.103
(model r^2=0.509)	Site(Stage)	16	29.554	6.658	<0.0001
	Error	147	4.439		
Stem volume	Stage	3	0.014	0.298	0.827
(model r^2=0.380)	Site(Stage)	16	0.048	5.345	<0.0001
	Error	147	0.009		
Pooled Data (Kruskal-Wallis)				X^2 (KW)	
DBH	Stage	3		7.602	0.055
Height	Stage	3		28.505	<0.0001
Stem volume	Stage	3		6.075	0.108

Mean dbh of *P. nigra* was lowest in forest edge sites (14.8cm ± 1.0) and highest in foredune sites (20.3cm ± 1.8; Table 2-3, Figure 2-4). Within each seral stage, mean dbh of the site with the highest mean dbh was more than two times that of the site with the lowest. Mean height was lowest in foredunes (6.9 ± 0.5m) and highest in forest edges (9.6 ± 0.3m, Table 2-3, Figure 2-5). Foredune and inland blowout stages were most variable: mean tree height of the site with highest mean height exceeded that of the lowest by more than two times. Wetpannes were least variable: the mean height of the site with lowest mean height was 80% that of the site with highest mean height.

Table 2-3. Mean size and stand characteristics ±S.E. for *P. nigra* in four seral stages at SDSP, Allegan Co., MI (data from 1994 and 1995) and for three seed lots in a 35-year old *P. nigra* plantation at Kellogg Experimental Forest, Augusta, MI (1996 data).

Seral Stage or Seed Lot	Height (m)	DBH (cm)	Stem Volume (m3)	Stand Density (trees per ha)	n
SDSP					# sites
Foredune	6.9 ± 0.5	20.3 ± 1.8	0.138 ± 0.03	274 ± 34	5
Forest Edge	8.9 ± 0.5	14.8 ± 1.0	0.110 ± 0.02	1176 ± 124	5
Wetpanne	9.6 ± 0.3	17.2 ± 0.8	0.137 ± 0.02	1173 ± 156	5
Inland Blowout	7.1 ± 0.4	15.6 ± 1.0	0.100 ± 0.01	693 ± 88	5
Kellogg Forest					# trees
Corsican	14.7 ± 0.6	14.9 ± 2.9	0.152 ± 0.05	1051	6
Austrian	15.4 ± 0.5	20.7 ± 0.9	0.277 ± 0.03	1051	19
Greek	16.6 ± 1.2	22.2 ± 2.4	0.378 ± 0.07	1051	15

Mean stem volume did not differ across seral stage. Variability of height and dbh was amplified in the calculation of stem volume, however. In foredunes, stem volume of the highest sites was more than seven times that of the lowest (Figure 2-5). Wetpannes were the least variable with just 2.5 times difference between the highest and lowest sites. Stem volume varied from a low of 0.019 ± 0.008m^3 in inland blowout site five to a high of 0.273 ± 0.079m^3 in foredune site four (Figure 2-5).

Allometric relationships.-- Despite similarities in mean stem volume among stages, tree morphology, as described by the combination of dbh and height, differed across seral stages. Foredune trees were shorter, but had larger dbh than wetpanne and forest-edge trees which were taller, and had lower dbh (Table 2-3, Figure 2-7). Inland-blowout pines were intermediate in height and dbh. Nonparametric Spearman's correlations showed a strong positive relationship between height and dbh across all seral stages (rho=0.6247, $p<0.0001$).

Environmental correlates.--Plant size was independent of site characteristics. None of the correlations between mean *P. nigra* size variables and slope of the site were statistically significant at SDSP (Table 2-4). Mean tree height per site differed with exposure to wind ($X^2=6.21$, df=2, $p<0.05$, n=20), but mean dbh and stem volume within sites did not ($X^2= 2.10$, and 0.37 respectively, df=2, $p>0.05$, n=20).

Table 2-4. Spearman's rank correlations between site slope and several measures of tree size in *P. nigra* at SDSP, Allegan Co., MI (n=20, size data taken in 1994 and 1995).

Size Variable	Rho	p
DBH	-0.235	0.318
Height	-0.216	0.316
Stem Volume	0.163	0.493

Stand density.--Stand density of planted *P. nigra* was lowest in the foredunes at an average of 274 ± 34 trees/ha (though no stands exceeded 0.04 ha in size), intermediate in inland blowouts (693 ± 88 trees/ha), and highest in wetpannes and forest edges (1173 ± 156 and 1176 ± 124 trees/ha, respectively; Table 2-3, Figure 2-8). Foredune and inland blowout stand densities were significantly different from those of forest edges and wetpannes (Tukey-Kramer HSD, q=2.86, p=0.05).

Relationships between tree size and stand density.-- Tree height and stand density were positively correlated, but only 28% of the variation in height was explained by density (rho= 0.28, p=0.0002, n=20). Dbh and stand density showed a weaker negative association (rho=-0.19, p=0.0137, n=20) and explained less of the variation. No statistically significant relationship was noted between stem volume and stand density (rho = -0.07, NS, n=20).

Comparisons with Kellogg Forest.--DBH for the 25-40 year old planted *P. nigra* on the dunes was comparable to that of the 35-year-old trees in Kellogg Experimental Forest, where it averaged between 14.9 ± 2.9cm and 22.2 ± 2.4cm depending on seed source (Table 2-3). Trees at Kellogg Forest were nearly double in height, however, ranging from 14.7 ± 0.6m to 16.6 ± 1.2m. Stem volume at SDSP was comparable to the Corsican seed lot at Kellogg Forest, but was less than half that of the Austrian seed lot. Stand density in foredunes and inland blowouts at SDSP was only 0.25 and 0.66 that of Kellogg Forest, but in wetpannes and at forest edges was 1.1 times that of Kellogg Forest.

Tree growth

Height growth.-- Tree height followed a linear trajectory across time in all seral stages (Figure 2-9, Table 2-5). The rate of height growth did not vary across seral stage, but it did with tree age (Figure 2-10). Growth rate was positively correlated with tree age (rho=0.6155; p<0.0001).

Radial growth.-- Radial growth rate differed among seral stage; foredune and inland blowout had the highest, and forest edge and wetpanne, the lowest rates of radial growth (Figure 2-11). In addition, average annual increment generally decreased with increasing age (Spearman rho= -0.4461; p<0.0001). In contrast, height growth increased with age.

Table 2-5. Linear regression of height against tree age (total number of whorls) in four seral stages at SDSP. Data taken in 1996, Allegan Co., MI.

Seral Stage	R^2	p
Foredune	.80	<.0001
Forest Edge	.89	<.0001
Wetpanne	.86	<.0001
Inland Blowout	.82	<.0001
Pooled Stages	.85	.0000

Table 2-6. Spearman's rank correlation between June precipitation (current and previous) and tree-ring width in four seral stages. Tree cores collected in Fall 1994, Allegan Co., MI.

	Month of Precipitation			
Seral stage	June		Previous June	
	Rho	p	Rho	p
Foredune	-0.0879	NS	-0.0121	NS
Forest Edge	0.4136	0.0150	0.3198	0.0652
Wetpanne	0.4350	0.0184	0.3911	0.0359
Inland Blowout	0.5480	0.0038	0.4154	0.0348

Tree growth and climate.--Annual increment was positively correlated with June precipitation of the year in which growth occurred in all but the foredune seral stage (Table 2-6). In inland blowout and wetpanne sites, a weaker positive correlation existed between ring width and precipitation during the previous June. None of the other correlations examined between annual increment and climatic variables were significant.

DISCUSSION

Overview

In order to examine the primary establishment success of *P. nigra* in a novel environment, its differential success was examined among seral stages in the dunes to determine if one habitat restricts *P. nigra* growth more than others, or if the introduced species is equally successful in all habitats. Environmental correlates with growth were also explored. Comparisons were then drawn with trees of similar age in North American *P. nigra* plantations growing under conditions less harsh than those in the dunes. Plantations are expected to represent the upper limits for measures of pine establishment since trees are managed as crops for which the highest possible productivity is desired. Primary establishment success at SDSP was also compared with that of a European plantation located in close proximity to the native distribution of the species. This was thought to give a more realistic picture of what constitutes successful establishment in its native distribution.

Finally, comparisons were made with the native distribution. Climatic comparisons were drawn to determine if the conditions at SDSP are similar to those within its native range. The size and stand-density characteristics of trees at SDSP were then compared with those in a natural uneven-aged stand within the native range. If primary establishment of trees at SDSP is comparable to that of a region in which the trees are known to persist naturally, it is likely that they have the potential to become successful invaders in the novel dune system.

Primary establishment of Pinus nigra at SDSP

Survivorship.-- Despite the depauperate soils and droughty conditions of the sand dunes, *P. nigra* survivorship has been high (estimated at approximately 80%) since planting at SDSP. In a study of primary establishment success of landscape plants derived from Yugoslavia and grown in a broad range of environments in the North Central United States, Widrlechner et al. (1992) found 10-year survivorship of *P. nigra* from two Slovenian seed sources to be 64% and 19%. The majority of mortality occurred during the first year after planting, and 10-year survivorship, calculated only for the individuals that survived the first year, was found to be approximately 75% (Widrlechner et al. 1992). Estimates of 16- to 32-year survivorship of *P. nigra* at SDSP exceed these values; therefore, early mortality after planting does not appear to be a major barrier to *P. nigra* invasion potential in the dune system.

Size.-- Tree size, as measured by dbh, height, and stem volume, differed more within seral stage than among seral stages at SDSP (Table 2-2, Figures 2-4 to 2-6). This indicates that the coarse-scale differences in environmental factors among stages account for only some of the variation in tree size. Some of the variation within seral stages may be due to genotype, because the trees were planted over a 15-year period and likely came from different seed sources during that time. In addition, tree height-growth may have been reduced by exposure to wind, as determined by the absence of trees (either native or exotic) surrounding the sampling sites ($X^2_{2,17} = 6.21$, $p<0.05$), but because categories of "wind exposure" were confounded with seral stage, this environmental factor does not help to explain within-stage height variation. For example, all of the foredune sampling sites were in the "most exposed" category; therefore, variation in foredune height could not be attributed to differing levels of wind stress. Additionally, initial planting densities may have influenced eventual tree dimensions, because stand density was positively correlated with height (rho=0.28) and negatively correlated with dbh (rho=-0.19). Further study is needed to determine the causes of variation in *P. nigra* size within seral stage, however.

Despite the intra-stage variation in size variables, pooled analyses showed differences in height across stages (Table 2-2). Wetpanne and forest edge trees were, on average, significantly taller than foredune and inland blowout trees. If dominant tree height is taken as an indication of site quality in even-aged stands (Oliver and Larson 1990), these data would suggest that wetpannes and forest edges were of higher site quality for primary establishment of *P. nigra* than either foredune or inland blowout seral stages (Table 2-3).

Because stem volume included measurements of both height and DBH, and was independent of stand density in this study (rho=-0.07, NS), establishment success may be better evaluated by this measure than either height or dbh. Contrary to tree height, stem volume did not vary across seral stage in pooled analyses (Table 2-2 and 2-3), suggesting that *P. nigra* was equally tolerant of very different conditions among seral stages. Stem volume estimates did not include branch volume, however, and therefore could not be taken as a complete evaluation of establishment success. Branches appeared to be more dense and numerous on foredune trees than on wetpanne or forest edge trees, possibly as a response to shading of the lower branches in the denser stands.

Stand density.--Much of the difference in *P. nigra* stand density among seral stages was likely attributable to differences in planting practices. In foredune sites, a single row or two of trees served as a windbreak, whereas in the sandy, destabilized inland blowouts and on the steep slopes of the forest edge, many rows of pines were introduced to reduce sand movement. In addition, fire occurred on the foredunes in 1972 and again in 1985 (Reynolds, unpublished data), and this may have reduced stand densities in foredune sampling sites. Fire scarring is still present on many of the standing foredune trees and charred, fallen trees are evident as well. Differential early mortality of the planted seedlings among seral stages may also have been responsible for some of the differences in stand density, but no records of this exist.

Pinus nigra growth.-- Tree height, when plotted as a function of age, generally follows a sigmoid curve (Oliver and Larson 1990). Stressful conditions can alter this general pattern, by reducing the rapid juvenile phase of growth and lengthening the decline phase, however (Fritts 1976). Height-growth patterns at SDSP suggest that *P. nigra* was still in a rapid phase of growth in all seral stages (Figure 2-9). Rates of height growth were still increasing in inland blowout and wetpanne sites, but had begun to level off and even decrease in foredune and forest edge sites (Figure 2-10), however. This suggests that the trees in these seral stages were approaching a size at which height becomes limiting (Oliver and Larson 1990). A decline in height growth rate occurred five years earlier in foredune than forest-edge trees, possibly indicating that the foredune seral stage was of poorest quality for primary establishment.

Despite their taller stature, wetpanne and forest-edge trees exhibited slower radial growth (Figure 2-11). Because woody plants preferentially allocate energy to height growth, however (Lanner 1985), radial growth data are inferior indicators of site quality (Oliver and Larson 1990). The larger annual increments of foredune and inland blowout trees may be related to increased wind stress in these seral stages (Telewski 1995). Foredune trees in particular were located in exposed areas, and because stand densities were also lowest in this seral stage, trees were least protected from the wind.

Environmental determinants of growth.-- Positive correlations between June rainfall and annual increment suggest that June precipitation was an important regulator of radial growth in all stages but the foredunes. Wind stress, which may be most extreme in foredunes is known to increase radial growth (Telewski 1995) and in this case, radial growth, as a response to wind stress, may obscure the precipitation-based variation across annual ring widths.

The moderate positive correlation between radial growth in wetpanne trees and precipitation suggests that radial growth was limited by June precipitation in even the wettest of the four seral stages. Observation during the field seasons of 1993 through 1996 showed that wetpannes soils were typically saturated, if not inundated during the month of June, yet the tree-ring analysis suggests that soils in wetpanne sites dried out in the driest years. Though annual radial increment was smaller in wetpannes than other stages, a negative correlation with precipitation would have been expected if waterlogged and anaerobic soils were limiting growth. There is no indication of this in the present analysis, however.

While *P. nigra* growth was correlated with precipitation in three seral stages, basal area increment (BAI) data indicated that biotic interactions and subsequent light limitation may also be regulating tree growth. Four patterns of growth were evident in BAI data for tree cores from three sites in each seral stage (Figure 2-12), and these patterns represent the dynamics of growth commonly experienced by trees in naturally occurring forest stands (Oliver and Larson 1990). The first growth pattern (A) is that of free or open growth, which is characterized by an upward trend in BAI over time as the tree gets larger and is able to garner more energy. Crown closure has not yet occurred so the trees are not in competition for light. Trees in sparsely planted stands would be expected to exhibit this type of growth pattern. The next growth pattern is that of competition (B), which occurs after canopy closure and is evidenced by a rapid decrease in BAI over time as light becomes more and more limiting. Trees in more densely planted stands would exhibit this growth pattern earlier. A third (C) is that of canopy closure and subsequent gap formation. Here the BAI decreases as a response to competition for light, and then increases rapidly again following an opening in the canopy. This pattern might be expected for a small proportion of the trees in the more densely planted stands. The fourth growth pattern (D) is that of trees in the understory which have always been limited by light and have grown slowly throughout their lives.

Two to four of these growth patterns were exhibited by trees from each site in all seral stages, perhaps as a response to their specific position in the stand. As might have been predicted, however, trees from the sparsely planted foredunes and inland blowouts showed primarily pattern A, that of open growth. Understory and canopy closure patterns were second most common in inland blowout sites (each pattern was represented in six of 28 trees), which were more than two times as dense as foredune stands. Trees in the more densely planted forest edge and wetpanne stands were mostly of pattern D (understory trees) with pattern C (gap formation) the second most common in both stages. Only one of 56 trees cored in wetpanne and forest edge sites exhibited the open growth pattern. These data suggest that intraspecific competition for light is a significant limitation to growth in forest edges and wetpannes, but less so in inland blowouts at SDSP.

Pinus nigra establishment in even-aged plantations

Pinus nigra height, dbh and, stem volume in plantations at Secrest Arboretum in Wooster, OH were comparable to that of Kellogg Forest (Table 2-7 (Burns and Honkala 1990); Table 2-3), but trees in both experimental forests were considerably taller than even the tallest trees in forest-edge sites in the dunes (11.1 ± 0.8m). Stem volume on the dunes was 0.5-0.75 that of 31-year-old stands at Secrest Arboretum. Management practices, including herbicide and fertilizer use, may have given these plantation trees an advantage over those in the dunes, although the differences are great enough that other factors, such as moisture availability and soil type, may have been involved. These differences in size for trees of similar age suggest that both experimental forests were of higher site quality than any seral stage in the dunes.

When compared with even-aged *P. nigra* plantations in France, however, stem volume per tree at SDSP was 25 to 75 percent higher than that of trees of the highest yield class of 30-year-old European stands (Table 2-7). Stand densities in France were two to nine times higher than on the dunes, however, and this may account for the greater stem volume of individual trees at SDSP.

Growth analysis: native habitat vs. SDSP

Climatic comparisons.--"Climate matching," or comparison of climatic and latitudinal variables of native and exogenous ranges is not always a good predictor of invasion potential (Mack 1996), but may give some baseline indication of habitat compatibility. The climate at SDSP is quite comparable to that of *P. nigra*'s native range. Annual precipitation averages 911mm at SDSP, well within the range of 600-1100mm for native European sites (Vidakovic 1991). Minimum temperature at SDSP (-15°C) is 15°C higher than in the northern range of *P. nigra*'s native distribution. Additionally, SDSP is located at the midpoint of the of native latitudinal range, though the European continent is subject to the moderating effects of the bodies of water surrounding it. The climate at SDSP appears to match well with that of the native distribution of *P. nigra,* and this undoubtedly contributes to the successful performance of the species at SDSP.

Primary establishment of native P. nigra .-- Native populations of *P.nigra* var. *pallasiana* growing in mixed stands with *Abies equi-trojani* in Turkey show similar

Table 2-7. Comparison of height, dbh, stem volume, and stand density for even-aged *P. nigra* plantations in Secrest Arboretum, Wooster, OH (Burns and Honkala 1990), and southwest France (Vannier 1984), and for uneven-aged native stands in Turkey (Ata 1989). Yield classes* are given only for France.

Tree Age or Yield Class	Height (m)	DBH (cm)	Stem volume (m3)	Stand Density (trees/ha)
Wooster, OH				
25-year	18.0	11.8	0.15	no data
31-year	17.8	14.5	0.18	no data
40-year	22.4	17.1	0.34	no data
France (30-year) Yield class				
Class 4	3.9	8.3	0.010	4549
Class 3	6.0	10.2	0.024	3760
Class 2	8.1	12.1	0.047	3067
Class 1	10.2	14.0	0.079	2509
France (40-year)				
Class 4	5.9	10.2	0.024	3782
Class 3	8.4	12.4	0.051	2995
Class 2	11.0	14.6	0.093	2327
Class 1	13.5	17.5	0.162	1812
Turkey				
30-year	6.5	9.0	0.021	no data
40-year	9.5	11.5	0.049	no data

*Yield class 1 represents the most productive conditions and yield class 4 the least.

patterns of establishment success to *P. nigra* at SDSP (Table 2-3, 2-7). Ata (1989) performed stem analyses on 30 individuals to determine average height and dbh at ten-year intervals and found a 30-year average height of 6.5 m and average dbh of 9 cm, and a 40-year average height of 9.5 m and average dbh of 11.5 cm. This range encompasses weakest (foredune) to strongest (wetpanne) *P. nigra* performance at SDSP (Table 2-3). Mean stem volume, however, was five to seven times greater on the dunes than in 30-year old trees in native stands in Turkey. This comparison suggests that primary establishment of *P. nigra* in all seral stages in the novel environment is as successful as it is in its native habitat. Ata (1989) indicated, however, that *P. nigra* was eventually overtopped by the faster growing *A. equi-trojani* and excluded from these mixed forests over time. *Pinus nigra* also grows in pure stands in its native range, and though no data were available for comparison, it is possible that the reduction in interspecific competition improves measures of establishment success in pure relative to mixed stands.

Stand densities of planted *P. nigra* in all seral stages on the dunes were similar to stand densities found in naturally occurring pure stands of *P. nigra* in Greece. Vergos (1985) defines five distinct phases of stand evolution in a study of pure stands of *P. nigra* in NW Greece (the forest of Krania-Monahition), including young forest stage (3809 trees/ha), optimum stage (904 trees/ha), aging stage (331 trees/ha), decomposition stage (267 trees/ha) and regeneration stage (1687 trees/ha). Foredune stand densities at SDSP were most similar to the decomposition stage densities, while forest edge and wetpanne stand densities were 1.3 times that of the optimum stage. Inland blowouts were more than three quarters that of optimum stage stand densities. As the planted trees age at SDSP, a decrease in stand density may be expected until regeneration becomes a significant factor. If *P. nigra* populations behave on the dunes as they do in natural stands in Greece, the density of regenerating foredune stands may be expected to be six times that of their current values, while forest-edge and wetpanne stand density may only increase by about 45 percent. As previously indicated, the stand densities observed at SDSP seem to have little effect on height, dbh or volume of *P. nigra* growing on the dunes, though height shows a slight positive correlation with stand density.

Conclusions

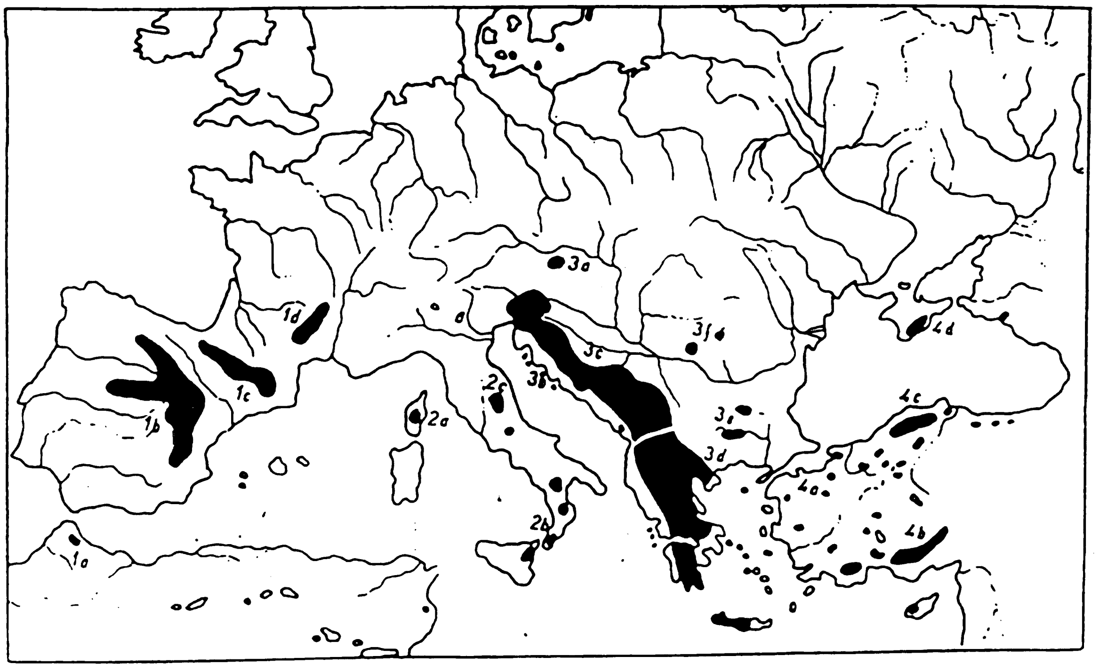
Comparable height, dbh, and stem volume of trees of similar age in the native region and in the Lake Michigan sand dune environment provides evidence that *P. nigra* has the potential to invade the fragile dune ecosystem. Within the dune system, *P. nigra* was highly tolerant of a variety of conditions, but as evidenced by significant intra-seral-stage variation, responded to environmental variables on a scale smaller than defined by seral stage.

An assessment of the differential success of *P. nigra* among seral stages is criterion-dependent. For example, tree height versus stem volume measurements lead to different conclusions regarding the primary establishment success of *P. nigra* among seral stages at SDSP. Height measurements indicate that *P. nigra* was more successful in forest edge and wetpanne seral stages (Table 2-8). Height growth rates were declining in forest edge trees, and not in wetpannes, however, therefore wetpanne trees appear to have been most successful in primary establishment. Foredunes, with the shortest trees and declining height growth rates, may be interpreted as least conducive to pine establishment. Stem volume did not vary across seral stage, however, which suggests that *P. nigra* established well in all these communities. Pine growth in all but foredune seral stages was limited by June precipitation. Biotic interactions which may have resulted in light limitations also appeared to regulate growth in wetpanne and forest edge stages, but not in inland blowouts or foredunes (Table 2-8).

Table 2-8. A comparison of measures of *P. nigra* establishment success among four seral stages at SDSP. Postulated growth regulators are also listed.

	Foredune	Forest Edge	Wetpanne	Inland Blowout
Height	Low	High	High	Low
DBH	No difference	No difference	No difference	No difference
Stem volume	No difference	No difference	No difference	No difference
Height growth rate	Declining	Declining	Increasing	Increasing
Annual radial increment	High	Low	Low	High
Limits to Growth	Wind exposure (?)	June precipitation Biotic interaction	June precipitation Biotic interaction	June precipitation

Pinus nigra has been successful through the primary establishment phase of invasion in foredune, forest edge, wetpanne, and inland blowout seral stages at SDSP. With the knowledge that it has passed through this critical phase in the invasion process and may have the potential to persist and invade the dune system, it becomes important to determine the consequences of its presence. Even though none of the seral stages investigated excluded the pine from primary establishment, are they differentially affected by its presence? In addition, *P. nigra* has recently begun to reproduce and recruit new offspring in the dune system, thereby passing into the next phases of the invasion process. A thorough understanding of the variation in reproduction and recruitment across seral stages will be essential in predicting long-term consequences of this introduction.



Range of *Pinus nigra*. *1. P.n.* ssp.*salzmanni: a) P.n. mauretanica, b) P.n. hispanica, c) P.n. pyrenaica, d) P.n. cevennensis; 2. P.n.* ssp. *poiretiana* : a) *P.n. corsicana*, b) *P.n. calabrica*. c) *P.n. barrea*; 3. *P.n.* ssp.*nigricans*: a) *P.n. austriaca*, b)*P.n. dalmatica*. c)*P.n. bosniaca*. d)*P.n. pindica*. e) *P.n.bulgarica*, f) *P.n.banatica*; 4. *P.n.* ssp. *pallasiana*: a) *P.n. caramanica*, b) *P.n. taurina*. c) *P.n. pontica*, d)*P.n. tatarica* (from Svoboda, 1953).

Figure 2-1. Native distribution of *Pinus nigra* in Europe and Asia (adapted from Vidakovic 1991; based on a map from Svoboda, 1953). Shaded areas indicate occurrence of *P. nigra*.

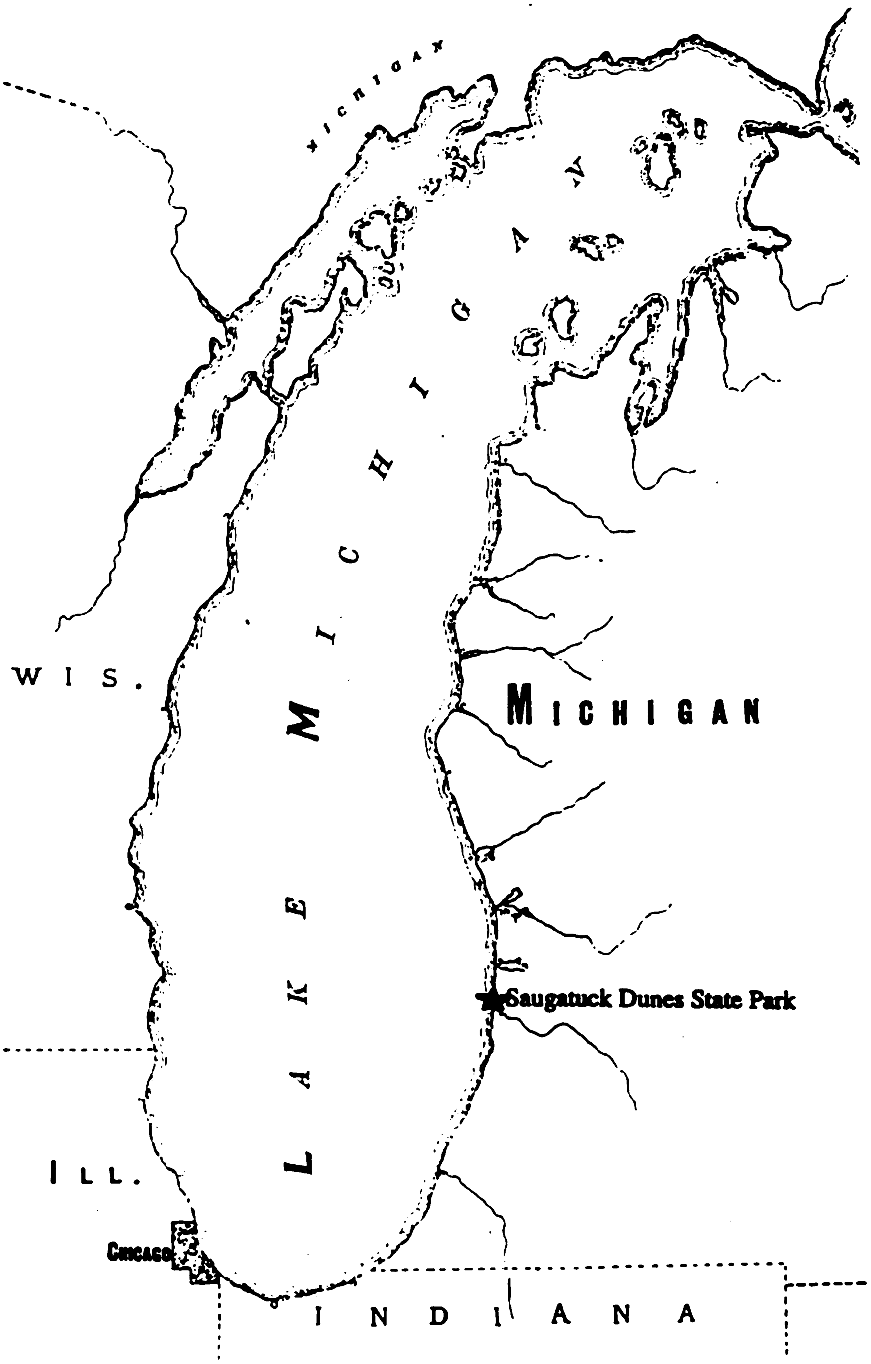


FIG. 1.—MAP OF THE SHORE OF LAKE MICHIGAN. SCALE, 1:2,850,000.

Figure 2-2. Location of study site (Saugatuck Dunes State Park) on eastern shore of Lake Michigan, Allegan, County, MI (from Cowles 1899).

Figure 2-3. Aerial photograph of the study site at Saugatuck Dunes Natural Area, and on adjoining private property, in Allegan County, Michigan (1988 MI DNR). *Pinus nigra* plantings are evident as dark lines in blowout areas and as scattered patches in foredunes. Sampling sites were located throughout four seral stages in areas with and without Austrian pine. Boundary of study area is demarcated with bold lines. One cm ≈ 120m.

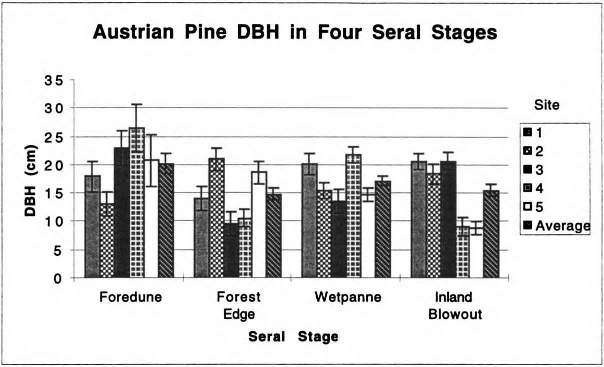


Figure 2-4. Mean diameter at breast height ± SE of planted *P. nigra* in five sites in each of four seral stages at SDSP, Allegan Co., MI (n=5).*

*Data taken from ten trees in each of five sites in forest edge, wetpanne, and inland blowout seral stages. Only three trees were measured in each of the five foredune sites because of their relatively small area.

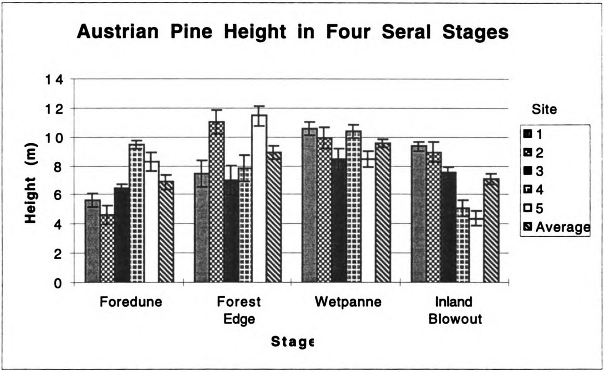


Figure 2-5. Mean height ± SE of planted *P. nigra* in five sites in each of four seral stages at SDSP, Allegan Co., MI (n=5).*

*Data taken from ten trees in each of five sites in forest edge, wetpanne, and inland blowout seral stages. Only tree trees were measured in each of the five foredune sites because of their relatively small area.

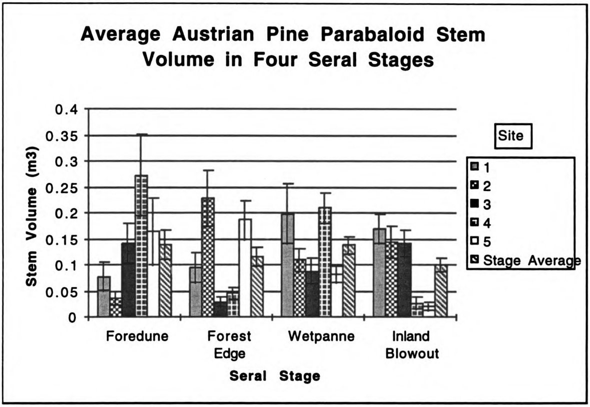


Figure 2-6. Mean stem volume ± SE of planted *P. nigra* in five sites in each of four seral stages at SDSP, Allegan Co., MI (n=5).*

*Data taken from ten trees in each of five sites in forest edge, wetpanne, and inland blowout seral stages. Only three trees were measured in each of the five foredune sites because of their relatively small area.

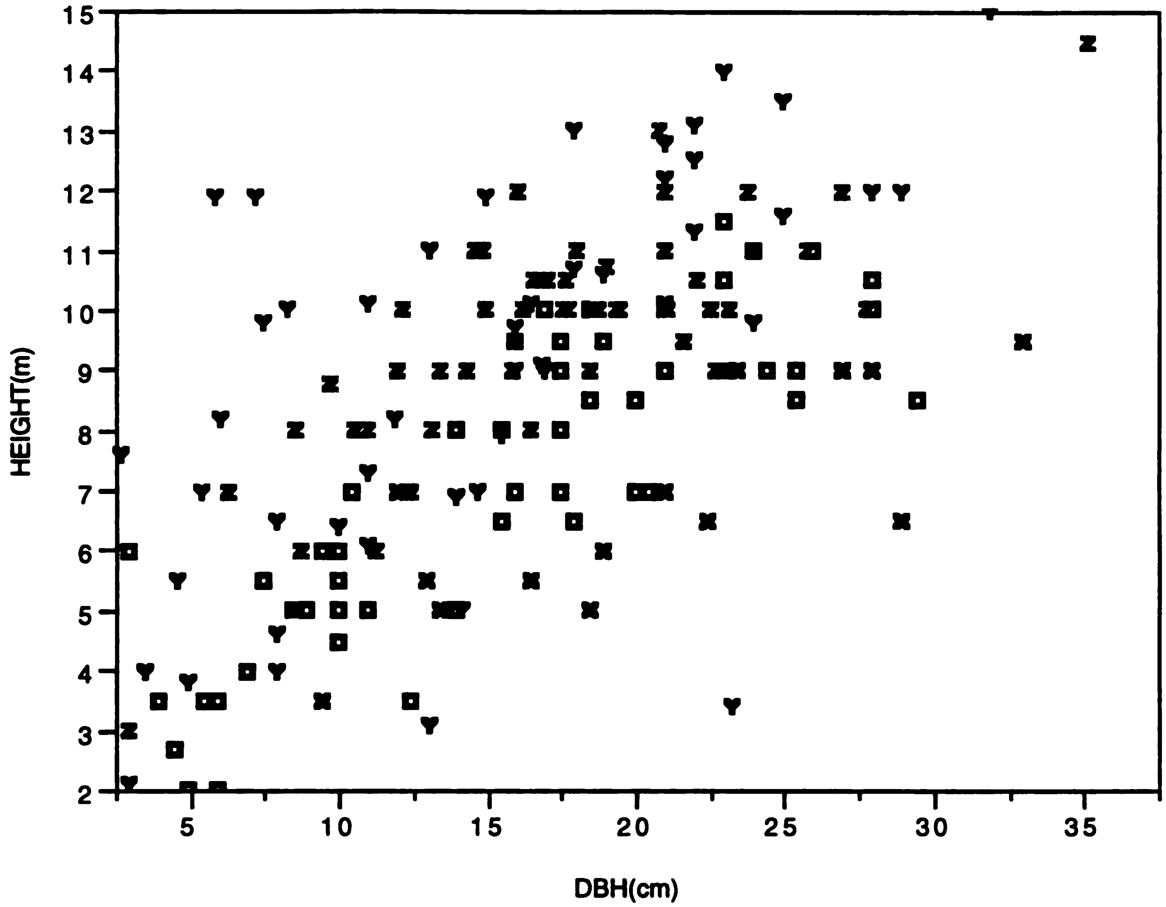


Figure 2-7. Scattergram of relationship between dbh and height in *P. nigra* planted in four seral stages, where x=foredune, y=forest edge, z=wetpanne, and o=inland blowout. Measurements taken June 1994 and 1995 at SDSP, Allegan Co., MI.

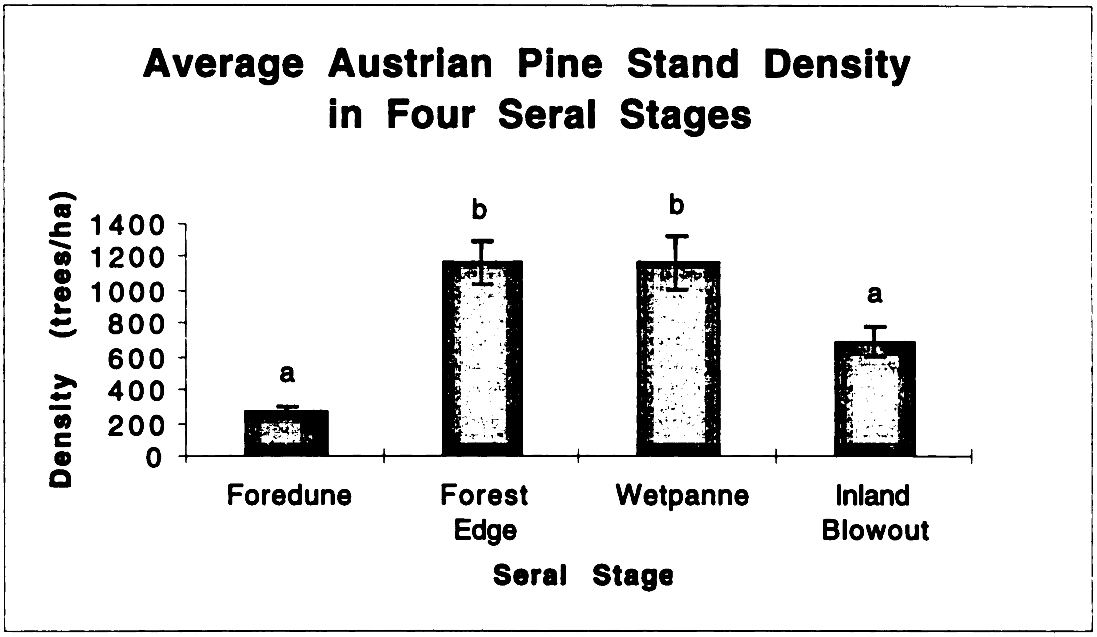


Figure 2-8. Mean stand density (± SE) of *P. nigra* in four seral stages at SDSP, Allegan Co., MI (n=5).*

*Data taken from total inventories of planted *P. nigra* in five sites in each seral stage. Significantly different densities are denoted with different letters (p<.0001, Tukey-Kramer HSD).

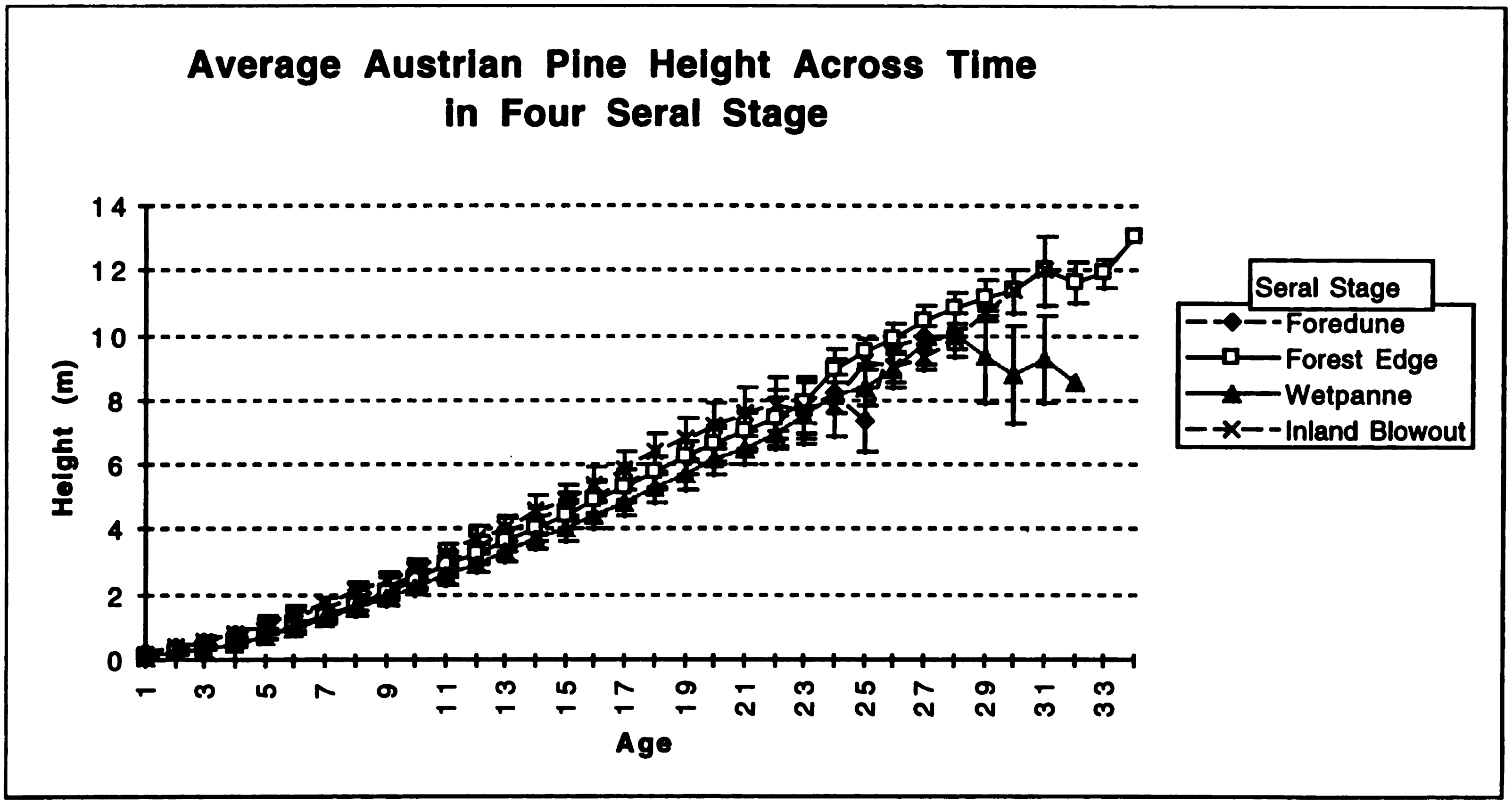


Figure 2-9. Mean tree height (± SE) across time in four seral stages at SDSP, Allegan Co., MI.*

*Means calculated from 10 trees in foredune and 11 in each of the remaining three seral stages. The cohort of trees sampled were of different ages, therefore n decreases across time. Number of whorls was used as an estimate of tree age.

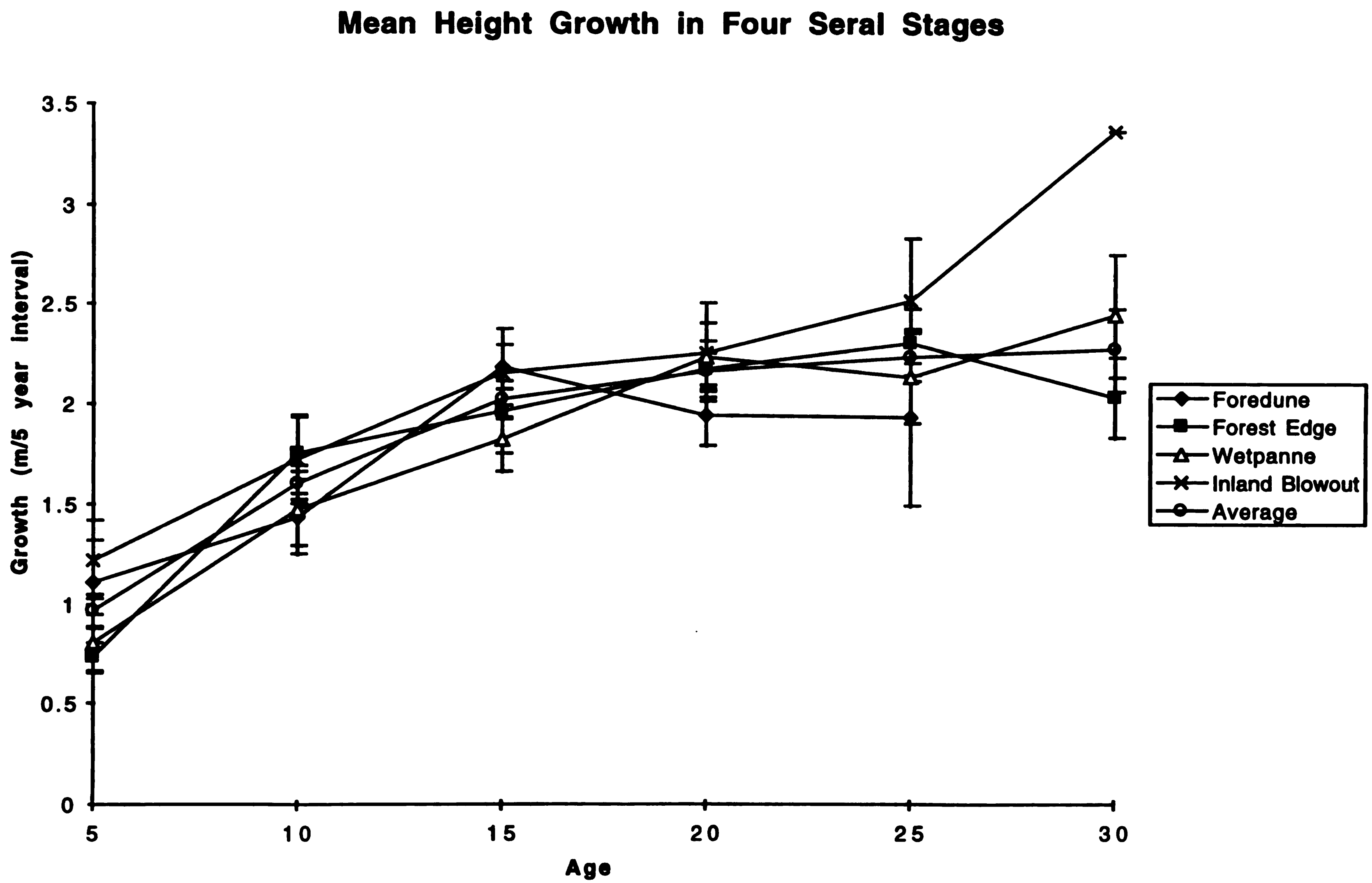


Figure 2-10. Mean height growth ± SE in *P. nigra* in four seral stages in five year increments. Number of whorls was used as an estimate of tree age . No S.E. is shown for the last value of inland blowout sites because it is based on a sample of one.

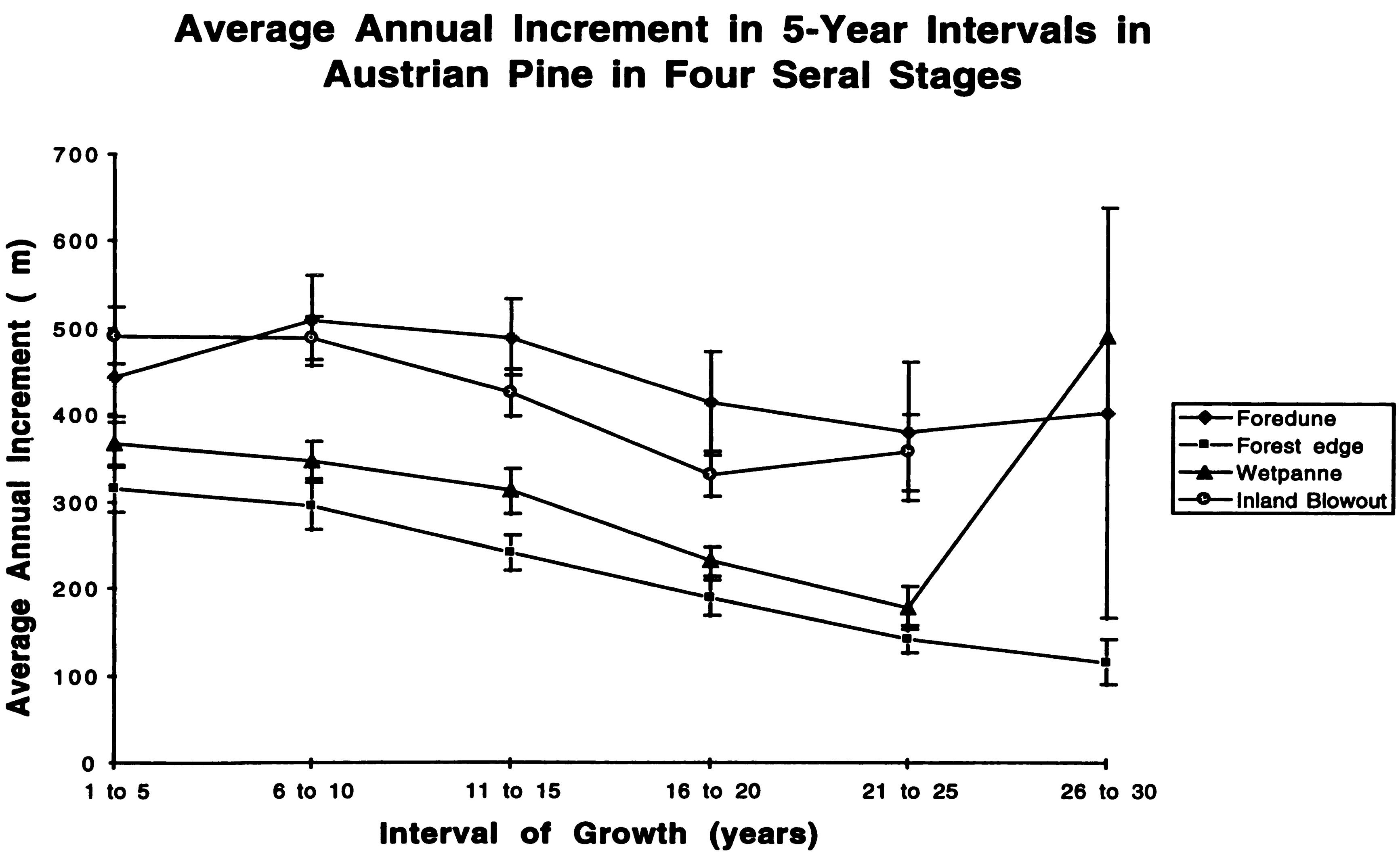
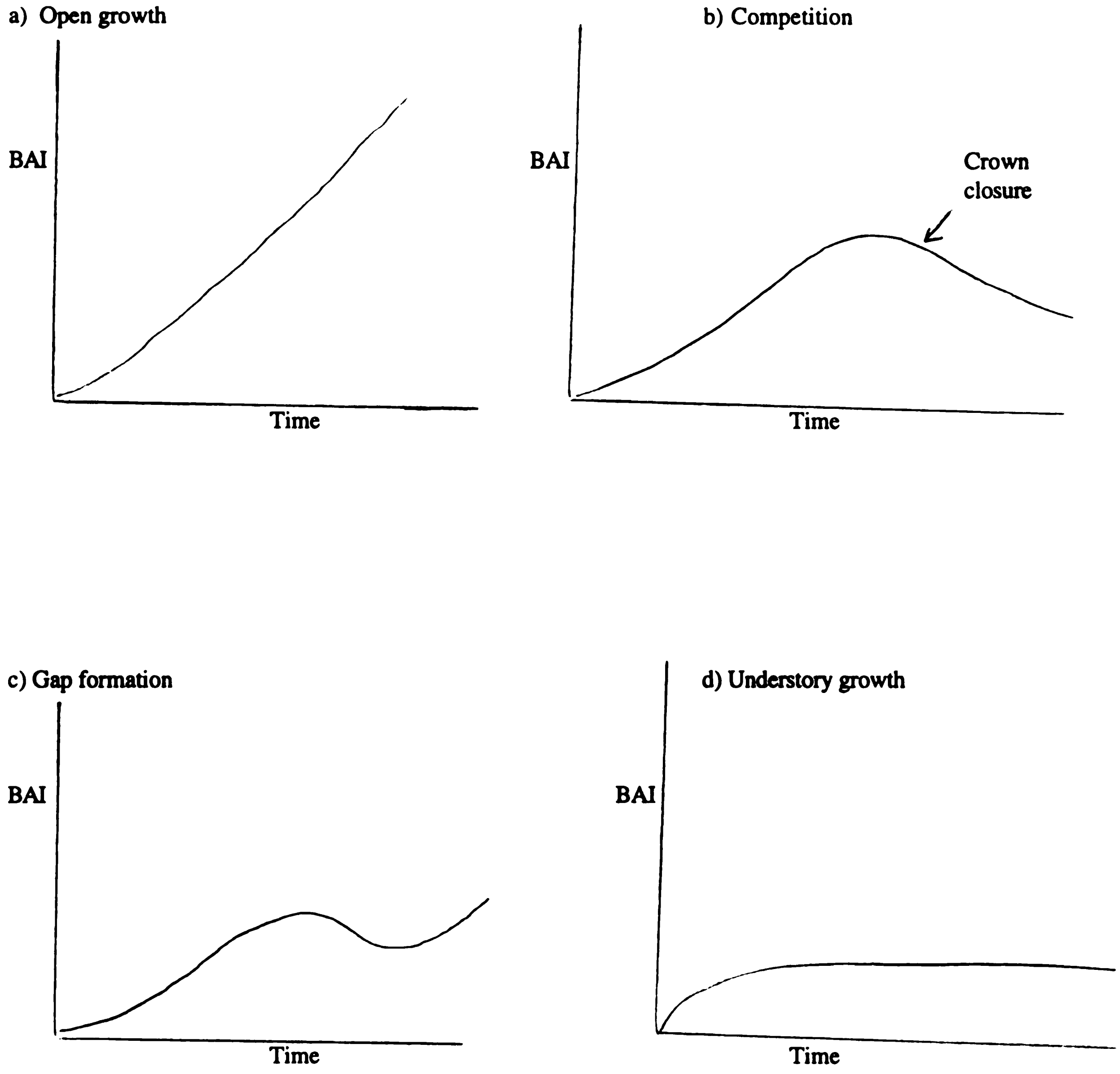


Figure 2-11. Mean radial growth ± SE for *P. nigra* in four seral stages. Mean annual increment calculated for five-year intervals. Data taken from 10 cores from each of three sites in forest edge, wetpanne, and inland blowout seral stages. Only three cores were taken from each of three sites in foredunes because of the limited number of trees available in these sites. Number of tree rings was used as an estimate of tree age.



a) Open growth

b) Competition

c) Gap formation

d) Understory growth

Figure 2-12. Diagrammatic representation of patterns of BAI (basal area increment) of *P. nigra* across time at SDSP, Allegan Co., MI.

CHAPTER 3

BIOTIC AND ABIOTIC ALTERATIONS OF FOUR SAND DUNE HABITATS BY THE INTRODUCED *PINUS NIGRA*

INTRODUCTION

Plants alter the environments in which they live. They occupy space, utilize soil moisture and nutrients, filter incident radiation, and add carbon to the soil, to name just a few of their effects. These changes in the abiotic environment, in turn, influence the plant communities of which these individuals are a part, and over many years, stable, self-sustaining communities are assembled and maintained.

When non-native plant species are introduced into novel habitats, they, too, alter their environments, sometimes in ways that the native species cannot tolerate. Loope (1992) and Williamson (1996) argue that plant introductions most often have little or no effect upon the biota of their recipient community. When they are successful, however, invaders can impact all levels of ecological organization of the recipient system. They alter population dynamics of native species by inhibiting germination or reducing growth and recruitment into larger size classes (Walker and Vitousek 1991, Equihua and Usher 1993, Hughes and Vitousek 1993). Effects of invaders on ecosystem function include changes in geomorphological processes, alteration of biogeochemical and hydrological cycles, and alteration of fire regimes (Macdonald et al. 1989 and references therein). Invasive species also alter community composition and structure. For example, in eastern deciduous forests, the introduced *Lonicera tatarica* reduces herb cover, tree seedling density, and species richness, most likely by shading out native species (Woods 1993). Similarly, *Rhododendron ponticum* is thought to inhibit recruitment of native forest species in Britain by dramatically reducing light intensity and producing a thick litter layer (MacDonald et al.

1989). Though many references are made to effects of invaders upon plant communities, clear documentation of this phenomenon is lacking (Woods 1993).

This paper documents the effects of an introduced pine (*P. nigra*) on both abiotic and biotic components of a sand dune system. Four seral stages, or dune habitats (foredunes, forest edges, wetpannes, and inland blowouts) were investigated, and population, community and ecosystem level effects of the pine introduction are discussed.

Invasive species may have important consequences in dune systems for a number of reasons. Continuous endogenous disturbance in the form of sand movement is an inherent characteristic of sand dunes which maintains the vigor of the native vegetation (Ranwell 1972). Any permanent change in the natural disturbance regime of the dune system would constitute an altered geomorphological process, an ecosystem level effect which could have irreversible consequences for the maintenance of the dune system. For example, the spread of European beachgrass (*Ammophila arenaria*) on the coastal dunes of California has altered dune topography, replaced native dune species and reduced species diversity (Mooney et al. 1986, Buell et al. 1995). The introduction of a large and potentially invasive conifer into a dune system where it represents a novel life form may alter sand movement patterns and disrupt the disturbance regime of the system. This, in turn, might have serious consequences for unique dune plants such as the federally threatened Pitcher's thistle (*Cirsium pitcheri*) which requires 70% open sand for germination and survival (McEachern 1992).

Additionally, invaders may influence dune succession. The endpoint of ecological succession in dune systems is thought to be influenced by initial conditions (Olson 1958, T. Poulson personal communication). The presence of a large, non-native evergreen in early successional stages may have the potential to accelerate the rate of succession or alter its trajectory by increasing nutrient inputs, developing soils, and redistributing water in the soil column (Ovington 1950, Anderson 1987).

Non-native pines, planted in dense stands, or plantations, are known to alter abiotic components of terrestrial ecosystems. Clough (1991) found reduced soil pH, Mg, K, and Ca, and increased Al in *Pinus elliotti* and *Pinus taeda* plantations relative to the indigenous medium-moist-coastal-platform-type forest in the South Cape, South Africa. In addition, litter under pine canopy was four to five times that of the indigenous forest. In a comparison of *Pinus radiata* plantations and native eucalypt forest in S.E. Australia, Feller (1983) documented decreased levels of nitrogen as well as base cations in plantation soils. The reduced fertility of plantations soils is likely due to the leaching of base cations elicited by decreased soil pH (Clough 1991). Water distribution in the soil column is also altered by pine plantations. In a British dune system forested with *Pinus nigra* ssp. *laricio*, water holding capacity was increased under pine cover, but the top layers of the soil were drier and soils reached the wilting point four months earlier in the growing season than in unforested dunes (Ovington 1950, Wright 1955).

Biotic effects of pine plantations include the inhibition of understory cover (Cowling et al. 1976, Hill and Wallace 1989, Richardson et al. 1989) and a reduction in species diversity (Cowling et al. 1976, Richardson et al. 1989, Lugo 1992). In other systems, however, pine plantations may have the reverse effect. Understory cover and species diversity were increased in serpentine systems forested with pines (Chiarucci 1995), and species diversity was increased in dune systems forested by pines (Ovington 1950, Hill and Wallace 1989).

The projected effects of an introduced pine on a dune system are numerous and potentially irreversible. This study seeks to answer the following questions regarding the effects of the pine on three separate components of the dune system.

1) The disturbance regime: How have the pines altered sand movement patterns relative to areas without pines?
2) Abiotic characteristics: How have light intensity, soil moisture, pH, and soil development within and around stands been altered by the pine introduction?
3) Community structure: How have the pines altered species diversity, composition and community structure under their canopy and in the surrounding habitat?

Three different outcomes of the introduction of *P. nigra* on the sand dunes of Lake Michigan are possible:

1) The presence of the introduced pine will facilitate the growth of native species because of favorable changes in microenvironment under pine canopy. Vegetation cover will be increased, particularly in blowouts and adjacent to deciduous forest, where cover is sparse under natural circumstances.
2) The presence of the introduced pine will inhibit the growth of native species because of unfavorable changes in microenvironment under pine canopy. Vegetation cover will be suppressed due to reduced light levels and competition with the pines for limiting resources.
3) The presence of the introduced pine will inhibit the growth of species native to each dune habitat, but will provide new microenvironments in which species not present in the adjacent dune habitat can establish.

Field observations suggested that either the second or third predicted outcome was most likely at SDSP. To determine the effects of *P. nigra* on the dunes, vegetation composition and structure and abiotic characteristics were compared under pines and in adjacent areas with similar vegetation in four seral stages.

METHODS

Study site

This investigation took place at Saugatuck Dunes State Park, as described in Chapter 2.

Biotic effects of P. nigra

To determine the effects of Austrian pine on dune community composition and structure, measurements of various plant and community characteristics were made in 1m X 2m quadrats at 1-m intervals along 20m X 2m belt transects established in foredune, forest edge, wetpanne, and inland blowout sites at SDSP. Most measurements were taken June-July 1994, with the exception of wetpanne sites, which were sampled in June and July 1995. Five additional transects were sampled in forest edge and foredune sites in July 1996 to increase the sample size. All transect locations were randomly selected from a larger set of possible sites with the aid of an aerial photograph.

Eight to ten belt transects (20m x 2m) were established at the edge of Austrian pine stands in four seral stages. The transects ran perpendicular to the border between native and pine vegetation (Figure 3-1). Up to 10m of the transect was located under pine canopy and 10m in the adjacent vegetation. Some variation in transect length was necessary in foredune and inland blowout sites, however, as pine stands did not extend the full 10m of the transect length. Transects always extended 10m into the native vegetation, but were 2-10m in length under the pine canopy. Data were collected in 2m x 1m quadrats at each 1-m interval along the transect.

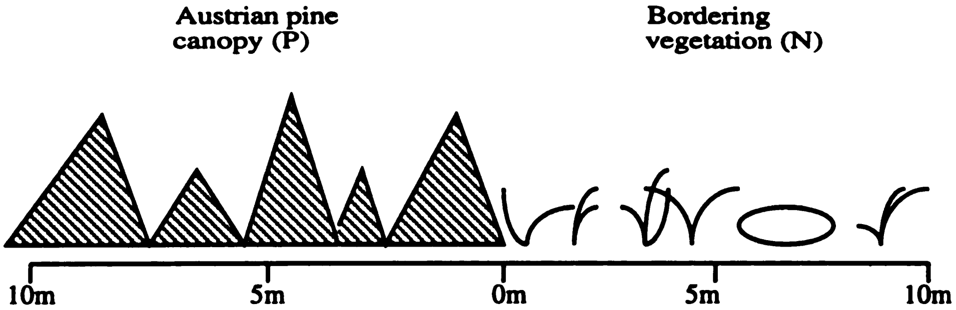


Figure 3-1. Diagrammatic representation of 20-m belt transect at the interface between pine and native dune vegetation. All measurements were taken at 1-m intervals. Multiple transects were located in each seral stage.

To compare *P. nigra* dune communities with dune communities unaffected by the introduced pine, transects were also established in the four seral stages in sites lacking *P. nigra* (Table 3-1). In foredunes, five transects were located at the interface between stands of *Populus deltoides* and native grasses which occur in the foredune. Transects were also established in 10 forest edge sites lacking *P. nigra*. Ten meters of the forest edge transect were located in inland blowout vegetation abutting the native deciduous forest (analogous to the portion of the transect under *P. nigra* canopy in pine sites). The remaining 10m of the transect were located under the native deciduous canopy. The border of the forest edge was located by identifying large native trees which were probably present at the time of the pine plantings. In wetpannes, 10 transects between native Jack pines (*Pinus banksiana*) and bordering wetpanne vegetation were also established. In blowouts, 10 1m x 2m quadrats were randomly located in 10 sites, because stands of native trees were lacking. (A map showing locations of all transects was filed with the Michigan Department of

Natural Resources in a 1994 Progress Report. The report is available at the Saugatuck Dunes State Park office in Holland, MI and with the Natural Heritage Program office in Lansing, MI. Additional location information is available from the author.)

Table 3-1. Vegetation types present in each portion of the transects in sites lacking Austrian pine. P indicates the portion of the transect analogous to that characterized by the presence of Austrian pine canopy in Austrian pine sites. N is the adjacent vegetation, similar in sites with and without Austrian pine.

Seral Stage	P: first 10m of transect	N: Adjacent vegetation (last 10m of transect)
Foredune	*Populus deltoides* canopy	Foredune grasses
Forest Edge	Blowout vegetation	Native deciduous canopy
Wetpanne	*Pinus banksiana* canopy	Wetpanne vegetation
Inland Blowout	10 1X2-m random plots measured	

In each 1m X 2m interval of established belt transects, cover of all vascular plant species was determined for grasses using ocular estimates and by taking crown area measurements of each forb species or woody seedling <1 cm dbh. Stem counts of all non-grass species, and the height and dbh of each woody plant >1cm dbh were also recorded. Plant species identification was verified using Voss (1972, 1985, 1996).

Disturbance regime: sand movement

In three of the four seral stages, observations of sand accumulation patterns around stands of Austrian pine were made to determine the effects of the trees on sand movement. In July and August of 1994, bamboo stakes (approximately 1m tall) were driven into the soil with 40cm remaining above ground. Net sand movement was measured against these stakes in September 1995, approximately one year later. Three series of stakes, 1m apart from each other, were established at the edge of the pine canopy on windward and leeward edges of pine stands in foredune, forest edge, and inland blowout sites. Wetpannes were not measured because of the lack of open sand surrounding stands in this seral stage. Each series consisted of three stakes: one each at canopy edge, 1m, and 5m into the unplanted region (see Figure 3-2). To compare the effects of the introduced pine and a native tree on sand movement, a duplicate set of stakes was established adjacent to native cottonwood stands (*Populus deltoides*).

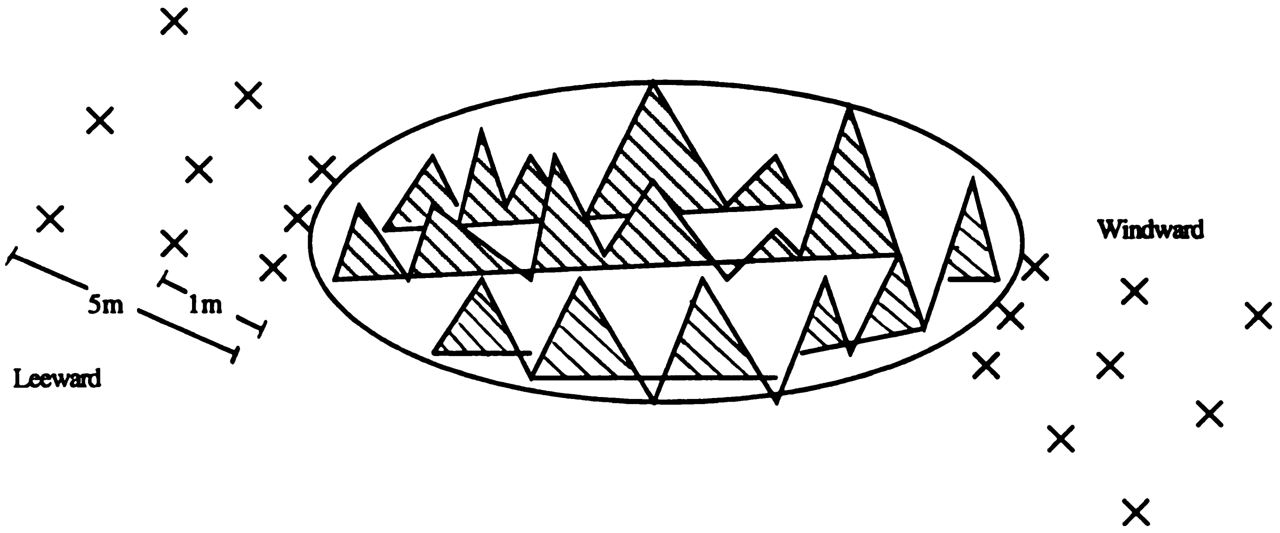


Figure 3-2. Measurement of sand movement patterns around *P. nigra* and *Populus deltoides* stands. Sand movement in both windward and leeward directions was determined. Each x represents a stake, used to measure sand movement.

Abiotic effects of P. nigra

In each of the four seral stages, a variety of physical factors were measured that were regarded as important to indigenous plants and which were likely to be altered by the presence of Austrian pine, including the solum depth, soil moisture, and light intensity.

Soil profile.--Soil profiles were examined during the summers of 1995 and 1996 for indication of the depth to which organic matter had been incorporated and soil development had taken place. Three to six soil profiles were examined at each of two locations (five meters into canopy and five meters into bordering vegetation: see Figure 3-1) along each of three to five established transects in sites with and without Austrian pine in all four seral stages. In Austrian pine, cottonwood foredune, and Jack pine wetpanne sites, soil profiles were examined at a point on the transect five meters under canopy and at another point five meters into the bordering native vegetation. In forest edge sites lacking pines, soil profile samples were taken at five meters into the blowout abutting the deciduous forest vegetation and five meters into deciduous forest cover.

To examine the soil profile, soil was exposed to a depth of at least 20 cm with a trowel or a soil core, and horizon designations and depths were determined in each exposed soil column. Soil samples of the top five cm of the soil column were collected and tested for physiological pH with an Oakton pH tester kit. Soil samples were stored in a freezer before testing,which was completed within 13 days of sample collection. Minimum, median and maximum pH values were calculated and compared within and among seral stages.

Soil moisture.-- Soil moisture content was determined monthly from May - August 1995 for four seral stages. Soil samples were collected to a depth of five cm with a soil core from points five meters into canopy and five meters into bordering vegetation on each of three of the ten established transects in sites with and without *P. nigra* in all seral stages. All soil was collected between 6:30 A.M. and 9 A.M., before significant drying and plant transpiration had taken place. Soil moisture content was determined gravimetrically. Water content of soil was compared within and among pine and control sites.

Light intensity.--To determine the effect of P. *nigra* stands on light levels, light intensity readings were taken with a Decagon Ceptometer at each one-meter interval of established 20-meter transects in all seral stages. Measurements were taken on clear days in July and August 1994 and 1995 between 11:00 A.M.and 2:30 P.M., when the rays of the sun were overhead.

ANALYSIS

Biotic effects

Understory cover.-- Total percent cover of the understory vegetation for each 1-m interval along each transect was calculated from forb and woody seedling crown area values and percent cover values for grasses. Understory vegetation included all vascular plants rooted in the plot with stems of less than 1cm dbh. Cover values for each one-meter interval were averaged across all transects, and compared among sites with and without *P. nigra* in each seral stage, and among seral stages.

Species richness and diversity.--Species richness per $2m^2$ plots (1mX2m transect intervals) and both Simpson (D) and Shannon-Weaver (H') indices of diversity were calculated for understory vegetation using percent cover values in 1-m intervals on each transect as a measure of abundance. Both diversity indices include a measure of evenness of species distribution in the community. The calculations for each follow.

$D = 1/\Sigma p_i^2$, and

$H' = -\Sigma p_i \ln p_i$

where p_i is the proportion of individuals of species i in the total sample of individuals.

Importance values.-- The relative importance of each species in the understory of the community was assessed for each seral stage and at each two-meter interval of the transect by summing relative frequency and relative cover values for each species in each two-meter interval along transects of the same seral stage (Brower et al. 1993). Relative density was not included in the calculation of importance, because stem density of grasses could not be determined. Species importance values were compared along transects and changes in community composition were identified in this manner.

Community similarity.--To further determine the changes in species composition along the 20-m transect gradient from *P. nigra* stands into the native vegetation, a quantitative index of similarity (IS_{Mo}) was calculated using mean percent-cover values for each species in each 2-m interval along transects. The index is a modification of Sorenson's similarity index which, in addition to similarity in species composition, also includes measures of species abundance (cover). The index was first applied by Motyka (Mueller-Dombois and Ellenberg 1974) and is calculated as follows:

$IS_{Mo} = 2Mw/(MA + MB) * 100$

where Mw = sum of the smaller quantitative values of the species common to the two plots,

MA = percent cover of all species in A, and

MB= percent cover of all species in B.

Similarity indices compared each two-meter interval on the transect with the first and last interval of the transect, as the first interval represents the core of pine community and the last interval represents the core of the neighboring dune community. Similarity indices were calculated for communities lacking pine in each seral stage as well.

Life form analyses.-- Understory species were classified by life form (graminoid, vine, forb, shrub, evergreen tree or deciduous tree) and compared across two-meter intervals of transects. Shrubs were defined as woody species which never reach the canopy, and included *Cornus stolonifera, Hudsonia tomentosa, Lonicera sp., Prunus pumila, Prunus virginiana* , *Ptelea trifoliata,* and *Salix sp.*.

Woody species : stem density and size structure.-- Stem density of woody species ≥1cm dbh was determined for 5m intervals in each transect and averaged across all ten transects within seral stage. No sapling or adult-sized woody species other than *P. nigra* occurred in foredune and inland blowout stands with pine. Similarly *Populus deltoides* was the only woody species beyond the seedling stage in foredune cottonwood stands, and for this reason, graphs of stem densities in these seral stages are not shown. Stem densities were compared for sites with and without *P. nigra* in forest edge and wetpanne seral stages.

In forest edge sites, two species, *Sassafras albidum* and *Quercus sp.* exhibited a range of size classes across transects in sites with and without Austrian pine, as did *P. banksiana* in wetpanne sites. The abundance of each species was determined for six DBH classes: S = seedlings <1cm DBH, Class 1 = 1-2.4cm, Class 2 = 2.5-4.9cm, Class 3 = 5-9.9cm, Class 4 = 10-19.9cm, and Class 5 = >20cm, and total counts of individuals in each size class were compared within species and seral stage.

Disturbance regime: sand movement

Sand accumulation and erosion in control plots and *P. nigra* stands were compared within and among seral stages to determine average cm of overall movement, average cm of gain and loss, and average percent of stakes gaining sand, losing sand, or stable. The above measurements for windward and leeward stakes were also compared within and among foredune *P. nigra* and *Populus deltoides* stands. Chi square tests were used to determine the differences in stakes gaining, losing, and stable, within and among seral stages.

Abiotic effects

Soil moisture.-- Variation in monthly soil moisture data for May - August 1995 within seral stage was analyzed with a repeated measure MANOVA, where the soil moisture values from each of four months were treated as the y response variables. Site type (Austrian pine (A) or lacking Austrian pine (C)) and sample location (under pine/cottonwood canopy (P), or in bordering native vegetation (N)) and their interaction were modelled as fixed effects, and site nested within site type was treated as a random effect. Replication was not sufficient to test 1995 forest edge seral stage data in this manner.

Light intensity.-- Light intensity was averaged across each one-meter interval of all transects of the same type and compared among sites with and without *P. nigra* within each seral stage. In addition, Spearman rank correlations between light intensity and species richness, as well as light intensity and total understory cover were calculated to determine the association between light and biotic variables.

Solum thickness.-- Soil development was compared within each seral stage using a two-way ANOVA with site type (Austrian pine (A) or lacking Austrian pine (C)) as one factor and sample location (under pine/cottonwood canopy (or in analogous locations lacking pine in forest edge sites) (P), or in bordering native vegetation (N)) as the other factor. The two main effects and their interactions were modelled as fixed effects in the ANOVA.

RESULTS

Biotic effects of Austrian pine

Understory cover.--Growth of understory vegetation was inhibited under *P. nigra* in all four seral stages (Figures 3-3 and 3-4). Understory cover in pine stands averaged 8% ± 1.5 over all seral stages compared to 45% ± 4.4 in the portion of transects bordering the pine stands.

In foredunes, the effect of Austrian pine clearly differed from that of cottonwoods (Figure 3-3a). Understory cover was 6.5 to 40 times higher in the first seven meters of transect under cottonwood stands than under Austrian pine canopy (refer to Figure 3-1 for locations on the transect). Understory cover increased rapidly in the final two meters under pine canopy, but was not equal to that of cottonwood sites until the tenth meter beyond the pine stand. In contrast, understory cover was not at all inhibited by cottonwood stands; 65 - 82% of the ground was vegetated across the length of transects in cottonwood sites.

Effects of pine canopy on understory cover were least pronounced in the forest edge seral stage where cover was two to ten times higher in sites without pine than under pine canopy (Figure 3-3b). Cover ranged from 6 - 24% under pine canopy, versus 28 - 59% in open dunes bordering the native forest canopy. Understory cover declined under deciduous canopy in sites without pine but increased under deciduous canopy abutting pine stands. Variance in understory cover under forest edge pine canopy was high due to an anomalous transect with a dense cover of bracken fern found nowhere else in Austrian pine forest edge sites.

Pinus nigra stand effect also differed from that of the native pine, *P. banksiana,* in the wetpanne habitat (Figure 3-4a). Understory cover was 3-13 times higher under the native pine stands than under *P. nigra* canopy. In addition, average cover in the bordering wetpannes was higher in the Jack pine sites until the seventh meter into the wetpanne, where Austrian pine wetpanne cover was 20% greater. Cover was very low under pine canopy in this seral stage, despite the fact that cover exceeded 100% in the portions of the transect bordering pine stands (due to multiple layers of understory cover) .

Understory cover was lowest under pine canopy in inland blowout sites, where it ranged from 0.2 - 4% (Figure 3-4b). Cover in the areas bordering pines was only 9-26%, but pine effect may have extended beyond the 10m sampled, since randomly selected inland blowout plots lacking Austrian pine averaged 24 to 45% in vegetation cover.

Species richness and diversity.-- Understory species richness was increased relative to cottonwood sites in Austrian pine foredune sites, but Simpson and Shannon diversity showed less of a difference between Austrian pine and cottonwood sites in foredunes (Figure 3-5, Table 3-2). In forest edges, species richness was slightly reduced under pine canopy relative to open blowout bordering the native forest, but Simpson and Shannon diversity indices differed little among sites with and without pine (Figure 3-6).

The greatest difference in species richness and diversity within a seral stage was between Austrian and Jack pine wetpanne sites (Figure 3-7). Richness was two to four times higher under Jack pine canopy despite the low vegetation cover. Shannon diversity was 1.5 to 6.7 times higher under Jack than Austrian pine canopy and Simpson diversity ranged from 0.98 to 2.49 under Austrian pine canopy and 1.94 to 3.89 under Jack pine canopy. Though species richness in inland blowouts was already low, it was decreased even further by the presence of *P. nigra* canopy (Figure 3-8).

Species composition.--

Importance values.-- In both cottonwood and Austrian pine foredune sites, *Ammophila breviligulata* was among the five most important species across transects (Table 3-3). *Calamovilfa longifolia*, another early successional graminoid, was important only in Austrian pine sites, however. It became important under pine canopy four meters from the edge of the stand, and maintained its position among the top five importance values to the end of the transect, ten meters beyond the pine border. *Quercus sp.* occurred only under pine canopy in foredunes, while *Artemesia campestris* and *Oenothera biennis* were important only beyond the canopy.

In the first 10m of forest edge sites, the composition of species with the top five importance values was almost completely different among sites with and without Austrian pine (Table 3-4). The graminoids *Andropogon scoparius, Ammophila breviligulata,*

Table 3-2a. Average diversity indices across transects in foredune and forest edge seral stages. S= species richness per $2m^2$ area, D= Simpson's index, and H'= Shannon-Weaver index. In foredunes, wetpannes and blowouts, intervals commence under pine or cottonwood canopy and progress out towards the bordering vegetation so that interval one is located at the edge of pine/cottonwood stand. In forest edge sites, intervals commence under pine canopy or in blowout vegetation in sites lacking pines and progress out towards the bordering deciduous vegetation. Interval one is the final meter before the forest vegetation.

Seral Stage	Interval	10	9	8	7	6	5	4	3	2	1
Foredune	Diversity Index										
P.nigra	S	3.00	5.00	2.33	2.33	2.33	2.40	2.43	2.71	2.38	2.63
	D	2.46	3.64	1.49	1.08	1.46	1.28	1.38	1.09	1.11	1.27
	H'	0.97	1.42	0.35	0.15	0.44	0.31	0.28	0.27	0.21	0.34
Cottonwood	S	1.75	1.25	1.00	1.00	1.00	1.25	1.60	1.80	1.20	1.00
	D	1.00	1.00	1.00	1.00	1.00	1.00	1.12	1.23	1.00	1.00
	H'	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.17	0.00	0.00
Forest edge											
P.nigra	S	2.70	3.10	2.89	2.89	2.67	3.89	2.90	3.50	3.50	3.30
	D	1.65	2.06	1.83	1.72	1.67	1.78	1.88	1.97	1.67	1.77
	H'	0.58	0.82	0.72	0.54	0.64	0.69	0.59	0.67	0.55	0.58
Lacking P.nigra	S	3.60	3.50	4.10	4.20	4.10	3.40	2.90	2.90	3.10	3.40
	D	1.74	1.64	1.94	1.97	2.05	1.72	1.54	1.97	2.02	1.65
	H'	0.58	0.49	0.75	0.75	0.83	0.56	0.44	0.72	0.75	0.64
Wetpanne											
P. nigra	S	1.10	1.70	1.90	1.80	2.20	2.90	3.60	3.70	4.40	5.70
	D	0.98	1.15	1.42	1.22	1.49	1.67	2.07	1.73	1.60	2.49
	H'	0.17	0.15	0.38	0.29	0.48	0.63	0.85	0.56	0.68	0.97
Jack pine	S	5.70	5.50	5.30	4.50	5.60	5.70	7.80	7.70	8.60	10.1
	D	2.15	2.43	1.94	2.46	2.50	2.67	3.47	3.10	3.50	3.89
	H'	1.05	1.00	0.84	1.05	1.06	1.24	1.38	1.34	1.39	1.46
Inland Blowout											
P. nigra	S	0.67	0.78	1.50	1.00	1.60	1.60	1.20	1.50	2.50	2.50
	D	0.46	0.67	0.97	0.78	1.06	1.09	0.97	0.90	1.64	1.44
	H'	0.07	0.20	0.25	0.12	0.36	0.34	0.29	0.45	0.69	0.51

Table 3-2b. Average diversity indices across transects in wetpanne and inland blowout seral stages. S= species richness per 2m^2 area, D= Simpson's index, and H'= Shannon-Weaver index. Interval one commences just beyond pine canopy and the transect progress out ten meters further into the bordering vegetation.

Seral Stage	Diversity Index	1	2	3	4	5	6	7	8	9	10
Foredune											
P.nigra	S	2.50	1.63	1.75	1.50	1.86	1.86	1.63	1.75	2.00	1.75
	D	1.16	1.05	1.02	1.00	1.15	1.04	1.05	1.15	1.27	1.18
	H'	0.25	0.09	0.05	0.01	0.12	0.09	0.09	0.15	0.26	0.17
Cottonwood	S	1.00	1.00	1.20	1.20	1.20	1.20	1.20	1.40	1.20	1.60
	D	1.00	1.00	1.02	1.00	1.20	1.00	1.00	1.08	1.00	1.03
	H'	0.00	0.00	0.04	0.00	0.14	0.00	0.00	0.09	0.00	0.07
Forest edge											
P.nigra	S	3.50	2.80	2.70	3.90	3.40	4.10	4.70	5.20	5.20	5.80
	D	1.52	1.67	1.61	1.61	2.28	1.90	1.80	1.84	2.47	2.68
	H'	0.43	0.51	0.49	0.53	0.64	0.61	0.61	0.68	0.90	1.01
Lacking	S	3.40	3.70	3.67	4.44	5.60	5.10	4.90	5.70	4.70	5.20
P.nigra	D	1.92	1.91	1.46	1.70	2.57	2.28	2.45	1.86	2.51	2.53
	H'	0.74	0.77	0.49	0.63	1.00	0.94	1.02	0.79	1.03	1.07
Wetpanne											
P. nigra	S	6.91	7.60	9.10	9.80	9.00	9.60	11.3	11.2	11.1	10.7
	D	2.75	2.93	3.41	2.71	3.09	2.91	3.29	2.90	4.70	4.14
	H'	1.18	1.23	1.36	1.23	1.32	1.27	1.42	1.36	1.74	1.64
Jack pine	S	9.60	9.60	9.90	9.00	8.50	8.80	8.30	9.80	7.60	9.80
	D	3.19	3.46	3.40	2.65	3.07	2.71	3.20	3.68	2.78	3.20
	H'	1.41	1.43	1.41	1.01	1.20	1.16	1.20	1.36	1.15	1.34
Inland Blowout											
P. nigra	S	2.88	2.56	3.11	3.22	3.22	2.67	2.89	2.33	2.33	2.33
	D	1.65	1.95	1.44	1.72	1.72	1.43	1.91	1.26	1.37	1.11
	H'	0.51	0.64	0.44	0.59	0.46	0.46	0.64	0.29	0.44	0.34
Lacking	S	2.50	3.20	3.10	3.40	3.10	3.80	3.30	3.70	4.50	3.60
P. nigra	D	1.14	1.90	1.90	1.70	1.37	1.55	1.97	1.69	1.94	1.81
	H'	0.50	0.62	0.79	0.61	0.53	0.68	0.65	0.60	0.69	0.60

Table 3-3. Top five important species in foredune sites along 20-m transect. Each number represents a 2-m interval, starting under cottonwood or pine canopy and ending 10m from the edge of the canopy in the bordering native vegetation. Data from 1994 and 1996.

Foredune Pinus nigra

Monarda punctata	MONPUN									
Quercus sp.	QUESP	QUESP								
Unidentified Poacae	UNKPOA	UNKPOA	UNKPOA							
Solidago sp.	SOLSP		SOLSP	SOLSP	SOLSP	SOLSP			SOLSP	
Ammophila breviligulata	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE
Pinus nigra		PINNIG	PINNIG							
Arabis lyrata		ARALYR				ARALYR				
Asclepius syriaca			ASCSYR	ASCSYR	ASCSYR		ASCSYR	ASCSYR	ASCSYR	ASCSYR
Aclepius sp.				ASCSP	ASCSP					
Calamovilfa longifolia				CALLON	CALLON	CALLON	CALLON	CALLON	CALLON	CALLON
Artemesia campestris						ARTCAM	ARTCAM	ARTCAM	ARTCAM	ARTCAM
Oenothera biennis							OENBIE	OENBIE		
Vitis riparia										VITRIP
	1	2	3	4	5	6	7	8	9	10
			Pinus nigra Canopy					Foredune Vegetation		

Foredune Cottonwoods

Prunus pumila	PRUPUM									PRUPUM
Asclepius syriaca	ASCSYR			ASCSYR	ASCSYR		ASCSYR	ASCSYR	ASCSYR	ASCSYR
Ammophila breviligulata	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE
Vitis riparia			VITRIP	VITRIP						
	1	2	3	4	5	6	7	8	9	10
			Populus deltoides Canopy					Foredune Vegetation		

Table 3-4. Top five important species in forest edge sites along 20-m transect. Each number represents a 2-m interval, starting under pine canopy or in blowout vegetation and ending 10m into native deciduous canopy.

Pinus banksiana Wetpanne

Lonicera sp	LONSP									
Toxicodendron radicans	TOXRAD	TOXRAD								
Quercus sp.	QUESP	QUESP								
Rumex acetosella	RUMACE	RUMACE	RUMACE	RUMACE						
Solidago sp.	SOLSP	SOLSP	SOLSP	SOLSP	SOLSP					
Prunus virginiana		PRUVIR								
Juncus balticus			JUNBAL		JUNBAL	JUNBAL	JUNBAL	JUNBAL	JUNBAL	JUNBAL
Panicum virgatum			PANVIR							
Calamovilfa longifolia			CALLON							
Fragaria virginiana				FRAVIR	FRAVIR	FRAVIR				
Rubus sp.				RUBSP		RUBSP	RUBSP	RUBSP	RUBSP	
Unknown19 (POACEA)				UN19	UN19	UN19	UN19	UN19	UN19	UN19
Unknown16 (POACEA)					UN16	UN16	UN16	UN16	UN16	UN16
Spiraea tomentosa							SPITOM	SPITOM	SPITOM	SPITOM
Populus deltoides										POPDEL
	1	2	3	4	5	6	7	8	9	10
			Pine Canopy					Wetpanne		

Pinus nigra Wetpanne

Pinus nigra	PINNIG									
Chimaphila maculata	CHIMAC	CHIMAC								
Ammophila breviligulata	AMMBRE	AMMBRE								
Calamovilfa longifolia	CALLON	CALLON	CALLON	CALLON	CALLON					
Solidago sp.	SOLSP	SOLSP	SOLSP	SOLSP	SOLSP	SOLSP	SOLSP	SOLSP	SOLSP	SOLSP
Toxicodendron radicans		TOXRAD								
Prunus virginiana			PRUVIR				PRUVIR			
Pinus banksiana			PINBAN	PINBAN						
Hieracium sp.			HIESP	HIESP	HIESP	HIESP				
Juncus balticus				JUNBAL	JUNBAL	JUNBAL	JUNBAL	JUNBAL	JUNBAL	JUNBAL
Unidentified Poaceae					UKNPOA			UKNPOA	UKNPOA	
Cornus stolonifera						CORSTO	CORSTO	CORSTO		
Salix sp.						SALSP	SALSP	SALSP	SALSP	SALSP
Rubus sp.									RUBSP	
Fragaria virginiana										FRAVIR
	1	2	3	4	5	6	7	8	9	10
			Pine Canopy					Wetpanne		

Panicum virgatum and *Calamovilfa longifolia,* as well as the dune shrub *Hudsonia tomentosa*, were of high importance in sites lacking Austrian pines, while none of these species appeared in the list of species of high importance in pine sites until the border between pine and deciduous canopy, when *Panicum virgatum* attained this status. In Austrian pine sites, woody species such as *Sassafras albidum, Quercus sp.*, and *Acer sp.* were important, both under pine canopy and in the bordering deciduous canopy.

In wetpannes, many of the important species in jack pine sites, such as *Rumex acetosella, Spiraea tomentosa,* and two unidentified graminoids, were unimportant in Austrian pine sites (Table 3-5). In contrast, the shrubs *Cornus stolonifera* and *Salix sp.* were important in the wetpannes bordering Austrian pine canopy, but unimportant in Jack pine sites. Additionally, *Solidago sp.* was important throughout the transects in Austrian pine sites, but was present only under pine canopy in Jack pine sites. The flora of Jack and Austrian pine sites was quite different, and that of Austrian pine sites more closely resembled blowout vegetation.

Austrian pine canopy in inland blowouts provided a colonization site for the woody shrubs, *Prunus virginiana* and *Prunus pumila* , as well as the small evergreen forb, *Chimaphila maculata* which were unimportant in the bordering blowout (Table 3-6). *Andropogon scoparius* was equally important under canopy and in the bordering blowout, but the common blowout species *Hudsonia tomentosa*, *Ammophila breviligulata*, and *Lithospermum canescens* were only among the top five importance values in the bordering blowout.

Life form.-- The proportion of species of a particular life form varied across transects and in sites with and without pine (Figures 3-9 to 3-14). Generally, graminoids were reduced under pine canopy in all seral stages. In foredune cottonwood sites, only

Table 3-5. Top five important species in wetpanne sites along 20-m transect. Each number represents a 2-m interval, starting under pine canopy and ending 10m into native wetpanne vegetation.

Blowout at Forest Edge

	1	2	3	4	5	6	7	8	9	10
Andropogon scoparius	ANDSCO	ANDSCO	ANDSCO	ANDSCO	ANDSCO	ANDSCO		ANDSCO		
Ammophila breviligulata	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE	AMMBRE			
Panicum virgatum	PANVIR	PANVIR	PANVIR	PANVIR	PANVIR	PANVIR	PANVIR			
Calamovilfa longifolia	CALLON	CALLON	CALLON	CALLON	CALLON	CALLON	CALLON		CALLON	
Quercus sp.	QUESP					QUESP		QUESP	QUESP	QUESP
Hudsonia tomentosa		HUDTOM	HUDTOM	HUDTOM	HUDTOM					HUDTOM
Vitis riparia							VITRIP	VITRIP		
Sassafras albidum							SASALB		SASALB	SASALB
Solidago sp.								SOLSP	SOLSP	SOLSP
Unidentified Poacae								UNKPOA	UNKPOA	UNKPOA
			Blowout Vegetation					Deciduous Forest		

Pinus nigra Forest Edge

	1	2	3	4	5	6	7	8	9	10
Acer sp.	ACESP	ACESP					ACESP			
Pinus nigra	PINNIG		PINNIG							
Chimaphila maculata	CHIMAC		CHIMAC							
Pteridium aquilinum	PTEAQU	PTEAQU	PTEAQU	PTEAQU	PTEAQU			PTEAQU	PTEAQU	PTEAQU
Quercus sp.	QUESP	QUESP	QUESP	QUESP	QUESP	QUESP	QUESP	QUESP	QUESP	QUESP
Celastrus scandens		CELSCA								
Sassafras albidum		SASALB	SASALB	SASALB	SASALB	SASALB	SASALB	SASALB	SASALB	SASALB
Unidentified Poacae				UNKPOA		UNKPOA				
Vitis riparia				VITRIP	VITRIP					
Panicum virgatum					PANVIR	PANVIR	PANVIR	PANVIR		
Smilacina stellata						SMISTE				
Cornus stolonifera							CORSTO		CORSTO	
Prunus virginiana								PRUVIR	PRUVIR	PRUVIR
Solidago sp.										SOLSP
			Pinus nigra Canopy					Deciduous Forest		

Table 3-6. Top five important species in inland blowout sites along 20-m transect. Each number represents a 2-m interval, starting under pine canopy and ending 10m into blowout vegetation. Data from 1994.

Pinus nigra in Inland Blowouts

	1	2	3	4	5	6	7	8	9	10
Prunus virginiana	PRUVIR									
Pinus niga	PINNIG	PINNIG	PINNIG	PINNIG						
Unidentified Poacae	UNKPOA			UNKPOA	UNKPOA					
Chimaphila maculata	CHIMAC	CHIMAC	CHIMAC	CHIMAC	CHIMAC					
Andropogon scoparius*	ANDSCO	ANDSCO	ANDSCO	ANDSCO	ANDSCO	ANDSCO	ANDSCO	ANDSCO	ANDSCO	ANDSCO
Panicum virgatum*		PANVIR						PANVIR		PANVIR
Solidago sp.		SOLSP								
Prunus pumila			PRUPUM							
Calamovilfa longifolia*			CALLON	CALLON		CALLON	CALLON	CALLON	CALLON	CALLON
Arabis lyrata					ARALYR	ARALYR				
Panicum sp.					PANSP	PANSP	PANSP			
Hudsonia tomentosa						HUDTOM		HUDTOM	HUDTOM	HUDTOM
Coryspermum hyssopifolium							CORHYS			
Ammophila breviligulata*							AMMBRE	AMMBRE	AMMBRE	AMMBRE
Lithospermum canescens									LITCAN	
Artemesia campestris*										
			Pinus nigra Canopy					Blowout Vegetation		

* Five most important species in blowouts lacking Pinus nigra

three life forms were present, and all portions of the transects were dominated by graminoids (Figure 3-9a). In Austrian pine foredune sites, evergreens, shrubs and vines were also present, though not abundant (Figure 3-9b). Graminoids made up an increasingly larger portion of the understory cover under pine canopy with increasing proximity to the interface with foredune vegetation, and then dominated the understory beyond the canopy.

In the forest edge seral stage, life form distribution differed most among sites with and without Austrian pine. In sites lacking Austrian pine, graminoids made up the largest portion of the understory cover until eight meters into the deciduous canopy, where they were replaced by forbs (Figure 3-10). Additionally, deciduous tree species and shrubs increased under deciduous canopy. In Austrian pine sites, little change in life form distribution took place across the transect (Figure 3-11). Deciduous tree species were the dominant life form throughout, and were exceeded only by graminoids at the junction of pine and deciduous canopies. Forbs made up approximately ten percent of the understory throughout, but shrubs increased slightly under deciduous canopy.

In Jack pine wetpanne sites, forbs were much more prevalent than graminoids under pine canopy, and they decreased closer to the wetpanne (Figure 3-12). In contrast, graminoids made up the greatest proportion of the understory vegetation in Austrian pine wetpanne sites. Additionally, in the wetpannes bordering Austrian pine canopy, shrubs made up a much greater proportion of the vegetation than in Jack pine wetpanne sites (Figure 3-13).

In inland blowouts, graminoids increased across the transect, while forbs decreased (Figure 3-14). Understory cover was much more evenly distributed among life forms under Austrian pine canopy than in the open blowout.

Similarity.-- In foredune cottonwood sites, understory vegetation under cottonwood canopy differed little from that in the bordering foredune (83-99.8% similarity, Figure 3-15a). This contrasted sharply with foredune pine sites, where the similarity of vegetation under pine canopy to that present 8-10 m from the canopy edge was only 5 - 54% (Figure 3-15b). Once beyond the pine canopy, however, similarity to the final 2-m interval was high (89 - 94%).

In forest edge sites without pine, species similarity with the first interval was more than 50% until the fourth meter into deciduous canopy (Figure 3-16a). The transition to a different flora did not occur until the sixth meter into deciduous canopy, where similarity to the final interval exceeded 30%. This pattern was quite different from that of forest edge pine sites (Figure 3-16b). The middle four meters of these transects appeared to have a different flora than either of the extremes, as exemplified by the low similarity of these intervals to either the first or final interval of the transect.

Measures of similarity in wetpanne sites differed for Jack and Austrian pine sites as well (Figure 3-17). Species composition under Jack pine canopy was much more similar to that of the final two meters of the transect (8 - 46%) than under Austrian pine canopy in Austrian pine sites (2 - 15%). In addition, similarity within Jack pine wetpannes beyond pine canopy was higher than that within Austrian pine wetpannes (67 - 74% vs. 41 - 61%).

Species composition in inland blowout sites differed dramatically from that under pine canopy (4-11% similarity to the first interval, Figure 3-18). Additionally, the middle six meters of the transect was quite different than either of the extremes, suggesting that this community was populated by different species than either the core of the canopy or the core of the blowout.

Woody species: stem density and size structure.--

Forest edges.-- Mean stem density of woody species ≥1cm dbh was 2.5 to 3.5 times higher under pine canopy than in the comparable blowouts lacking pine, adjacent to native forest (Table 3-7). In addition, a wider range of species was represented in pine sites (Figure 3-19, 3-20). In the 5m abutting native deciduous forest vegetation in forest edge sites where *P. nigra* was present, five different woody species were represented in size classes ≥1cm dbh. Of the three species represented in sites lacking pines, one, *Populus deltoides*, is found only very rarely in mature deciduous forest vegetation. In the first 5m under deciduous canopy, six species were present in sites with pine and three in sites without pine. By the final 5m under native deciduous canopy, eight species were present in size classes beyond the seedling stage in sites with and without pine.

Table 3-7. Mean stem density (# stems/m^2) ± SE (n=10) of all woody species ≥1cm DBH across four 5-m intervals in forest edge and wetpanne seral stages. Data from 1994-1996.

	Transect Interval*			
	1	2	3	4
Forest Edge Austrian pine	0.14 ± 0.04	0.19 ± 0.05	0.16 ± 0.04	0.41 ± 0.10
Forest Edge Lacking pine	0.04 ± 0.02	0.08 ± 0.04	0.13 ± 0.05	0.37 ± 0.10
Wetpanne Austrian pine	0.20 ± 0.05	0.18 ± 0.07	1.12 ± 0.05	0.34 ± 0.13
Wetpanne Jack pine	0.65 ± 0.09	0.50 ± 0.10	0.13 ± 0.05	0.21 ± 0.09

* 1= first 5m under pine or in blowout, 2= 5m abutting deciduous forest or wetpanne, 3=5m deciduous forest or wetpanne abutting pine or blowout, 4= last 5m in deciduous forest or wetpanne.

Size structure data for two species, *Quercus sp.* and *Sassafras albidum*, indicate that the seedling component of these populations was 2.5 to 16 times greater in sites where Austrian pines were present (Table 3-8). The representation of individuals ≥1cm dbh was only slightly higher under Austrian pine canopy than in blowouts abutting deciduous forest. In the first five meters of the adjacent deciduous forest, however, the populations of *Quercus* in size classes other than seedlings in Austrian pine sites are double those of sites without Austrian pine. The non-seedling portion of *S.albidum* populations is only half that in sites without Austrian pine in the first 5m under deciduous canopy, but these proportions are reversed in the final 5m of the transect, where 14 individuals are present in Austrian pine sites as compared to the seven in sites lacking Austrian pine.

Table 3-8. Size structure of two tree species in 5-m intervals across transects in forest edge sites with and without Austrian pine. Values represent number of individuals in each DBH class. Data from 1994 and 1996.

	Aust. pine sites					Sites lacking Aust. pine					
	DBH class*					DBH class					
Transect Interval**	S	1	2	3	4	S	1	2	3	4	5
Quercus sp.											
1	55	1	0	0	0	13	1	0	0	0	0
2	55	1	0	0	1	7	2	0	0	0	0
3	59	2	0	1	3	7	1	2	0	0	0
4	137	1	2	2	3	40	1	1	2	5	1
Sassafras albidum											
1	10	0	0	0	0	0	0	0	0	0	0
2	48	0	1	0	0	3	0	0	0	0	0
3	121	2	1	0	0	22	7	0	0	0	0
4	136	3	5	5	1	59	4	3	0	0	0

*DBH classes: S= seedling (<1cm DBH), 1= 1-2.4cm, 2= 2.5-4.9cm, 3= 5-9.9cm, 4= 10-19.9cm, 5= >20cm

**Transect intervals: 1= first 5m under pine or in blowout, 2= 5m abutting deciduous forest, 3=5m deciduous forest abutting pine or blowout, 4= last 5m in deciduous forest.

Wetpannes.--In Jack pine wetpanne sites, the density of woody species ≥1cm DBH decreased along the gradient into wetpannes and reached its lowest point in the first five meters of the wetpanne (0.13 / m^2, Table 3-7). The pattern in Austrian pine sites was quite different, however; stem density was very low under pine canopy and increased nearly tenfold in the first five meters of the wetpanne, due to the high stem density of *Salix sp.* (0.9/m^2, Figure 3-22). The number of species represented in the shrub/tree layer was highest (four) in the center of the wetpanne in both Jack and Austrian pine sites (Figure 3-21, 3-22).

Pinus banksiana seedlings did not occur in the first 5m interval under Jack or Austrian pine canopy, but increased from that point on into the wetpanne proper in Austrian pine sites (Table 3-9). Seedling population sizes reached their peak before the wetpanne in Jack pine sites and decreased in the wetpanne proper. Individuals $\geq$1cm dbh were most prevalent in the Jack pine stand and were reduced to 1/8 that number in the wetpanne proper. Sapling populations reached their peak in the wetpanne in Austrian pine sites.

Table 3-9. Size structure of *Pinus banksiana* across transects in Austrian and Jack pine wetpannes. Values represent number of individuals in each DBH class. Data from 1995.

	Aust.	pine	sites			Jack	pine	sites		
		DBH	class*				DBH	class		
Transect Interval**	S*	1	2	3	4	S	1	2	3	4
P. banksiana										
1	0	0	1	1	3	0	15	5	24	12
2	23	2	1	1	0	41	7	13	10	12
3	45	2	5	2	0	31	2	2	0	1
4	50	2	4	0	1	32	1	1	0	0

*DBH classes: S=seedling (<1cm DBH), 1= 1-2.4cm dbh, 2= 2.5-4.9cm, 3= 5-9.9cm, 4= 10-19.9cm, 5= >20cm

**Transect intervals: 1= first 5m under pine, 2= 5m abutting wetpanne, 3=5m wetpanne abutting pine, 4= last 5m in wetpanne.

Disturbance regime: sand movement

Average erosion ranged from no erosion in forest edge sites lacking pine to 3.9cm on the leeward edges of inland blowout *P. nigra* stands (Table 3-10). Sand accumulation ranged from 1.8cm in leeward *P. deltoides* stands in foredunes and in forest edges lacking pine to 3.6cm at leeward edges of inland blowouts. There was a general trend of accretion from 1994 to 1995, only leeward inland blowout *P. nigra* stands had more stakes losing sand than gaining.

Number of stakes gaining, losing and stable varied across seral stages around *P. nigra* stands ($X^2_{4,231}$=13.41, p=0.009). Sand movement patterns did not vary within stage among *P. nigra* stands and sites without pine (foredune $X^2_{2,104}$=0.44, p=0.80; forest edge $X^2_{2,86}$=1.22, p=0.54; inland blowout $X^2_{2,58}$=1.66, p=0.44), nor did they vary among *P. nigra* and *Populus deltoides* stands in foredunes ($X^2_{2,130}$=2.82, p=0.245).

Furthermore, leeward to windward sand movement patterns did not vary in foredune and forest edge pine stands, but proportionally more stakes were gaining sand on windward sides of both foredune *Populus deltoides* and *P. nigra* stands in inland blowouts ($X^2_{2,32}$=5.31, p=0.005; $X^2_{2,48}$=7.56, p=0.02).

Abiotic effects of P. nigra

Light intensity.-- Light intensity was greatly reduced under Austrian pine canopy cover in all four seral stages (Figures 3-23, 3-24). In foredune stands, light intensities were 1.5 to six times higher under cottonwood canopy than under pine, but were the same in the bordering foredune vegetation (Figures 3-23a). Light intensity under cottonwood cover was 25 to 91% that of mean values in neighboring vegetation, however.

In forest edge transects with pine, light intensity was consistently low under both pine and deciduous canopy and ranged from only 14 to 123 microeinsteins*m-^{2}*s^{-1}

Table 3-10. Sand movement around pine stands in three seral stages during the period of 1994-1995.

Site Type	Stake Location	Avg cm overall	Avg cm loss	Avg cm gain	% Losing	% Stable	% Gaining	n
Foredune								
No Pine		1.3	-1.0	1.9	10.0	30.0	60.0	10
P. nigra	leeward	1.9	-1.5	2.9	16.7	27.1	56.3	48
P. nigra	windward	1.4	-1.6	2.1	18.0	34.0	48.0	50
Populus deltoides	leeward	1.2	-1.6	1.8	22.2	33.3	44.4	18
Populus deltoides	windward	2.4	-2.3	2.4	16.7	0.0	83.3	18
Forest Edge								
No Pine		1.2	0.0	1.8	9.3	14.0	76.7	3
P. nigra	leeward	2.0	-1.5	2.4	20.5	20.5	59.1	43
P. nigra	windward	2.3	-1.4	3.3	0.0	33.3	66.7	44
Inland Blowout								
No Pine		2.0	-2.0	2.1	18.5	25.9	55.6	10
P. nigra	leeward	2.8	-3.9	3.6	52.0	8.0	40.0	27
P. nigra	windward	2.5	-2.9	2.4	20.0	10.0	70.0	25

(Figure 3-23b). In forest edge sites lacking pine, however, light intensities gradually decreased with proximity to the deciduous canopy (1670 to 88 microeinsteins*m-^{2}*s^{-1}), but were still seven times higher than in *P. nigra* forest edge transects at five meters into the deciduous forest vegetation. Light intensity was up to 58 times higher in sites without Austrian pine than in sites with pines in the forest edge seral stage.

Light intensity was reduced under both Jack pine and Austrian pine canopy in wetpanne sites, but was still 1.2 to 4.8 times higher under Jack pines (Figure 3-24a). In addition, light intensities in Austrian pine sites did not equal those in Jack pine sites until eight meters from the edge of pine canopy.

In inland blowout sites (Figure 3-24b), light intensity was very low under pine canopy, but increased 20-fold by the third meter from the canopy edge.

Solum thickness.--Soil development was four and 11 times greater under pine canopy (P) in foredunes and blowouts, respectively, than it was in the bordering native vegetation (N) (Table 3-11). Solum thickness under cottonwood (7.3 ± 2.1 cm) also exceeded that of the area bordering the stand (4.3 ± 1.0 cm). In wetpanne and forest edge sites, however, solum thickness did not differ significantly between Austrian pine canopy and bordering vegetation.

In comparing sites with and without Austrian pine within seral stages, only forest edge sites differed in solum thickness (Table 3-11). Soil was far less developed in sites lacking pine than in sites where pines had been planted, and a significant interaction term indicates that P and N solum thickness varied among sites with and without Austrian pine.

Soil pH.-- The highest pH of the top 5 cm of soil was found in the foredune sites under pine and cottonwood stands with pH up to 7.8 (Table 3-12). The lowest pH values were found in wetpanne sites, under both Austrian and Jack pine canopy (4.3 and 3.9, respectively). In addition, pH values of 4.2 were seen under deciduous canopy bordering Austrian pine and under Austrian pine canopy in inland blowout sites. Minimum pH is lower under pine canopy than under bordering vegetation in foredune, wetpanne, and inland blowout seral stages. In forest edge sites, however, minimum pH is lower under

Table 3-11. Solum thickness in four seral stages under canopy and in bordering vegetation. Significance of main effects and interactions in two-way ANOVA for each within-seral stage comparison is shown. Data from 1995-1996.

	Bordering Vegetation (N)		Pine, Cottonwood, or Lacking Pine (P)		Two-Way-ANOVA Significance		
Seral Stage and Stand Type (A/C)	Mean Solum Thickness (cm) ± s.e.	n	Mean Solum Thickness (cm) ± s.e.	n	(A/C)*	(P/N)**	A/C* P/N
(A) Foredune Austrian Pine	1.8 ± 0.5	5	7.6 ± 1.9	5	NS	0.01	NS
(C) Foredune Cottonwood	4.3 ± 1.0	4	7.3 ± 2.1	4			
(A) Forest Edge Austrian Pine	8.0 ± 1.3	5	8.7 ± 0.5	5	0.001	NS	0.055
(C) Forest Edge Lacking Austrian Pine	5.8 ± 1.5	5	1.6 ± 1.1	5			
(A) Wetpanne Austrian Pine	8.1 ± 0.2	3	9.9 ± 2.7	3	NS	NS	NS
(C) Wetpanne Jack Pine	12.1 ± 2.1	3	8.6 ± 3.2	3			
(A) Inland Blowout Austrian Pine	0.6 ± 0.2	4	6.8 ± 0.7	4		0.00002	

* A=Austrian pine sites, C= sites without Austrian pine

** P=Under pine or cottonwood canopy, or open blowout bordering native deciduous forest, N=in native vegetation bordering Austrian pines, cottonwoods, or native deciduous forest.

Table 3-12. Minimum, median, and maximum pH in four seral stages. Data from 1995.

	Bordering Vegetation (N)**				Pine, Cottonwood, or Lacking Pine (P)**			
Seral Stage and Stand Type (A/C)*	Min pH	Median pH	Max pH	n	Min pH	Median pH	Max pH	n
Foredune Austrian Pine	6.0	6.9	7.4	9	5.4	6.8	7.8	9
Foredune Cottonwood	6.4	6.8	7.1	5	6.9	7.6	7.8	6
Forest Edge Austrian Pine	4.2	6.1	6.9	9	4.5	5.2	6.2	9
Forest Edge Lacking Pine	5.0	5.4	7.3	9	4.6	5.8	7.5	9
Wetpanne Austrian Pine	4.9	6.2	6.6	9	4.3	5.1	7.1	9
Wetpanne Jack Pine	4.9	5.7	6.6	9	3.9	4.9	6.4	9
Inland Blowout Austrian Pine	4.9	5.4	6.0	9	4.2	5.0	6.4	9

* A=Austrian pine sites, C= sites without Austrian pine

** P=Under pine or cottonwood canopy, or open blowout bordering native deciduous forest, N=in native vegetation bordering Austrian pines, cottonwoods, or native deciduous forest.

the bordering deciduous vegetation (4.2) than under the pine canopy (4.5).

Soil moisture.--Repeated-measure MANOVA showed a significant site type effect in foredunes and wetpannes (Tables 3-13 to 3-15). *Pinus nigra* sites were drier than *P. banksiana* sites in wetpannes, while *P. nigra* sites had higher soil moisture than *Populus deltoides* sites in foredunes (Figures 3-25 to 3-26). Soil moisture was higher under canopy than in the bordering vegetation in foredune and inland blowout sites, but the reverse was true in wetpanne sites. Time effect was significant only in foredunes, where soil moisture decreased as the growing season progressed.

Biotic correlations with light intensity.-- Understory cover was highly positively correlated with light intensity in wetpannes, inland blowouts and in foredune Austrian pine sites (rho= 0.53 to 0.68; Table 3-16), but was not correlated with light intensity in foredune cottonwood sites. Within seral stages, correlations between understory cover and light intensity were stronger for sites with Austrian pine than those without.

The association between two measures of species diversity (species richness and Simpson's index) and light intensity were not as strong as those between light intensity and understory cover. Species diversity decreased with increasing light intensity in both forest edge site types and in foredune Austrian pine sites, but was positively correlated with light intensity in all other circumstances.

Table 3-13. Repeated measure MANOVA for foredune soil moisture across the 1995 growing season.

Source	Wilks Lambda	Exact F	DF Num	DF Den	Prob>F
Between Subjects					
A/C*	0.313	13.1468	1	6	0.0110
P/N**	0.131	39.5245	1	6	0.0008
A/C*P/N	0.524	5.4448	1	6	0.0584
Site(A/C)	0.318	2.1492	6	6	0.1870
All Between	0.066	9.5065	9	6	0.0063
Intercept	0.045	126.5514	1	6	<.0001
Within Subjects					
Time	0.071	17.3738	3	4	0.0093
Time*A/C	0.238	4.2681	3	4	0.0974
Time*P/N	0.489	1.3936	3	4	0.3667
Time*A/C*P/N	0.371	2.2607	3	4	0.2235
Time*Site(A/C)	0.116	0.7464	18	11.799	0.7206
All Within Interactions	0.018	1.3460	27	12.324	0.2980

* A=Austrian pine sites, C= cottonwood sites

** P=Under pine or cottonwood canopy, N=in native vegetation bordering Austrian pines or cottonwoods.

Table 3-14. Repeated measure MANOVA for wetpanne soil moisture across the 1995 growing season.

Source	Wilks Lambda	Exact F	DF Num	DF Den	Prob>F
Between Subjects					
All Between	0.104	4.9130	7	4	0.0715
Intercept	0.078	47.2011	1	4	0.0024
A/C*	0.275	10.5204	1	4	0.0316
P/N**	0.224	13.8291	1	4	0.0205
A/C*P/N	0.430	5.2993	1	4	0.0828
Site(A/C)	0.458	1.1856	4	4	0.4365
Within Subjects					
All Within Interactions	0.013	1.0681	21	6.293	0.5068
Time	0.183	2.9770	3	2	0.2615
Time*A/C	0.243	2.0743	3	2	0.3417
Time*P/N	0.244	2.0665	3	2	0.3426
Time*A/C*P/N	0.226	2.2877	3	2	0.3186
Time*Site(A/C)	0.120	0.5704	12	5.583	0.8059

* A=Austrian pine sites, C= sites without Austrian pine

** P=Under pine canopy, N=in native vegetation bordering pines,

Table 3-15. Repeated measure MANOVA for soil moisture in inland blowout sites across the 1995 growing season.

Source	Wilks Lambda	Exact F	DF Num	DF Den	Prob>F
Between Subjects					
All Between	0.2470928	12.1883	1	4	0.0251
Intercept	0.0476379	79.9668	1	4	0.0009
P/N*	0.2470928	12.1883	1	4	0.0251
Within Subjects					
All Within Interactions	0.1647099	3.3809	3	2	0.2366
Time	0.3448	1.2668	3	2	0.4697
Time*P/N	0.1647099	3.3809	3	2	0.2366

* P=Under pine canopy, N=in native vegetation bordering Austrian pines.

Table 3-16. Correlations between light intensity and understory cover, species richness/2m^2, and Simpson's diversity index in four seral stages. Values are Spearman's rho. Data from 1994-1996.

Seral Stage and Stand Type	Understory rho	p	Richness rho	p	Simpson's rho	p	n
Foredune Austrian Pine	0.53	****	-0.30	**	-0.23	*	94
Foredune Cottonwood	-0.24	NS	0.33	*	0.33	*	40
Forest Edge Austrian Pine	0.34	**	-0.19	NS	-0.33	**	60
Forest Edge Lacking Pine	0.25	**	-0.31	***	-0.25	**	118
Wetpanne Austrian Pine	0.68	****	0.53	****	0.442	****	200
Wetpanne Jack Pine	0.57	****	0.39	****	0.24	***	200
Inland Blowout Austrian Pine	0.65	****	0.54	****	0.52	****	89

* $0.01 < p \leq 0.05$, ** $0.001 < p \leq 0.01$, *** $0.0001 < p \leq 0.001$, **** $p \leq 0.0001$

DISCUSSION

Geomorphological effects: Disturbance regime

The *P. nigra* trees were planted in 1956-1972 at SDSP to stabilize the shifting sand. According to the results presented here, however, sand movement patterns did not vary in areas with Austrian pines compared to areas without pines within each seral stage. The sites sampled showed slight overall accumulation, but the presence of the pines did not appear to significantly alter the sand movement patterns of the dune system. Buckley (1987) found a reduction in sand transport rate with increasing plant cover and with increasing k, as described by the following equation:

$$q = B\,[V(1-kC)-V_t]^3$$

where q is sand transport rate, B is Bagnold's constant, V is wind velocity, k is a constant dependent upon plant geometry, C is percent plant cover, and V_t is threshold wind velocity. Though the constant for the geometry of the pines (k) would be expected to be larger than that of typical dune plants in foredune, inland blowout and forest edge sites, vegetation cover tends to be reduced around the pine stands, and this may account for the lack of difference in sand movement patterns in areas with and without pine. It is important to consider the changes in sand movement patterns over the life span of the trees as well, because k and C will change as the pines grow taller and as vegetation surrounding them is gradually reduced. In addition, sand movement patterns may vary across years due to differences in climatic conditions and wind speeds, and the time period measured in this study may not necessarily be representative of those in the past. This information provides an argument against using Austrian pines as stabilizers of the dune system.

Population and community level effects

Foredunes.--The inhibition of understory cover under Austrian pine canopy in foredunes indicates that the changes in microenvironment brought about by the pines were unfavorable to the vegetation that normally occupies this dune habitat (Figures 3-3 and 3-4). The effect of pine upon community structure extended beyond the pine canopy since understory cover was inhibited relative to that of cottonwoods up to ten meters from the pine stand. At first glance, this inhibition of understory cover directly under Austrian pine canopy might be attributed to the 32-84% decrease in light intensity (Figure 3-23). The high correlation between light intensity and understory cover in pine sites and the absence of the same correlation in cottonwood sites in the foredunes, however, might be interpreted to suggest that a factor or suite of factors other than light (but correlated with light in Austrian pine sites) is responsible for reduced understory cover. It is also possible that a minimum level of light intensity is required by the understory vegetation. Because the light intensity under cottonwoods is 1.5-6.2 times higher than under pines, the grasses below cottonwoods may be receiving adequate light for growth even at the reduced levels relative to the light levels received by the vegetation beyond the canopy. Light intensity under pine canopy, however, may be too low to support the maintenance and growth of the understory. In addition, species that occur beneath the pine canopy are always in deep shade, whereas the deciduous habit of the cottonwoods would allow for full light intensities in the early growing season when grasses are first emerging.

Though establishment of typical foredune species was inhibited by the presence of Austrian pines, there was an increase in species richness in pine sites (Figure 3-5, Table 3-2). This suggests that the pines provided a microenvironment conducive to colonization by non-foredune species. Species that were normally competitively excluded by the dominant

Ammophila breviligulata, or limited by low soil moisture in typical foredune sites were then able to colonize the pine understory. The altered species composition under pines included a higher proportion of deciduous trees and shrubs absent from the cottonwood sites. This might suggest that the pines will accelerate the rate of ecological succession to forest. None of these young woody individuals had developed into saplings, however, perhaps because they had only just recently been dispersed to the site. More likely, they could not compete with the dominant pines beyond the seedling stage. If the latter is the case, the plant communities under the pines in foredunes will continue to be impoverished until the pines are removed.

Species composition beyond the pine canopy was also altered; *Calamovilfa longifolia*, a foredune species less tolerant of burial (Olson 1958), was of high importance under the pines and up to 10m beyond. This species did not occur in or around cottonwood stands. This suggests that sand movement was decreased by the presence of the pines and had encouraged the colonization of a species representative of a later stage of succession. The presence of buried A horizons in soil under the cottonwood canopy but not under pines also suggests a stabilizing effect of the pines across time, despite data to the contrary in 1994-1995 sand movement studies (Table 3-10).

Forest Edge.-- While the growth of understory cover did not increase under Austrian pine canopy in forest edge sites, it was only slightly suppressed relative to growth under native deciduous forest canopy (Figure 3-3b). Species richness and diversity were only slightly reduced under pine canopy relative to the deciduous forest as well (Table 3-2). The similarity of abiotic conditions under pines to those of the bordering deciduous forest may account for the similarity in understory cover and species diversity across transects; soils in both understories were developed to 8cm, soil pH was similar, though slightly lower in deciduous forest, and light intensities did not differ (Tables 3-11 and 3-12, Figure

3-23).

The effect of Austrian pine on plant community composition was least dramatic in forest edge sites. The relatively high similarity in species composition and life forms across most of the transect, was most likely a reflection of the similar abiotic conditions. The only place where the biotic composition varied was where the Austrian pine canopy met the forest canopy (Figure 3-16). Here, an increase in graminoids and a reduction in deciduous tree species was most likely due to an increase in light intensity where the two canopies met.

The Austrian pines appear to have created a microenvironment similar to that under deciduous canopy further into the blowouts, and tree and shrub species from the native forest have begun to colonize and establish under pine cover. Tree and shrub densities (Figure 3-7) indicate that native deciduous forest species were dispersing to and establishing under pine canopy. The size structure of these individuals (Table 3-8) suggests that *Quercus sp.* and *Sassafras albidum* were beginning to recruit into the sapling size class as well. *Sassafras albidum* is a clonal tree, which relies heavily upon vegetative reproduction to invade new areas (Bosela 1995). The root connection to the parent plant gives the new shoot the carbohydrate reserves it needs to become established under the shade of the pine canopy. In addition, this species has large leaves which may allow it to collect incident radiation at very low light levels (Bazzaz et al. 1972, Barnes and Wagner 1981). *Quercus* is a large-seeded species which benefits from extra food reserves present in the seed in early germination and establishment. Additionally, the frequent mammalian dispersal of acorns may allow for establishment further from the parent, as reflected by the large number of seedlings present 10-m distant from the native deciduous trees. Both of these characteristics may aid its entry into the understory of the introduced pine.

In sharp contrast, microenvironmental conditions and species composition of native blowout vegetation in forest edge sites lacking pine were quite different from the neighboring deciduous forest. Higher light intensity and decreased soil development may be responsible for the increased understory cover and greater prevalence of graminoids in these sites (Figures 3-3b, 3-10). *Quercus* and *S. albidum* seedlings were present, but in much lower numbers than in pine sites (Table 3-8). Population age structure of these species indicated that seedling recruitment was very low, and that recruitment into the sapling stage did not occur except under deciduous canopy. This suggests that either seeds were not dispersed to these sites or that predation and/or environmental conditions limited their germination and establishment.

The contrast between sites with and without pine provides evidence that Austrian pine plantings at the forest edge act to change the pattern of succession in areas that would otherwise be vegetated by blowout species.

Wetpannes.-- The wetpanne habitat provided an opportunity to compare the effects of the introduced pine with those of a native pine on abiotic and biotic components of the wetpanne. Both pines inhibited the growth of understory vegetation relative to the bordering wetpanne, but species richness and cover under Austrian pine canopy were much lower than under Jack pine (Figure 3-7,Table 3-2). Higher light intensities under Jack pine may be due to the narrower crowns of this species and to the age structure of the Jack pines; they circle the wetpanne in different heights with the shortest trees at the edge of the wetpanne and the tallest trees deeper into the stand. Both understory cover and richness are strongly positively correlated with light intensity (Table 3-16) indicating that higher light intensities may be responsible for the higher cover and diversity of the native stands . The Jack pine wetpannes occurred further from the beach than the Austrian pine wetpannes, however, which might suggest that they have had a longer time in which to develop a more diverse plant community.

Austrian pine sites were significantly drier than Jack pine sites (Table 3-25), and this may have contributed to the differences in the understories of the two site types. The shrubs *Cornus stolonifera* and *Salix sp.* made up a much larger component of wetpanne vegetation in Austrian pine sites (Figure 3-22), and more upland species such as *Solidago sp.* were more prevalent under the canopy and in the adjacent wetpanne than in Jack pine sites (Table 3-5). Though the differences in soil moisture and vegetation suggest that the Austrian pines are drying down the wetpannes, the initial conditions of these wetpannes is not known. It is possible that the sites where Austrian pines were planted were always drier than the Jack pine sites sampled. In studies of the effects of forestation on British dune systems, it was found that over a period of twenty to forty years, the water table was lowered in two dune systems planted with *P. nigra* var. *maritima* (Ovington 1950, Hill and Wallace 1989). It was unclear, however, whether this was a result of increased transpiration by the pines or of other factors.

The continued drying of the wetpannes may mean the successional replacement of unique dune communities as shrubs continue to encroach and the character of the sites changes. The wetpanne communities surrounded by Austrian pine are in a later stage of succession than those surrounded by Jack pine, but it is unclear if this is simply a response to initial conditions or a response to increased transpiration and a lowering of the water table by the introduced species.

Inland blowouts.-- As in other seral stages, understory cover and species richness were depressed under *P. nigra* canopy in inland blowouts, but the changes in microclimate encouraged colonization by non-blowout species, as in foredunes (Figures 3-4 to 3-8, Tables 3-6). Two- to 32-fold differences in light intensity were likely responsible for the decrease in cover (see Table 3-16 for correlation), while increased soil moisture under pine canopy might have encouraged the germination and colonization by the increased woody component of the vegetation (Figure 3-14). Woody species seed sources are quite a distance away, but the majority of the woody species present (*Prunus pumila, Prunus virginiana*) are bird-dispersed. The increased number of perching sites in pine stands relative to open dune habitat may account for increased dispersal to these sites. As in foredunes, the woody species that colonize the site under pine canopy have not recruited into the sapling class. Time lags in dispersal and/or competition with Austrian pines for moisture, nutrients, and light during establishment may limit recruitment into the sapling class. If the latter is the case, as is also possible in foredune sites, cover and species diversity will remain low until the pines are removed.

Assessment of Austrian pine effects

The actual outcome of Austrian pine introduction on each seral stage is summarized in Table 3-17. The growth of native species is facilitated only in forest edge sites, where blowout species are lost from the community and forest species successfully replace them.

Inhibition of native vegetation.--The presence of Austrian pines inhibited the growth of native vegetation in all four dune habitats (Table 3-17). Pine introductions have often been associated with a reduction in understory cover (Cowling et al. 1976, Hill and Wallace 1989, Richardson et al. 1989). Lugo (1992) found a 50% reduction in understory biomass in tropical pine plantations (*Pinus caribaea*) relative to secondary forests of similar age in Puerto Rico. Other introduced species have had similar effects. In eastern deciduous forests, Woods (1993) attributed a reduction in understory cover associated with an invasive shrub, *Lonicera tatarica*, to seasonal competition for light. At this site, evergreen herbaceous and vining or sprawling species were more abundant beneath the invader, suggesting that they were more tolerant of reduced light.

Enrichment or impoverishment of soils by conifers may also influence vegetation cover. In a serpentine system with poor soils, Chiarucci (1995) found increased understory cover under pine canopy accompanied an increase in organic matter content and an improved microenvironment for plant establishment. Generally, however, forestation with conifers alters soils by decreasing soil pH and levels of base cations (Ca, K, Mg), increasing exchangeable aluminum, and altering organic matter content, which may have negative consequences for the native vegetation in these sites (Ovington 1950, Wright 1958, Hill and Wallace 1989, Clough 1991, Chiarucci 1995).

Table 3-17. Actual outcome of *P. nigra* introduction and projected future trajectory of native dune populations in four seral stages at SDSP.

Potential Outcome	**Foredune**	**Wetpanne**	**Forest Edge**	**Inland Blowout**
1. Facilitate native species.	No	No	Native woody forest species successful	No
2. Inhibit native species.	Understory growth suppressed	Drying: Loss of cover and species diversity	Blowout species (graminoids) reduced, cover slightly lower	Loss of cover and species diversity
3. New colonists in new habitat.*	Unsuccessful: colonize but do not grow	Successful: Vigorous shrub growth in wetpanne	Successful: Deciduous tree growth under pine canopy	Unsuccessful: colonize but do not grow
Projected trajectory	Depauperate w/o gap formation	Loss of unique wetpanne flora	Facilitation of forest species	Depauperate w/o gap formation

* Includes native woody and other species not present in the dune communities adjacent to *P. nigra* stands.

Reduced species diversity.-- At SDSP, Austrian pines reduced species diversity in all dune habitats but the foredunes, where it was slightly increased. Species diversity has been shown to both decrease (Cowling et al. 1976, Richardson et al. 1989) and increase (Ovington 1950, Hill and Wallace 1989, Chiarucci 1995) under pine canopy, depending upon the initial conditions. In Great Britain, the new species entering a dune system forested with pines included those common in waysides and woodlands (Hill and Wallace 1989). Reduced light intensity may be associated with the decrease in diversity; species richness was negatively correlated with overstory cover in sclerophyllous communities in Australia (Sprecht and Sprecht 1989). Increased diversity under pine canopy may reflect a release from competition in communities dominated by one or several vigorous species disadvantaged by pine cover (Ovington 1950), or as a result of enrichment of poor soils (Chiarucci 1995).

Austrian pine and succession.--At SDSP, the presence of Austrian pines was associated with colonization by species not present in the adjacent dune communities (Table 3-17). In foredunes and blowouts, the increased woody component of the understory vegetation will not result in the eventual overtopping of the Austrian pines by native woody species because these individuals never transitioned beyond the seedling stage. Their presence in the seedling pool was not interpreted as an acceleration of ecological succession. The presence of Austrian pine at the edge of native deciduous forest, however, appeared to facilitate an invasion by native deciduous species which may eventually replace *P. nigra* as dominants in the community. In this dune habitat, the introduced pine accelerated the rate of succession. Austrian pines may have been responsible for the drying of wetpannes and the acceleration of succession in this seral stage, as represented by the increased shrub component in vegetation bordering the pines.

Conclusions

It is clear that the introduction of Austrian pine into the dune system has had serious consequences for community structure. The magnitude and direction of Austrian pine effects varies by seral stage, however, and this is a response to the interaction of the pines with the initial conditions of each dune habitat. Further experimental work will be necessary to elucidate the factors controlling these differences in the outcome of invasion, though relative development of soil and proximity to seed source may play an important role. The results of this study suggest that precautions must be taken in assuming uniformity of the effects of an invasive species on community structure. The consequence of invasion are likely to vary with initial conditions.

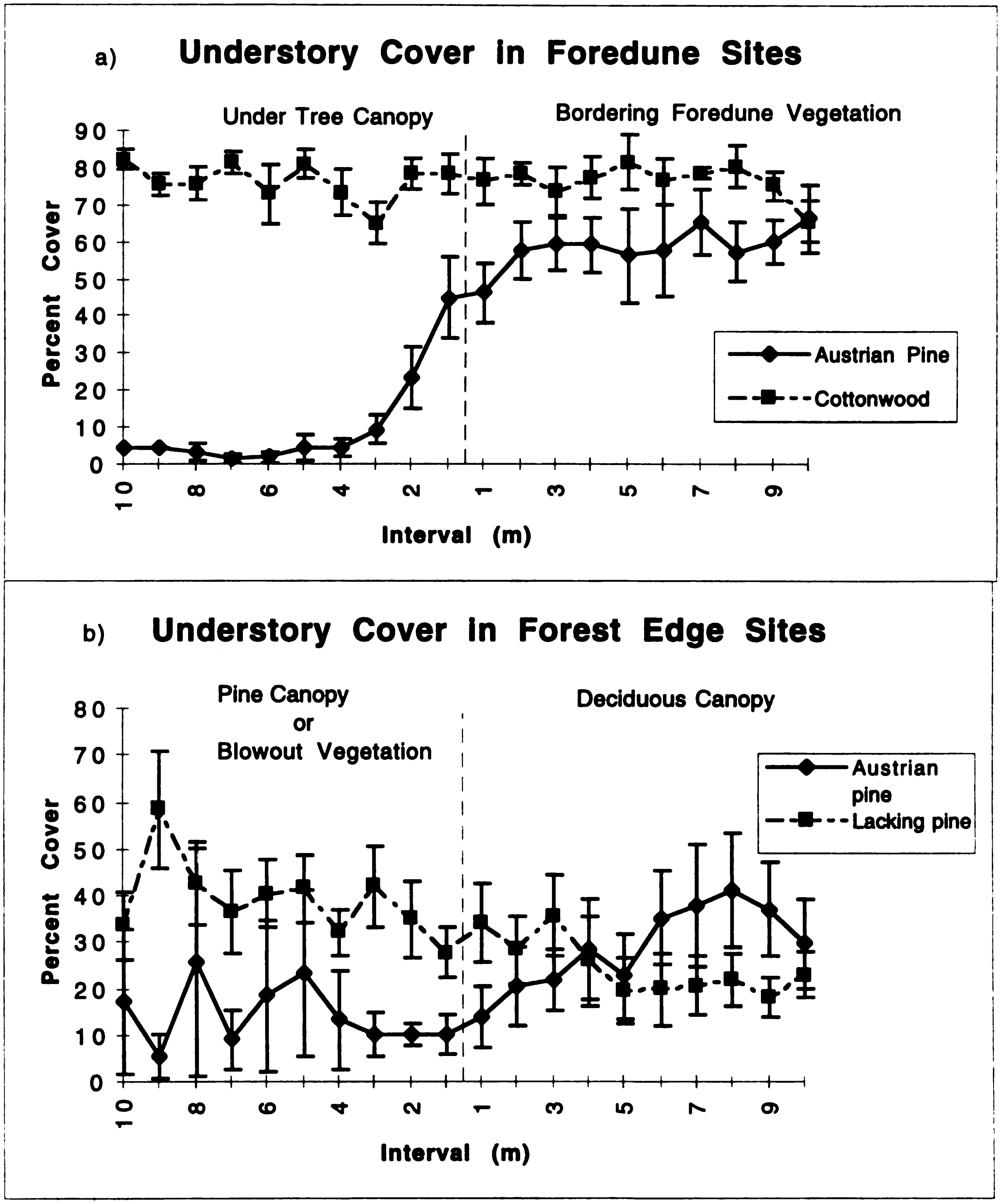
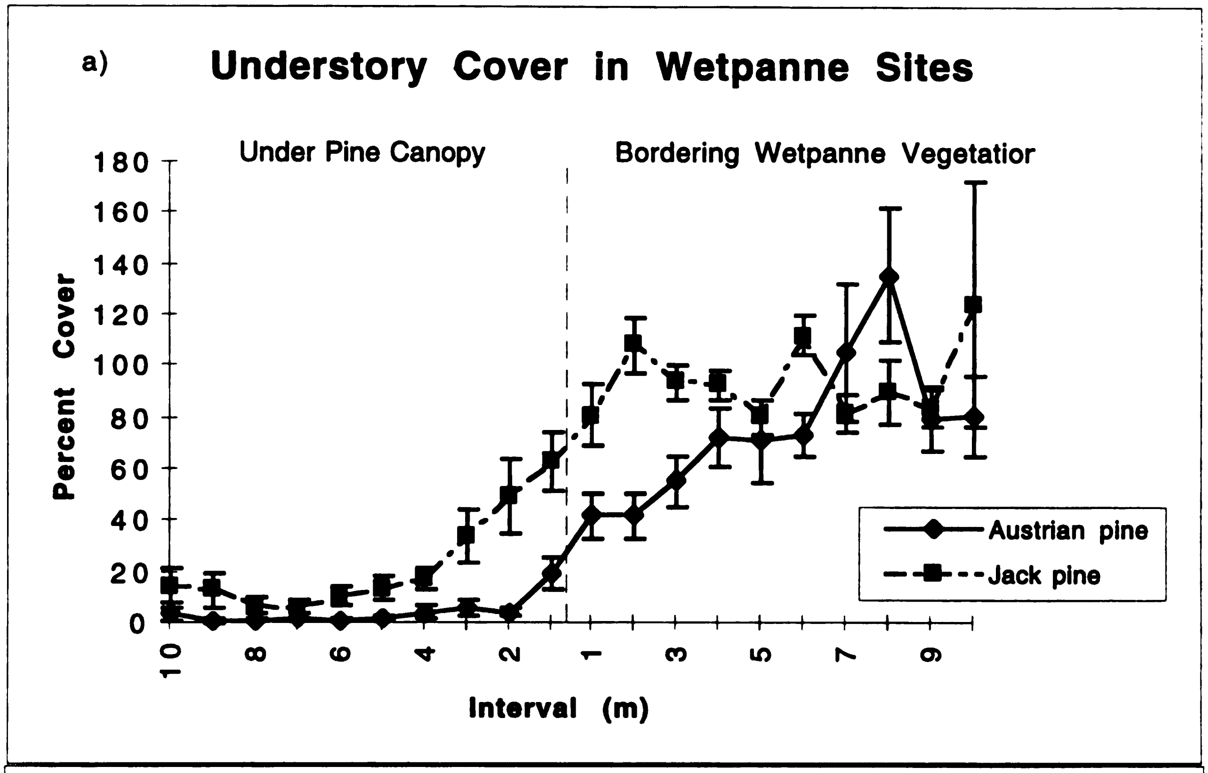


Figure 3-3. Understory cover ± SE in a) foredune sites with Austrian pine or Cottonwood and b) forest edge sites with and without Austrian pine. Data from 1994 and 1996.



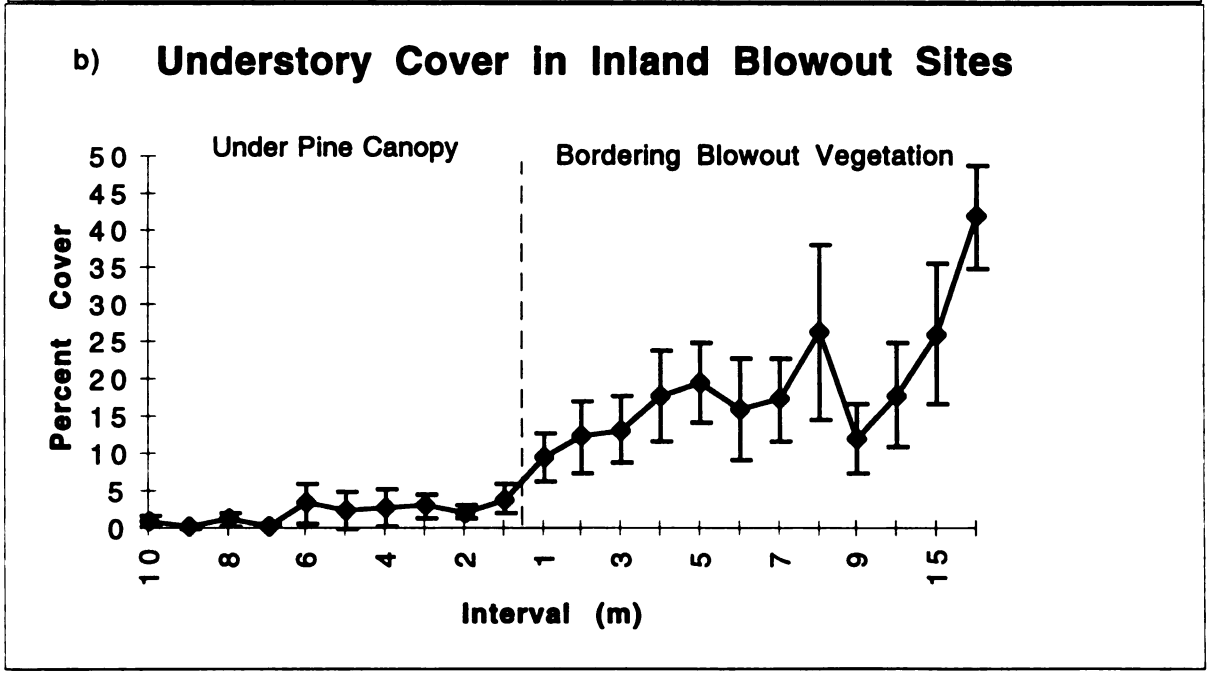


Figure 3-4. Understory cover ± SE in a) wetpanne sites with Jack or Austrian pine (1995 data) and in b) inland blowout sites with Austrian pine (1994 data).

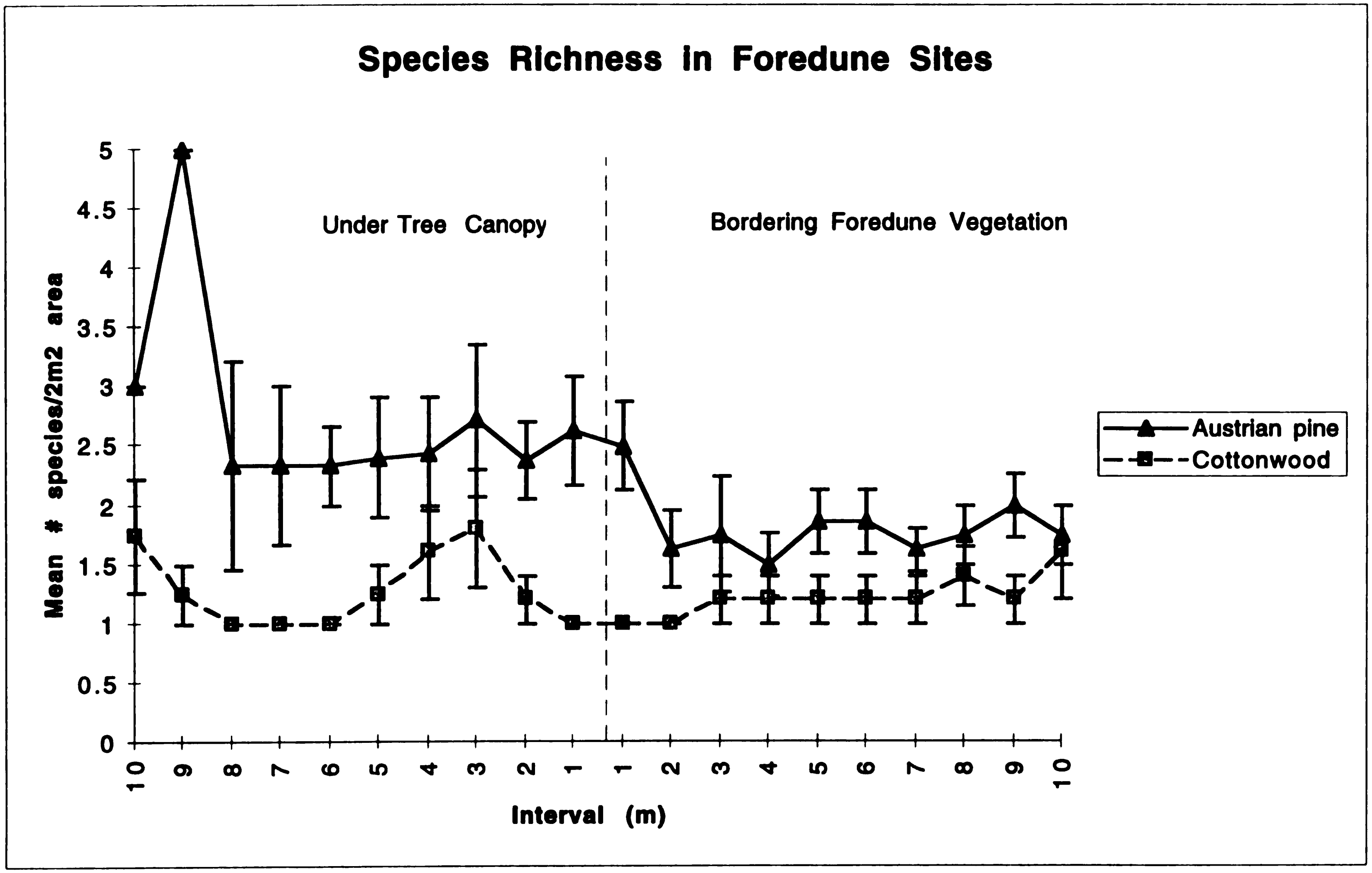


Figure 3-5. Mean species richness/2m^2 ±SE across 20-m transects in foredune sites with cottonwoods or Austrian pines. Data from 1994 and 1996.

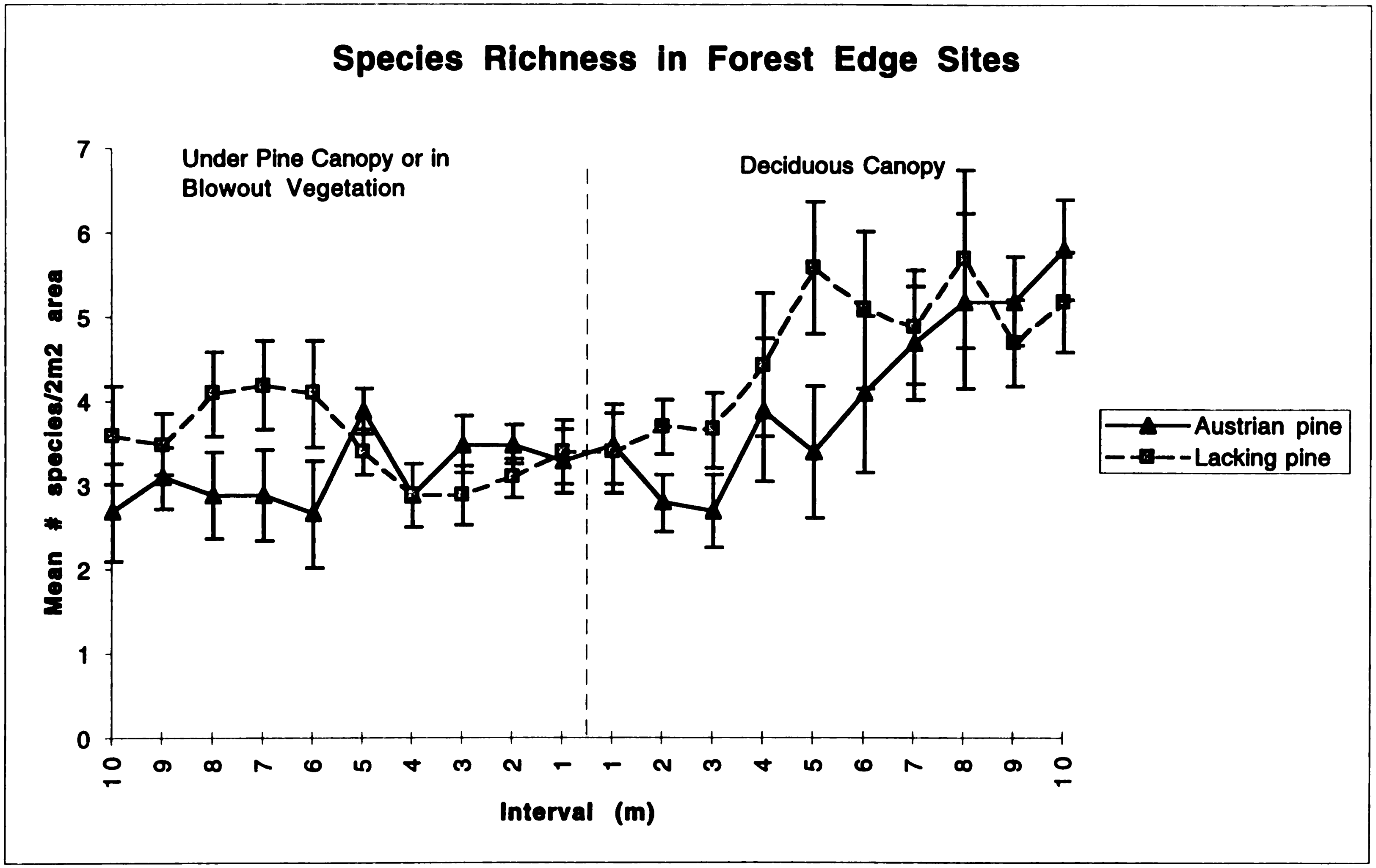


Figure 3-6. Mean species richness/2m² ±SE across 20-m transects in forest edge sites with and without Austrian pine. Data from 1994 and 1996.

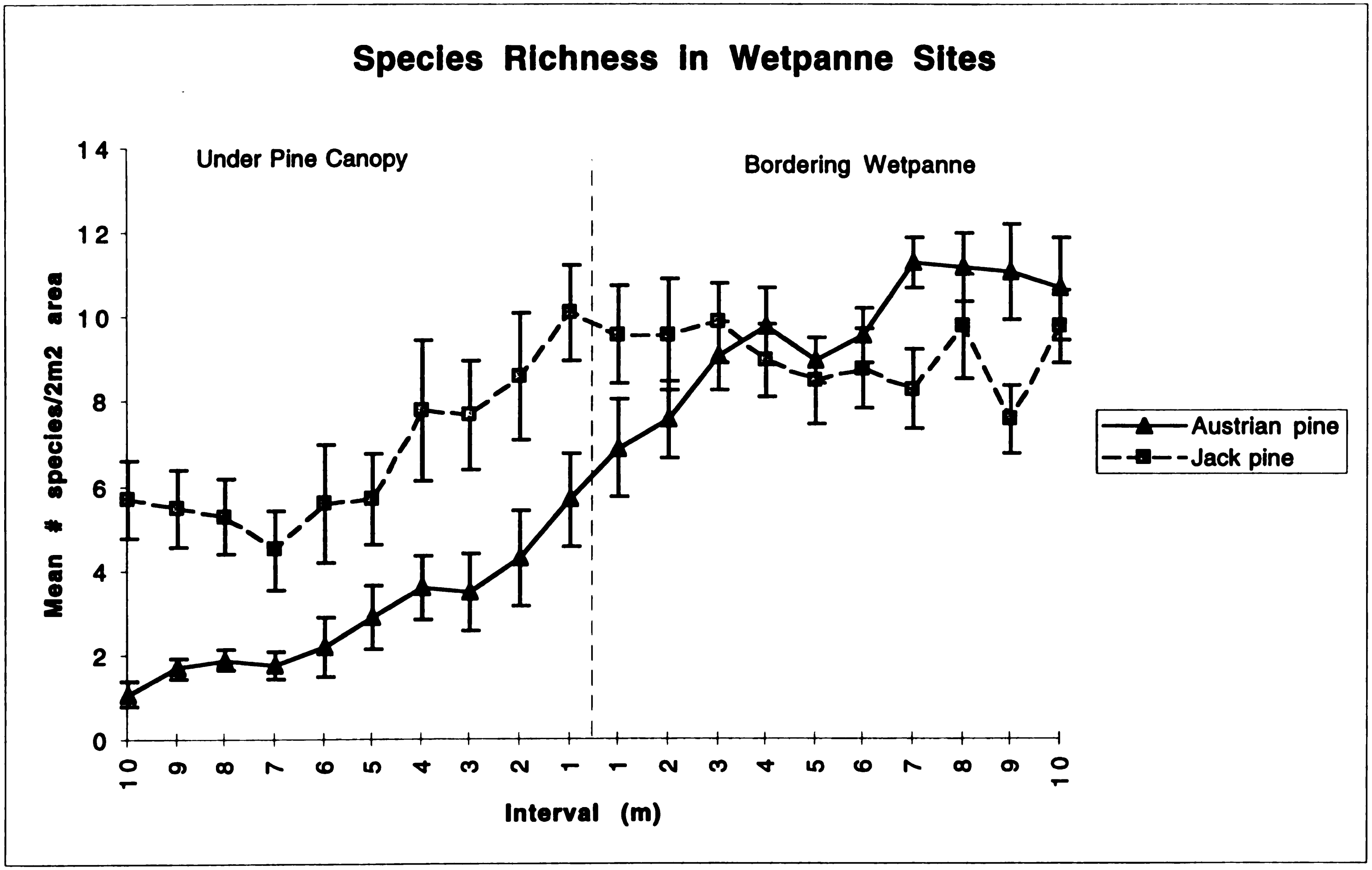


Figure 3-7. Mean species richness/$2m^2$ ±SE across 20-m transects in wetpanne sites with Jack or Austrian pines. Data from 1995.

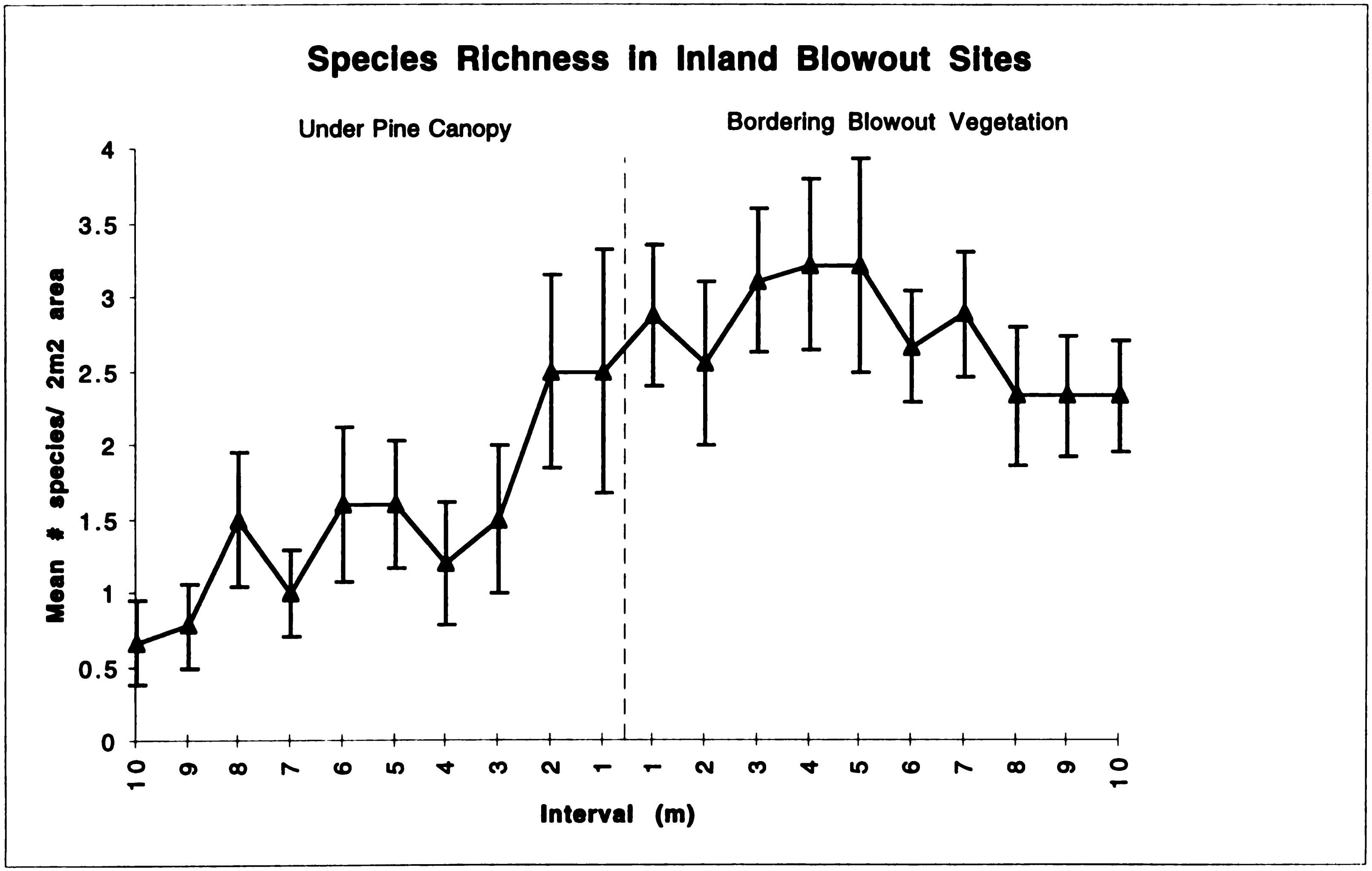


Figure 3-8. Mean species richness/$2m^2$ ±SE across 20-m transects in inland blowout sites planted with Austrian pine. Data from 1994.

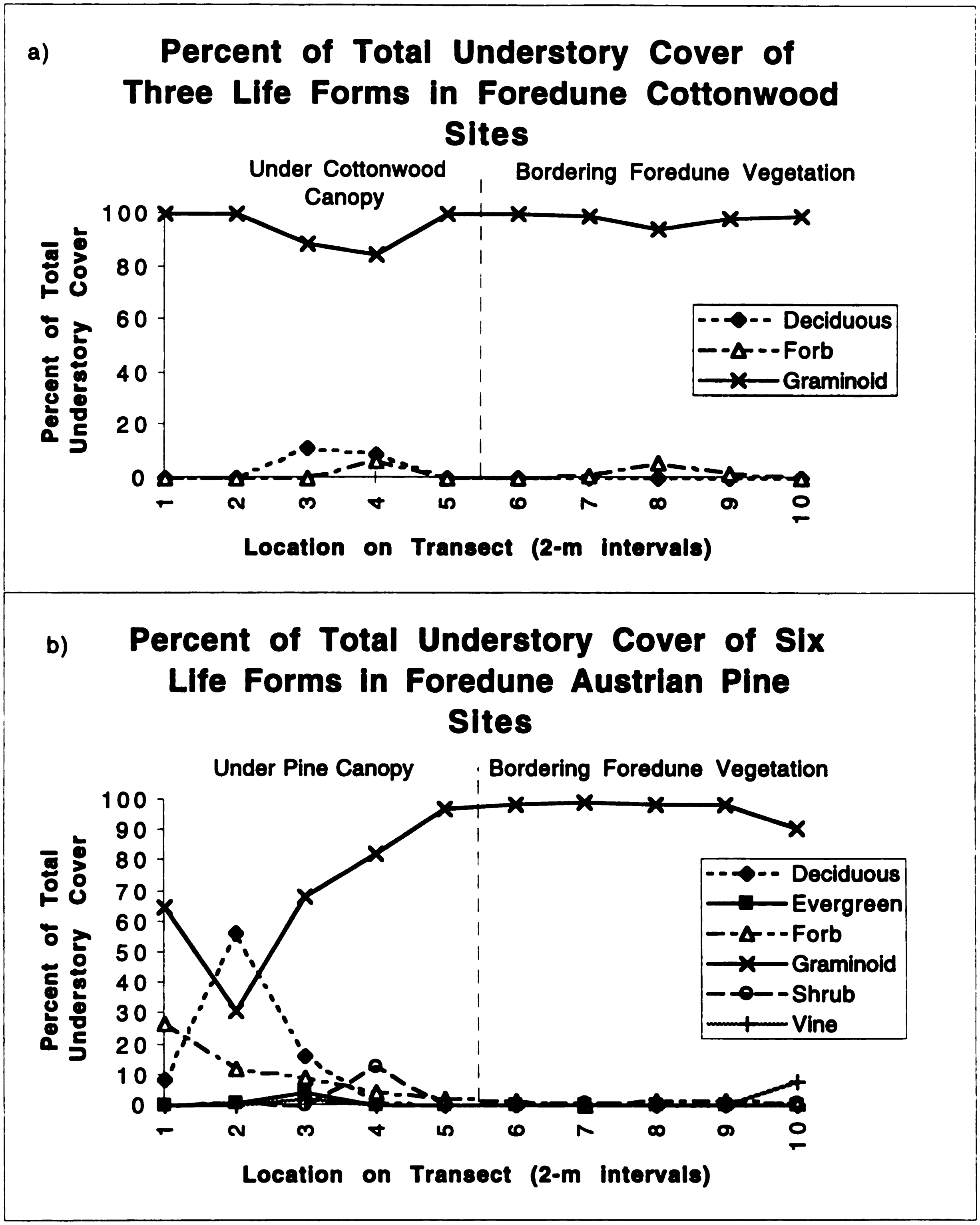


Figure 3-9. Life form composition of understory cover in a) cottonwood and b) Austrian pine sites in foredunes. Data from 1994 and 1996.

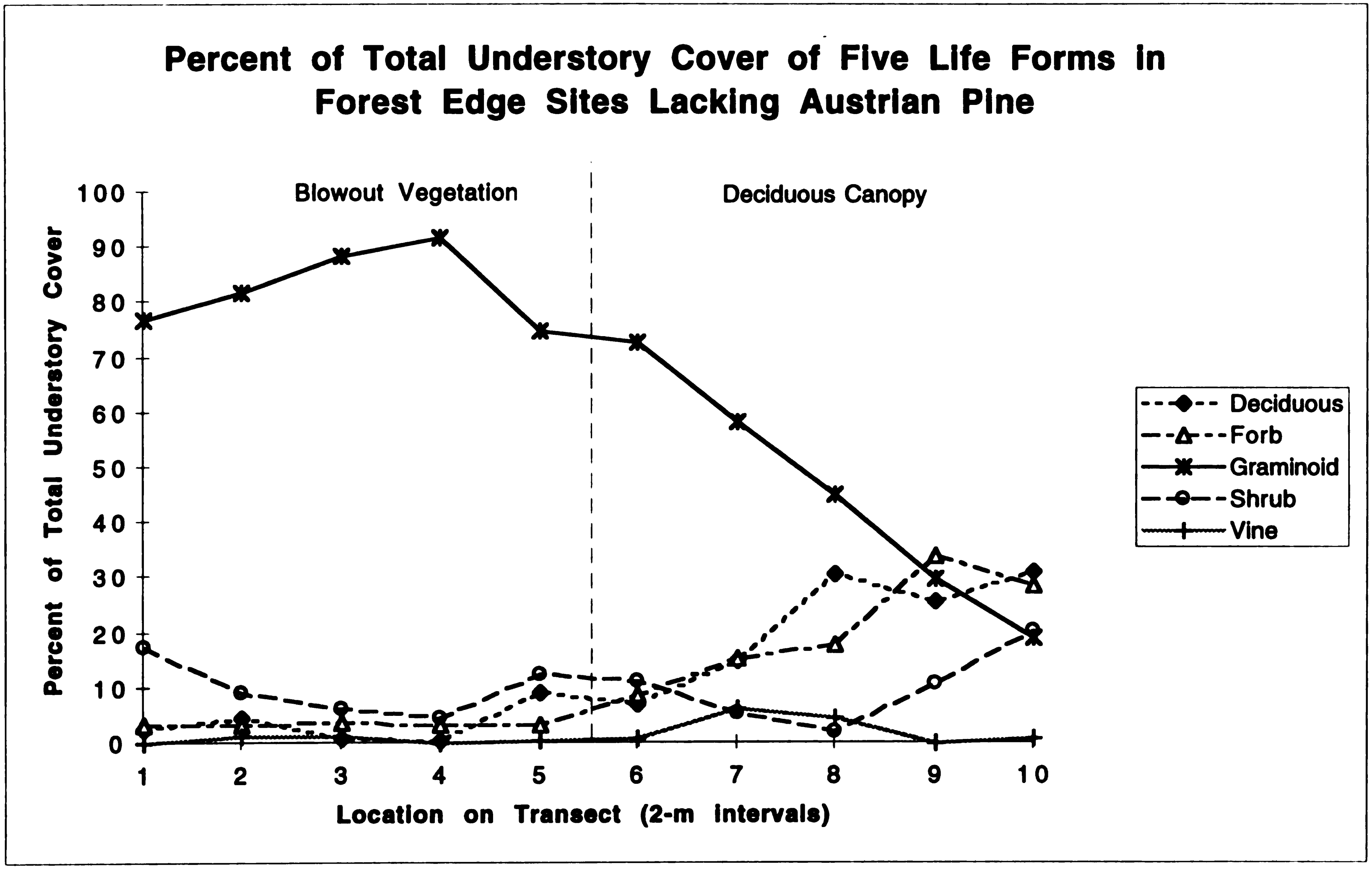


Figure 3-10. Life form composition of understory cover in forest-edge sites lacking Austrian pine. Data from 1994 and 1996.

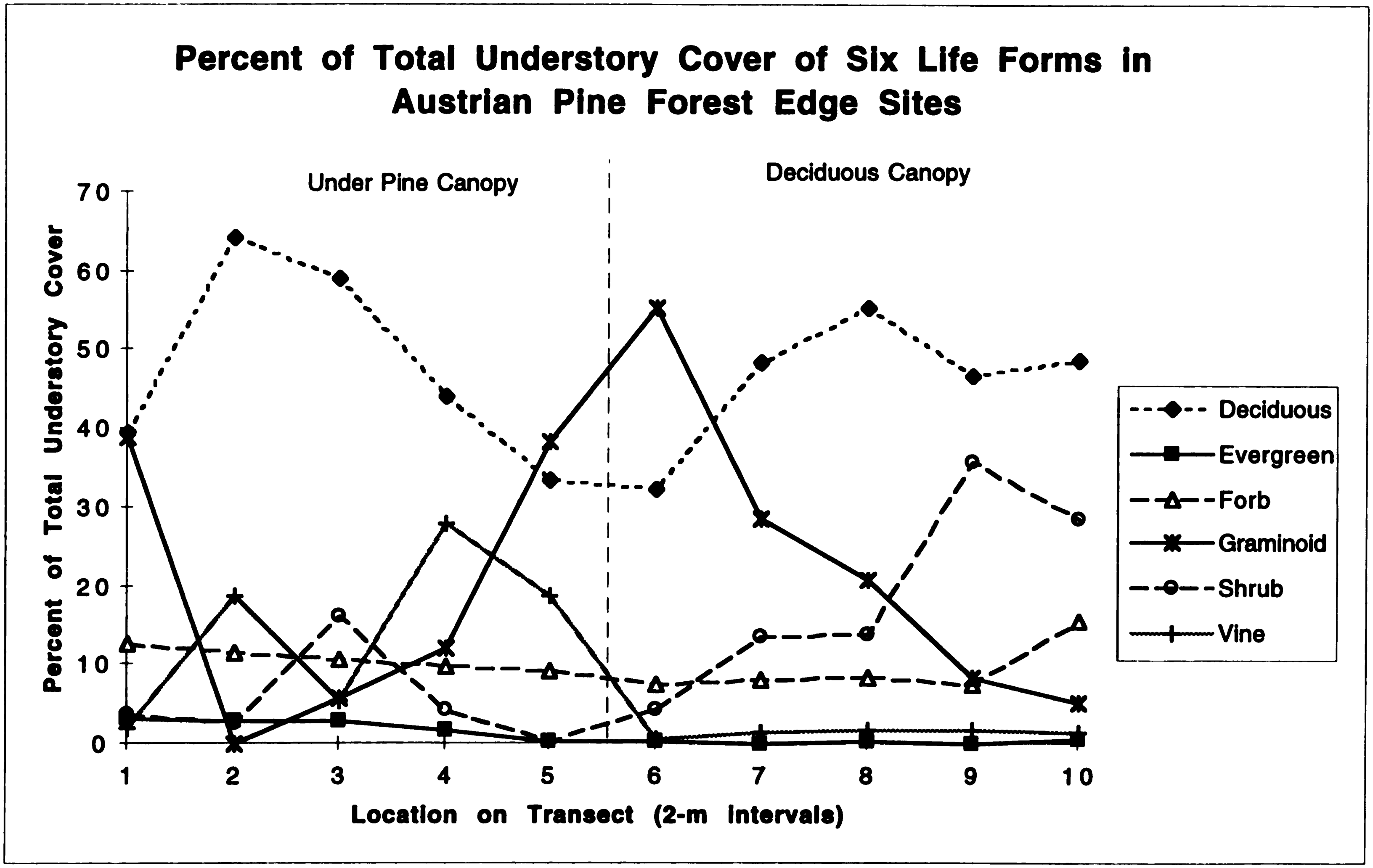


Figure 3-11. Life form composition of understory cover forest-edge sites with Austrian pine. Data from 1994 and 1996.

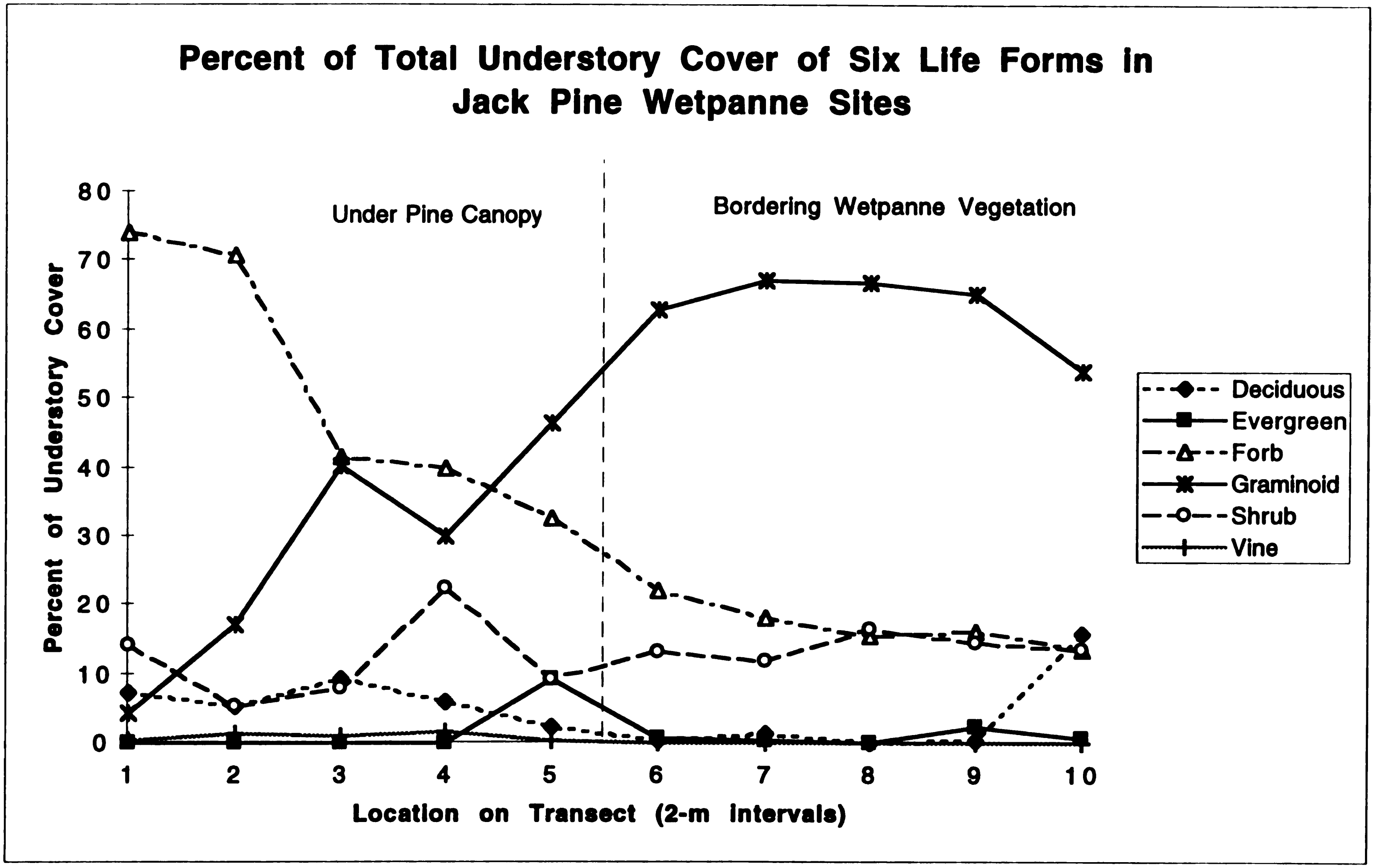


Figure 3-12. Life form composition of understory cover in Jack pine wetpanne sites. Data from 1995.

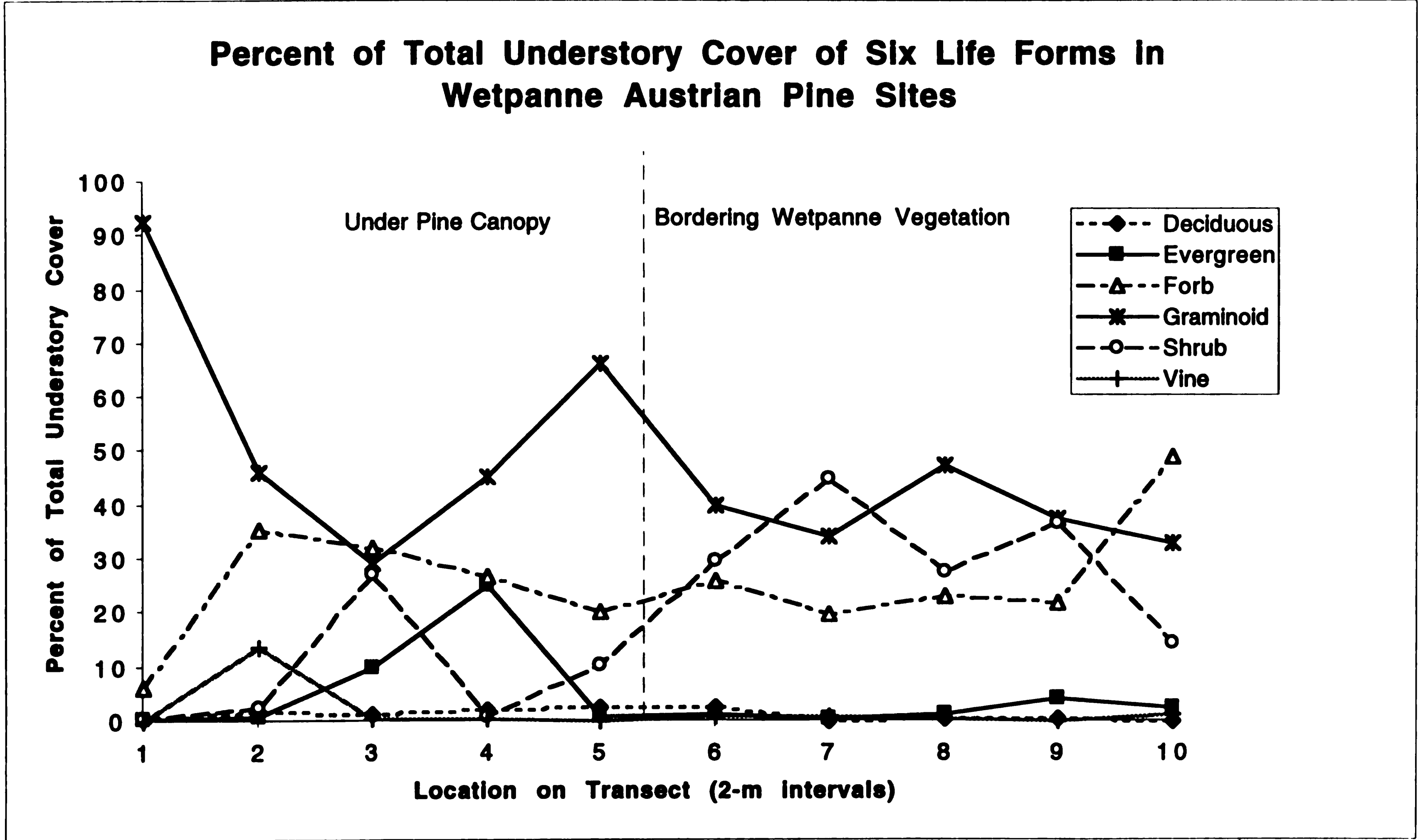


Figure 3-13. Life form composition of understory cover in Austrian pine wetpanne sites. Data from 1995.

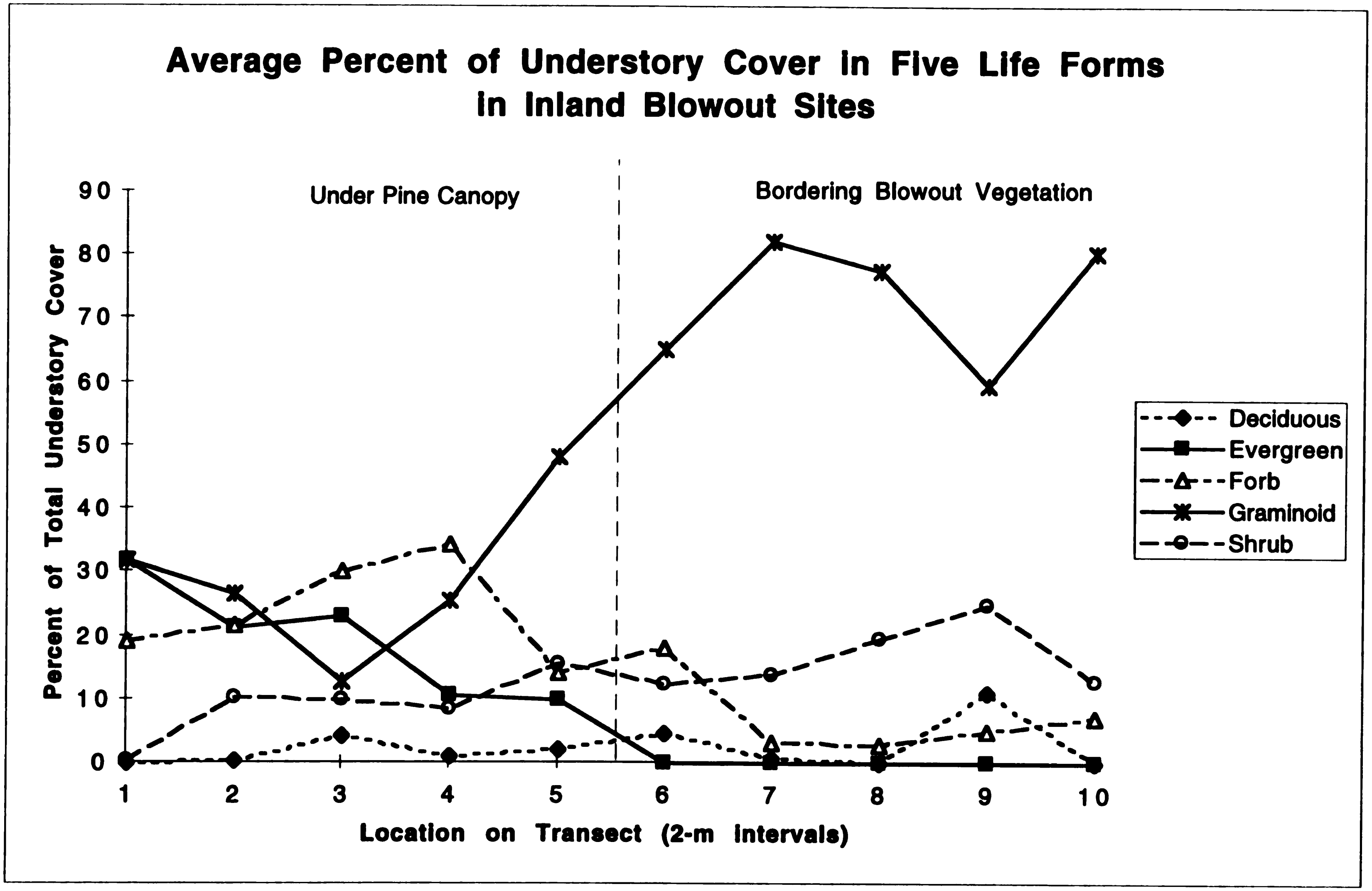


Figure 3-14. Life form composition of understory cover in Austrian pine inland blowout sites. Data from 1994.

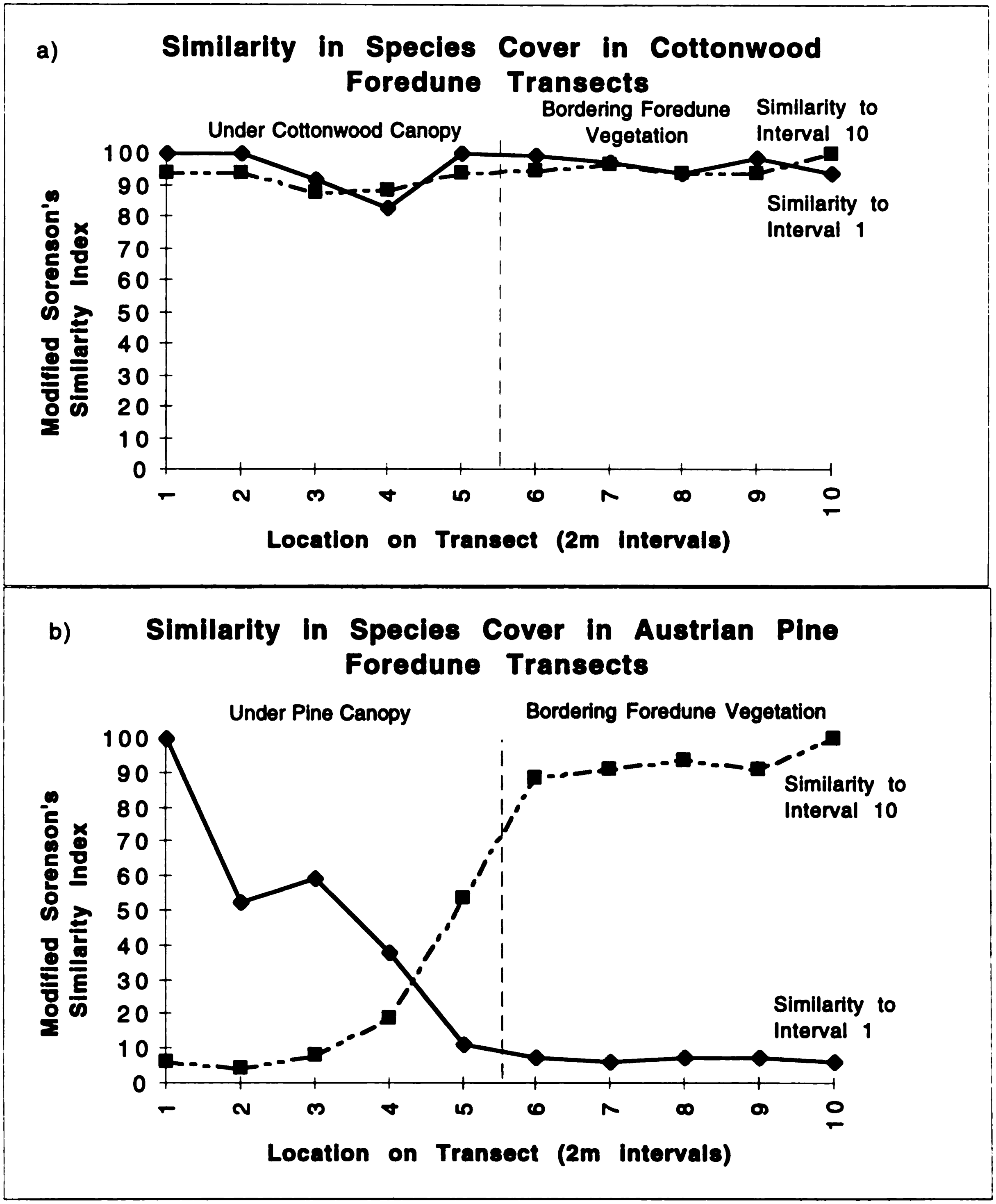
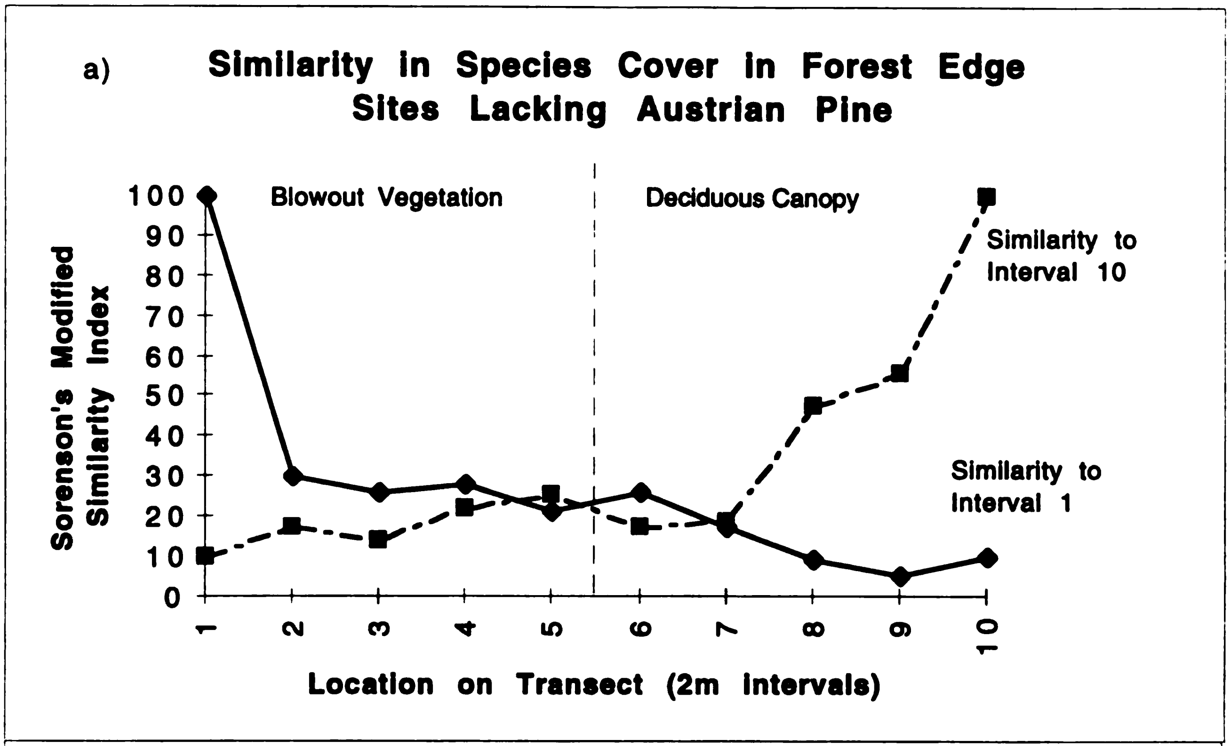
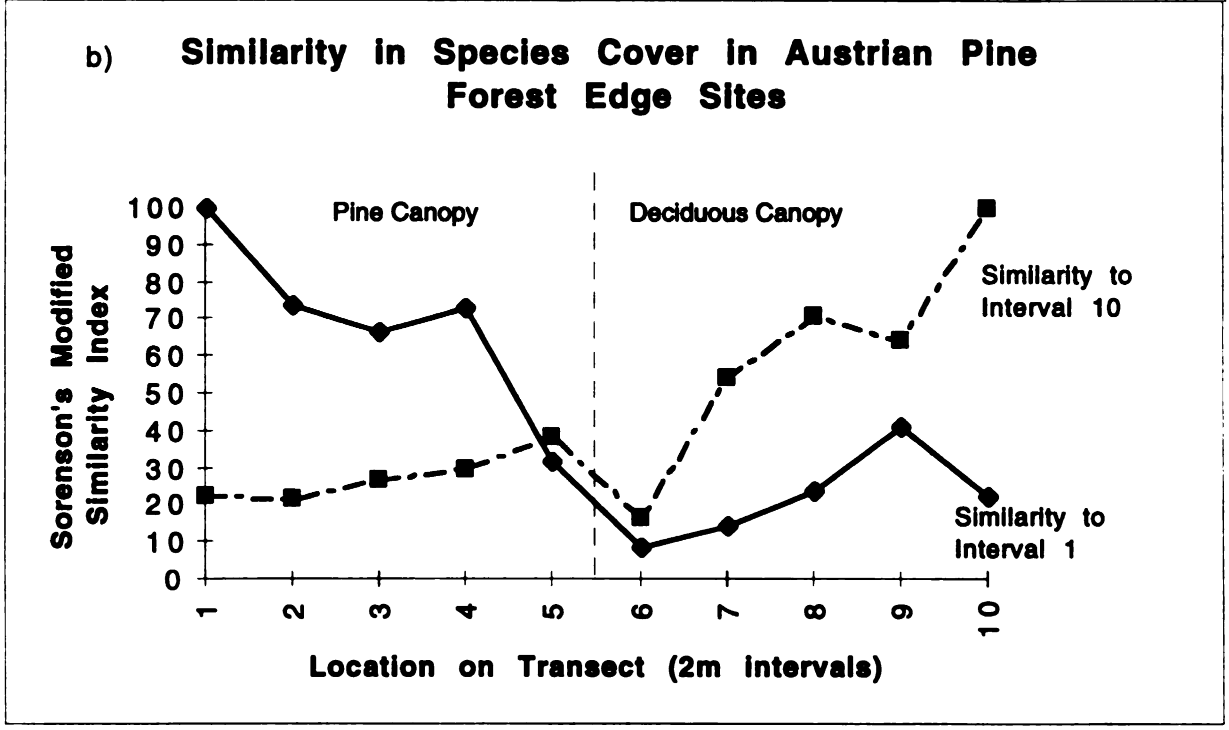


Figure 3-15. Similarity in community composition and cover across a) Cottonwood and b) Austrian pine foredune transects. Solid lines indicate similarity of the community to that of interval one, in the core of the Cottonwood/Austrian pine community, and dotted lines indicate similarity of the community to that of interval 10, in the core of foredune vegetation. Data from 1994 and 1996.



a) Similarity in Species Cover in Forest Edge Sites Lacking Austrian Pine



b) Similarity in Species Cover in Austrian Pine Forest Edge Sites

Figure 3-16. Similarity in community composition and cover across a) forest edge sites lacking pine and b) Austrian pine forest edge transects. Solid lines indicate similarity of the community to that of interval one, in the core of the Blowout/Austrian pine community, and dotted lines indicate similarity of the community to that of interval 10, in the core of deciduous forest vegetation. Data from 1994 and 1996.

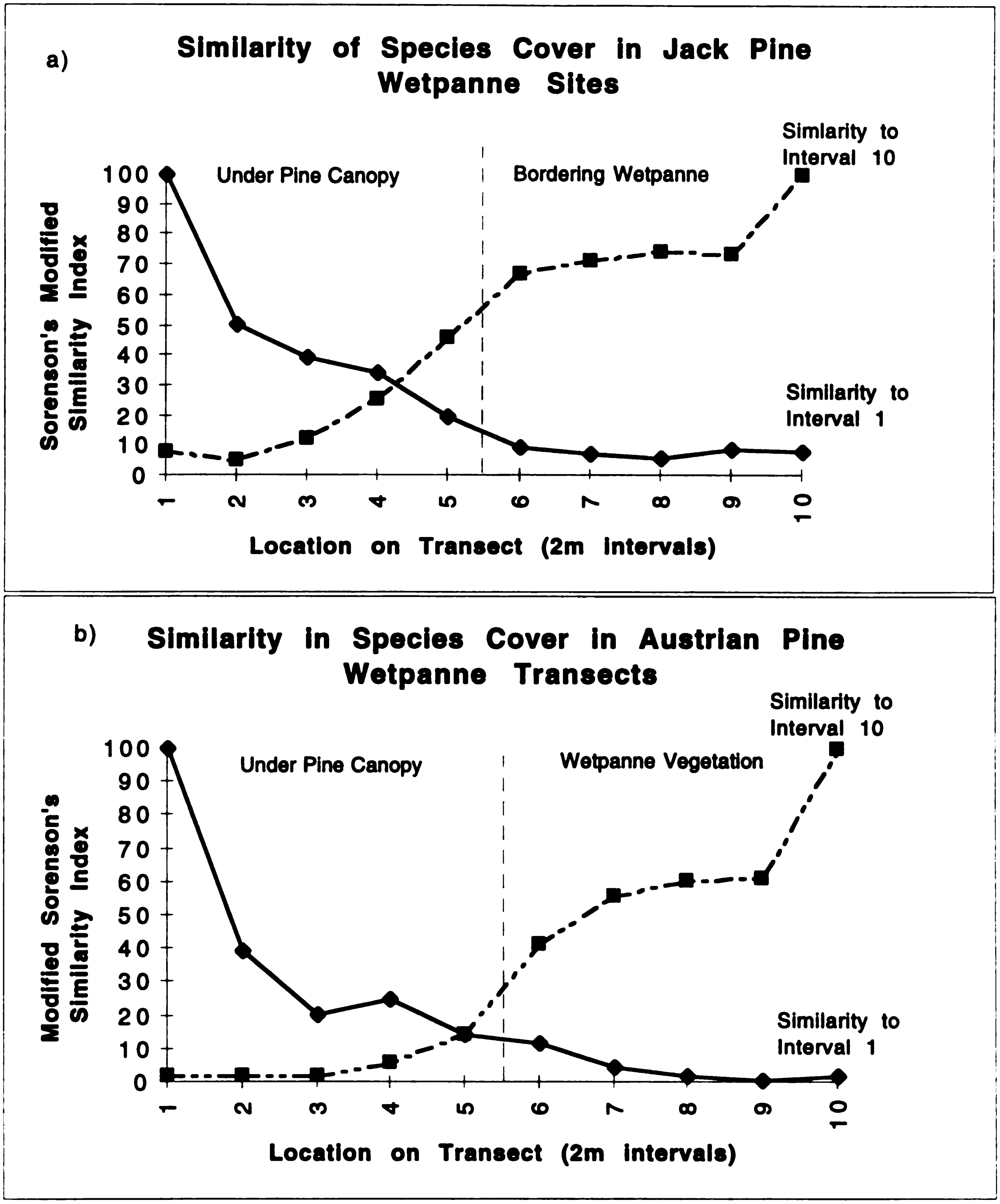


Figure 3-17. Similarity in community composition and cover across a) Austrian pine and b) Jack pine wetpanne transects. Solid lines indicate similarity of the community to that of interval one, in the core of the Austrian/Jack pine community, and dotted lines indicate similarity of the community to that of interval 10, in the core of wetpanne vegetation. Data from 1995.

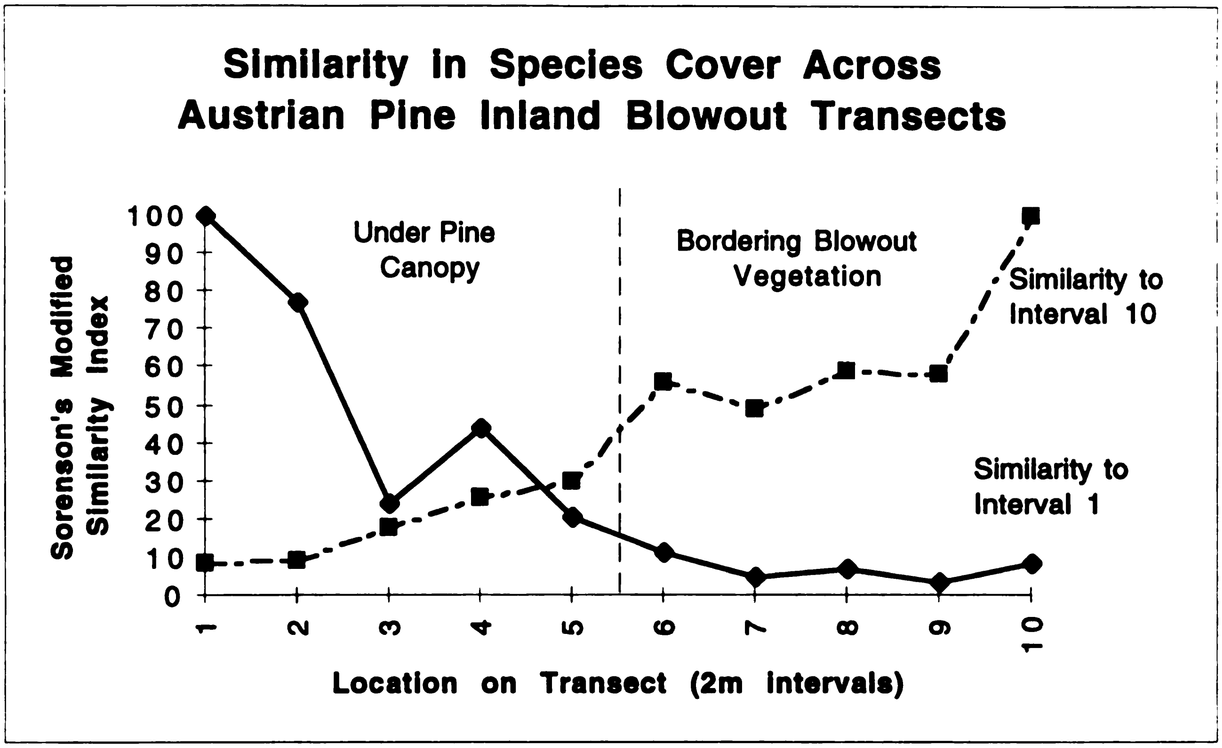


Figure 3-18. Similarity in community composition and cover across Austrian pine inland blowout transects. Solid lines indicate similarity of the community to that of interval one, in the core of the Austrian pine community, and dotted lines indicate similarity of the community to that of interval 10, in the core of blowout vegetation. Data from 1994.

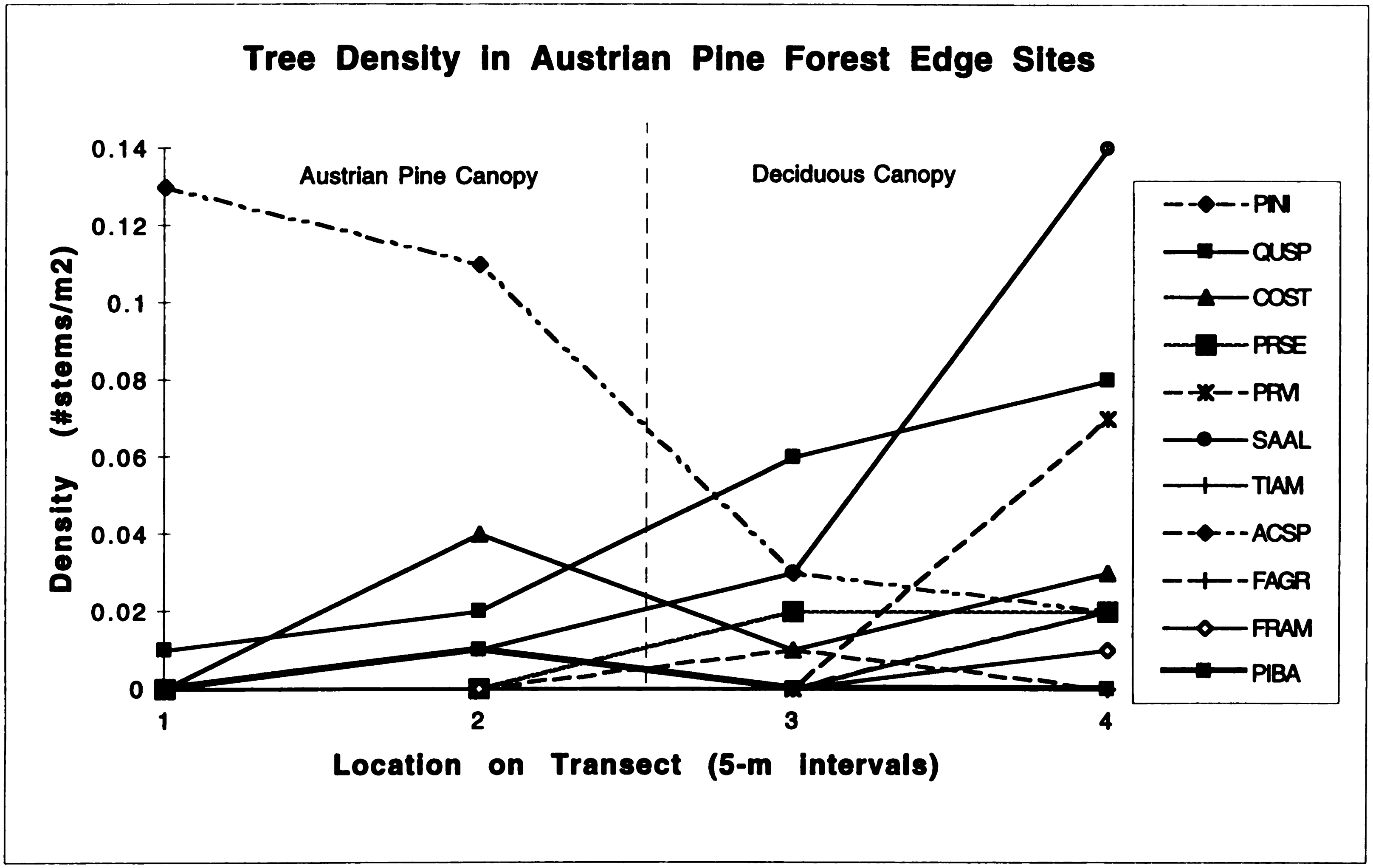


Figure 3-19. Density of trees (≥1cm dbh) across Austrian pine forest-edge transects. PINI = *Pinus nigra*, COST = *Cornus stolonifera*, PRSE = *Prunus serotina*, PRVI = *Prunus virginana*, SAAL = *Sasafras albidum*, TIAM = *Tilia americana*, ACSP = *Acer sp.*, FAGR = *Fagus grandifolia*, FRAM = *Fraxinus americana*, PIBA = *Pinus banksiana*. Data from 1994 and 1996.

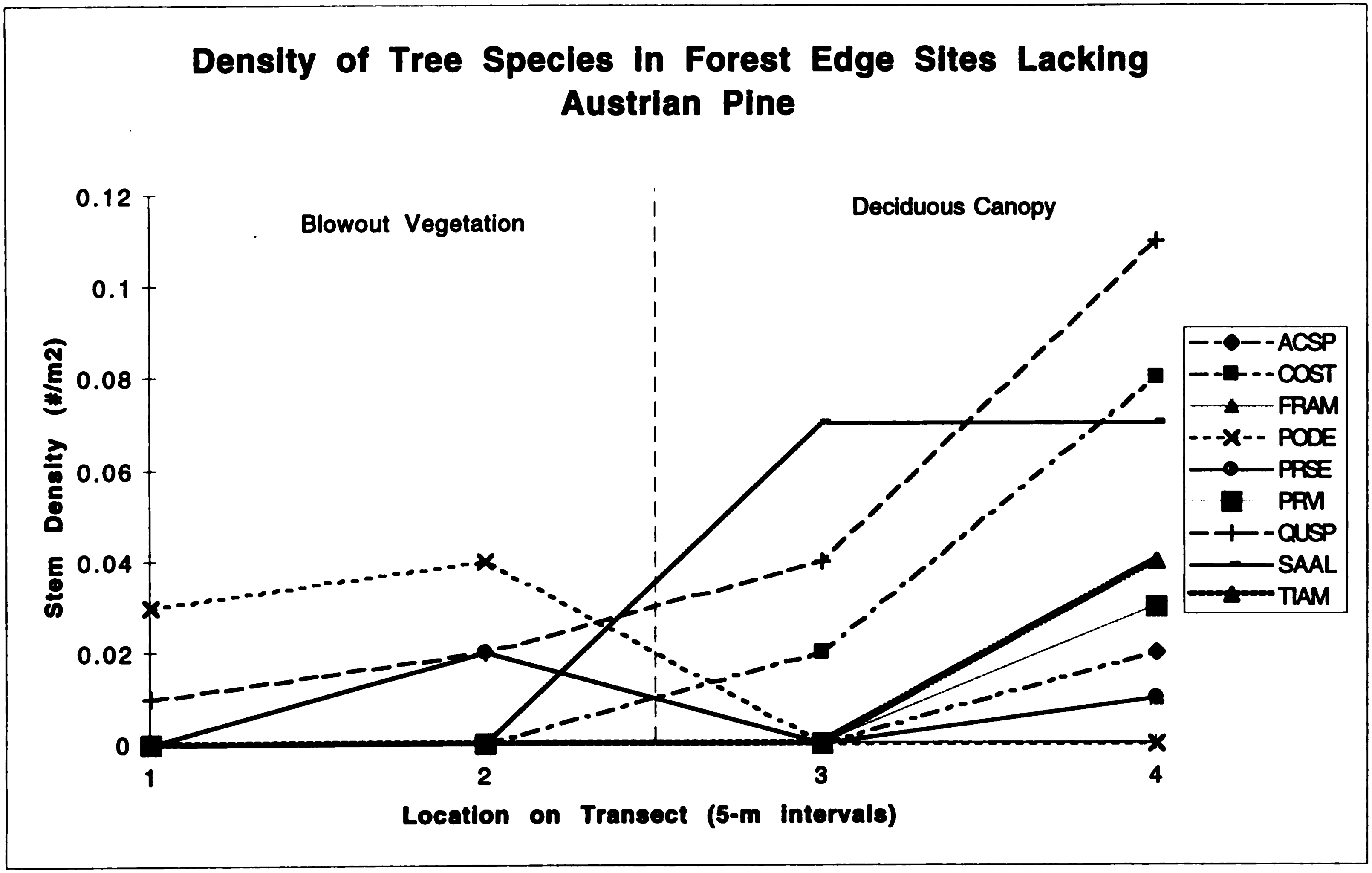


Figure 3-20. Density of trees (≥ 1cm dbh) along transects in forest edges lacking Austrian pine. QUSP = *Quercus sp.*, COST = *Cornus stolonifera*, SAAL = *Sasafras albidum*, PODE =*Populus deltoides*, TIAM = *Tilia americana*, PRVI = *Prunus virginiana*, ACSP= *Acer sp.*, FRAM = *Fraxinus americana*, PRSE = *Prunus serotina*. Data from 1994 and 1996.

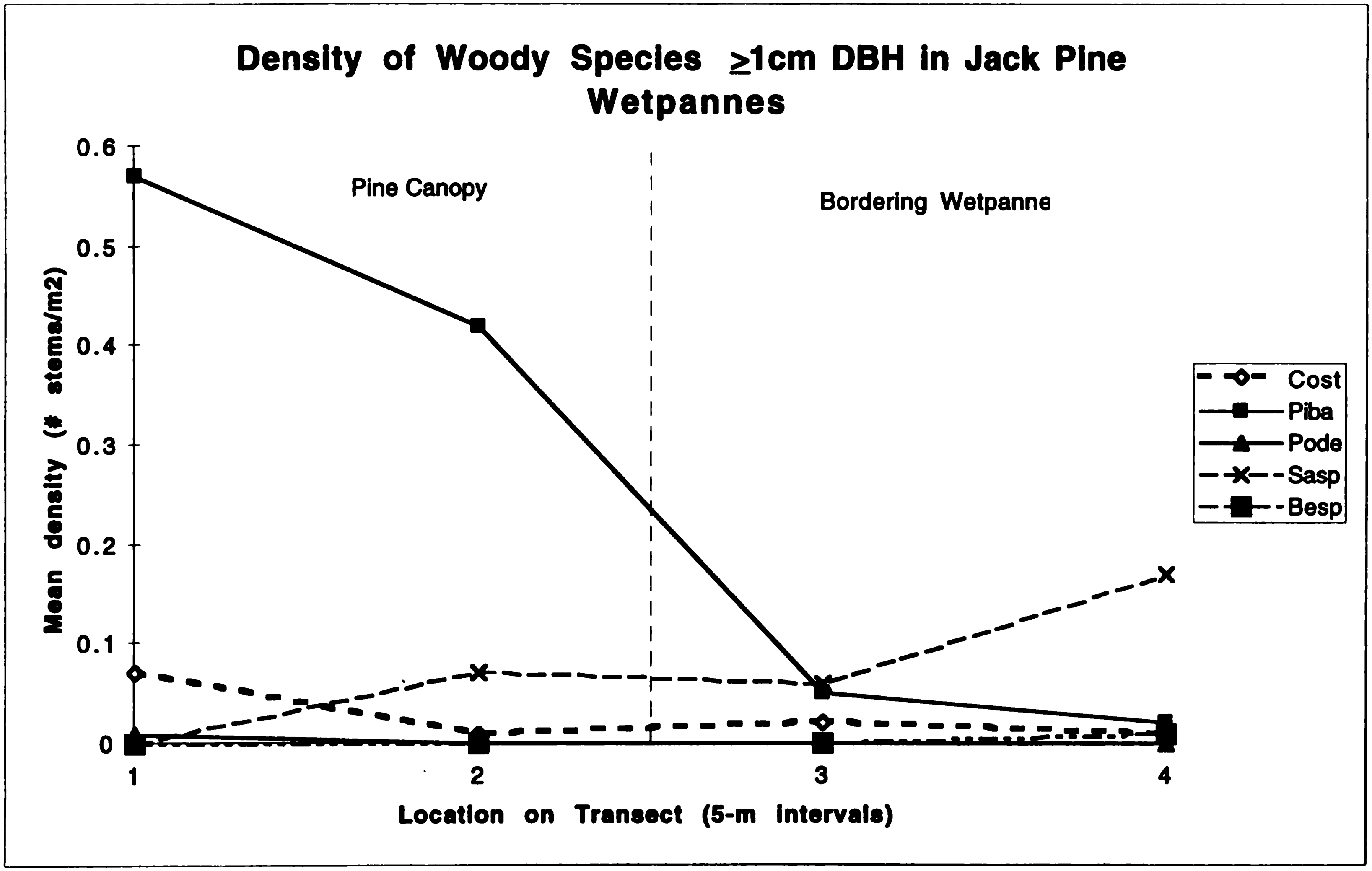


Figure 3-21. Density of woody species (≥ 1cm dbh) along transects in Jack pine wetpannes. Cost = *Cornus stolonifera*, Piba = *Pinus banksiana*, Pode =*Populus deltoides*, Sasp = *Salix sp.*, Besp = *Betula sp.* Data from 1995.

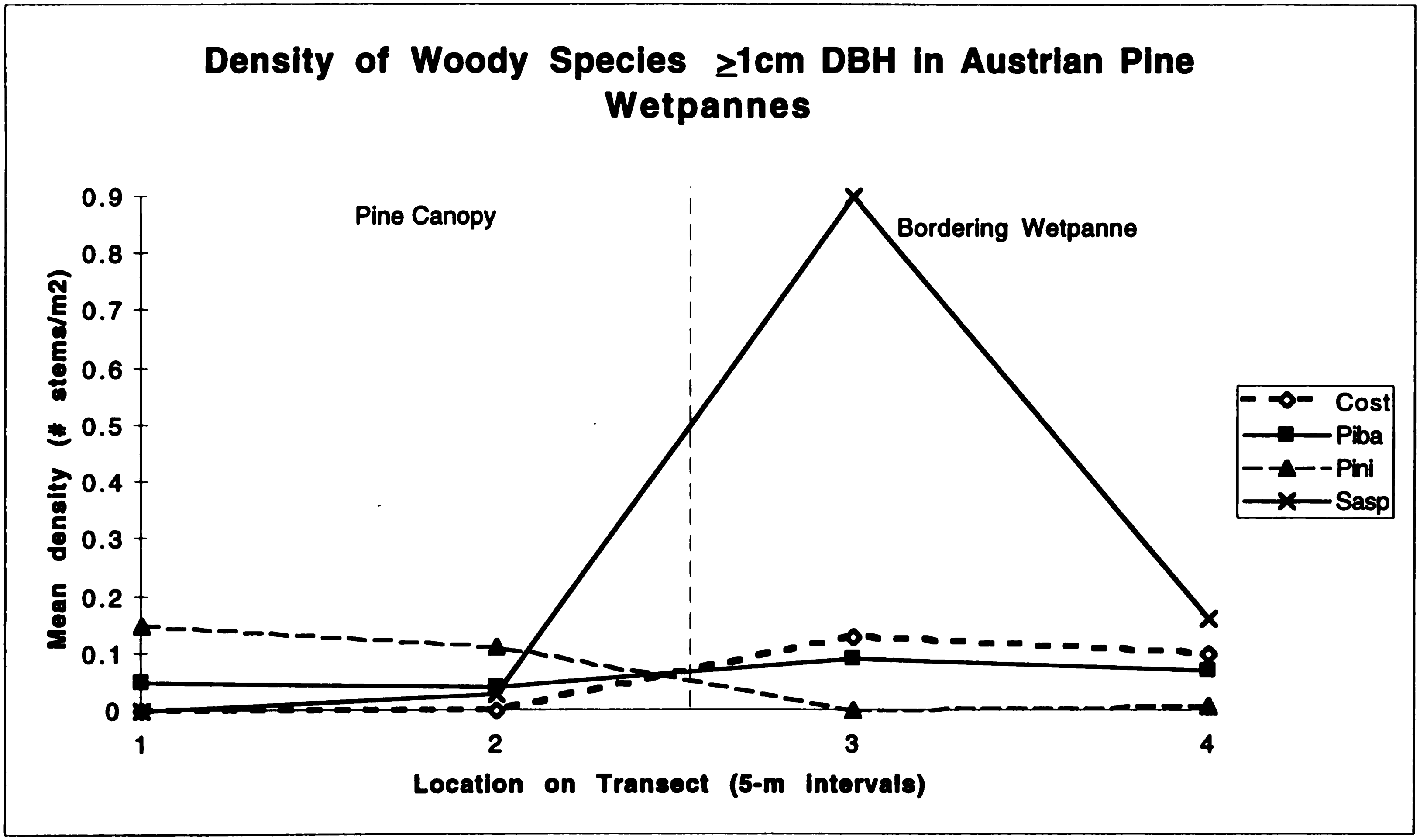


Figure 3-22. Density of woody species (≥ 1cm dbh) along transects in Austrian pine wetpannes. Cost = *Cornus stolonifera*, Piba = *Pinus banksiana*, Pini =*Pinus nigra*, Sasp = *Salix sp*. Data from 1995.

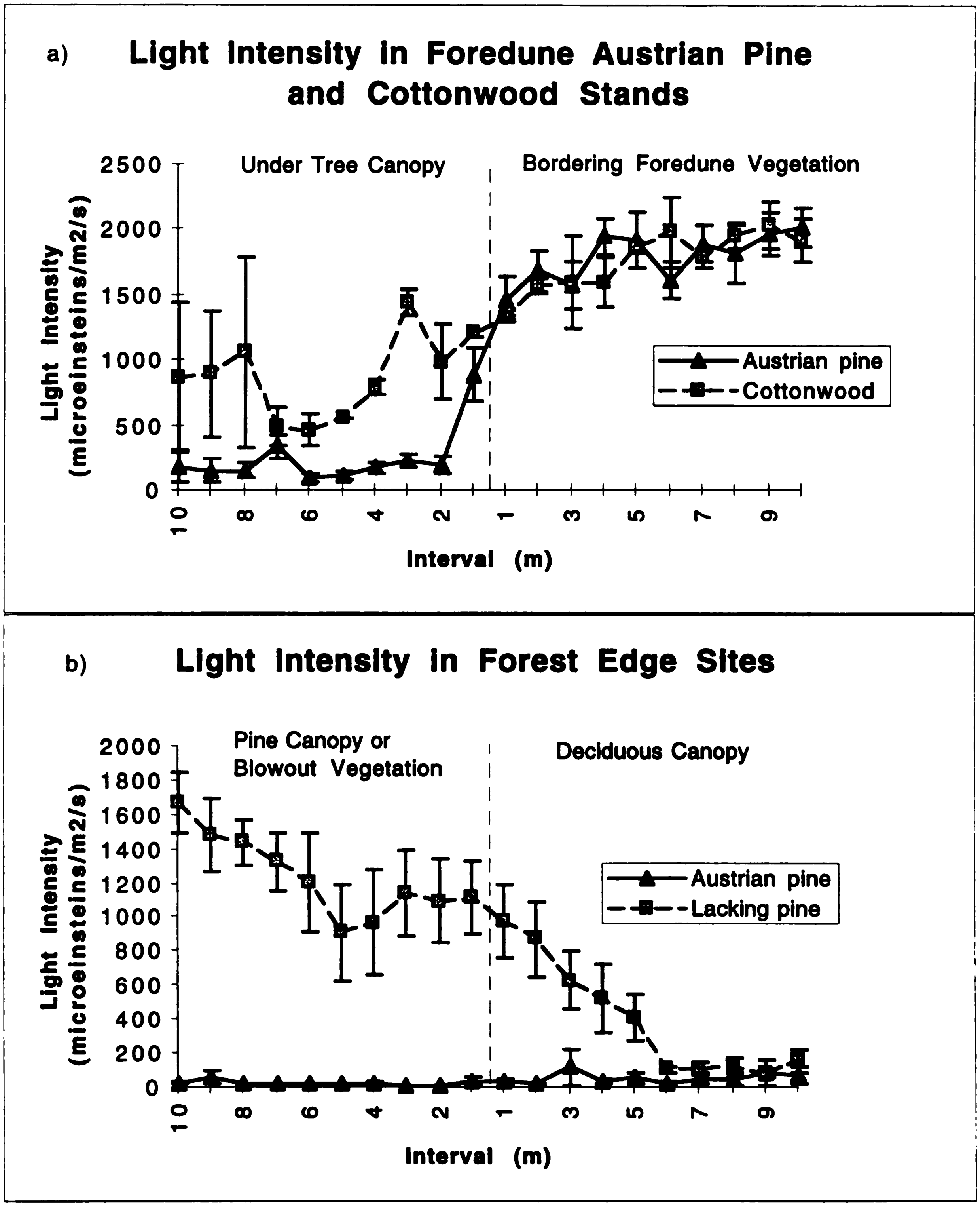


Figure 3-23. Light intensity ± SE across a) foredune cottonwood and Austrian pine transects and in b) forest edge sites with and without Austrian pine. Data from 1994.

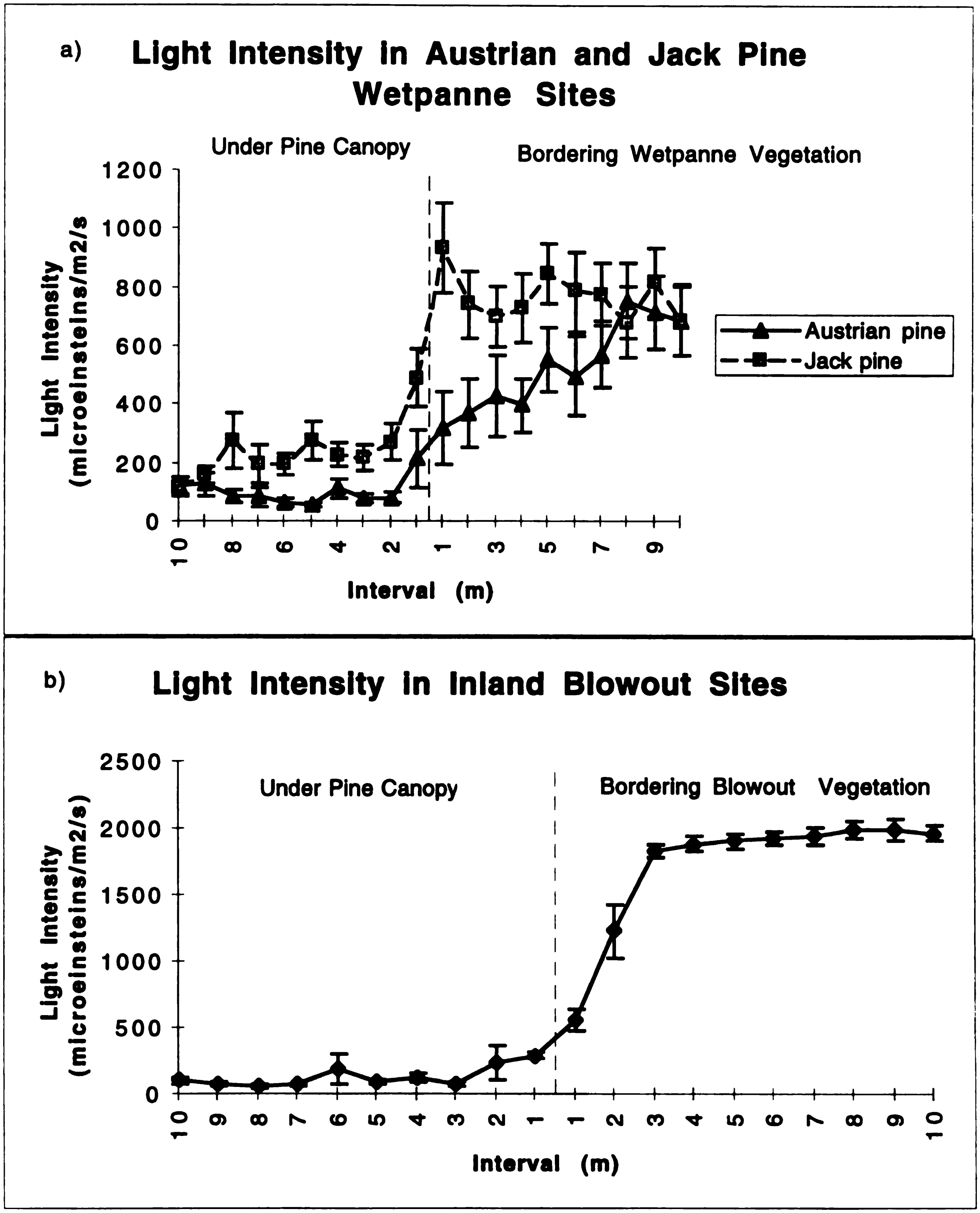
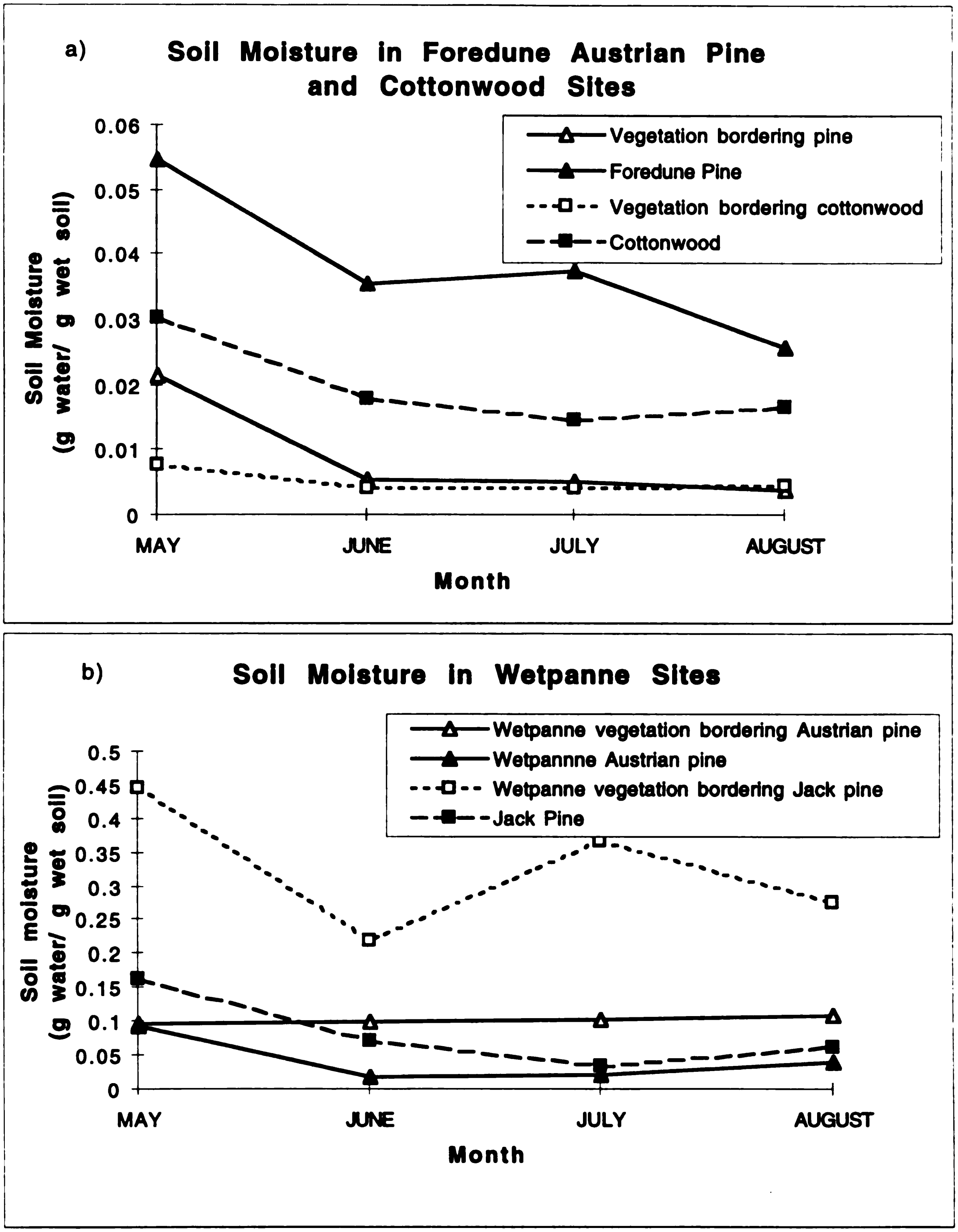


Figure 3-24. Light intensity ± SE across in a) Jack and Austrian pine wetpanne sites (1995) and in b) inland blowout sites with Austrian pine (1994).



a) Soil Moisture in Foredune Austrian Pine and Cottonwood Sites

b) Soil Moisture in Wetpanne Sites

Figure 3-25. Mean monthly soil moisture in a) foredunes and b) wetpannes across the 1995 growing season. Note difference in scales.

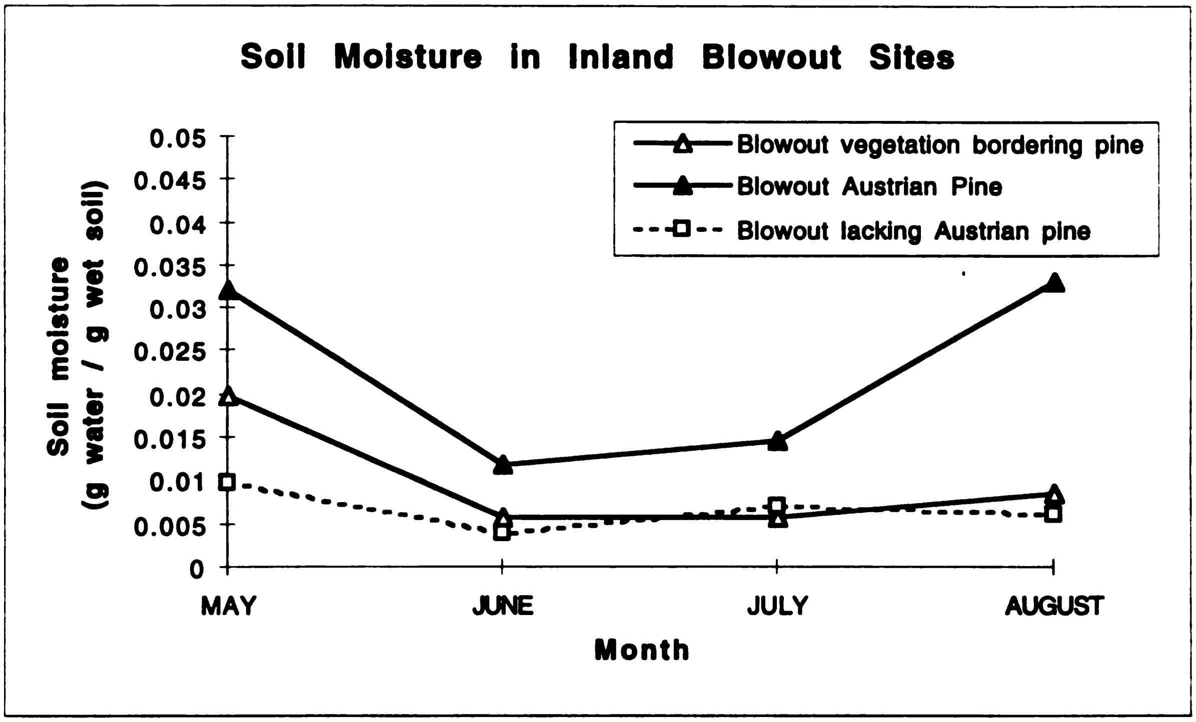


Figure 3-26. Monthly soil moisture in inland blowout sites across the 1995 growing season.

CHAPTER 4

REPRODUCTION AND RECRUITMENT OF THE INTRODUCED *PINUS NIGRA* ACROSS DUNE SUCCESSION: DEMOGRAPHIC AND COMMUNITY CONSIDERATIONS

INTRODUCTION

The concept of habitat choice has recently gained favor among plant ecologists, despite the fact that it has traditionally been applied only to organisms which are mobile throughout their lives (Bazzaz 1991, Schupp 1995). It is during the motile dispersal phase of the life history of a plant that "habitat choice" occurs, or more technically, is imposed upon the plant by its habitat (Bazzaz 1991, Schupp 1995). Seeds are dispersed into an array of habitats surrounding the parent plant and the selective forces of the environment upon them shape the evolution of an optimal dispersal-germination-establishment life history strategy (Schupp 1995). Invasive plant species present a unique opportunity to study habitat choice, because they are new to the system and have yet to be evolutionarily influenced by it.

Among the factors that influence germination and subsequent establishment of seedlings are light (Augspurger 1984, Pons 1992, Gray and Spies 1996), litter (Facelli 1991, Silman 1996), understory vegetation (Maguire and Forman 1983), moisture (Streng et al. 1989, Laman 1995), and microtopography (Harper 1977, Hamrick and Lee 1987). Since most mortality in long-lived perennials occurs in early life history stages, the interactions between the early life history stages of a plant and its environment may determine its eventual adult distribution (Harper 1977, Bullock et al. 1996, Silman 1996).

Recruitment limitation can occur prior to seedling germination, however. Seed production can be constrained by flower set, pollination and subsequent fertilization, floral abortion, and finally embryo abortion (Owens 1995). Limitation at any of these steps will reduce seed production and subsequent recruitment.

An understanding of recruitment limitation in the context of non-native plant species introductions is of particular importance if we are to determine the potential for their invasion into a novel habitat. In order for a plant to be a successful invader, it must be able to reproduce and replace itself. While it is important to study the reproductive characteristics of an invader to determine its reproductive output, invasion success in a variety of habitats will ultimately be determined by both the reproductive output of the invader and the environmental factors of the receptor community which regulate survivorship of young seedlings.

Invasion ecology

Generalized characteristics common to successful invaders have been proposed and used as early indicators of potential spread (Baker 1974, Crawley 1986, Moulton and Pimm 1986, Noble 1989). Rejmanek and Richardson (1996) found three characteristics of pines to be predictive of their invasion potential: small seeds, short juvenile period and short mean interval between large cone crops. The latter two characteristics imply rapid early reproduction, while small seeds are often associated with high seed output, long dispersal distance, or early germination (Rejmanek 1995). While this approach has been quite successful in retroactively predicting the invasive potential of pine species, it ignores the interactions with the environments into which these pines were introduced.

Other workers have identified characteristics correlated with community invasibility; these include frequent exposure to disturbance, low species richness, low plant cover, and favorable interactions of the invader with the biota of the receptor community (Crawley 1986, Fox and Fox 1986, Orians 1986). Communities invasible by pines, in particular, provide limited competition with regenerating pine seedlings, are lacking in species of a similar growth form, and are exposed to intermediate to severe disturbance which results in the reduction of plant cover (Richardson and Bond 1991). These community studies disregard the characteristics of the potential invaders, however. Though few studies have combined investigation of both invader and invaded community (but see D'Antonio's 1993 study of *Carpobrotus edulis* invasion in three coastal communities), it is generally accepted that a thorough understanding of the invader must be combined with an understanding of the characteristics of the receptor community in making predictions about invasion.

Population projection models

The projection matrix model approach combines demographic information about the invader with information about the community into which it has been introduced. The response of the life history stages of a species to its environment is embedded in matrix transition probabilities which are determined from empirical data. The construction of Lefkovitch or stage-based transition matrices facilitates comparisons of future invasion success of non-native species in a variety of habitats by projecting population sizes across time and by determining population growth rates. Matrix elasticities, which pinpoint the proportional contributions of each life history stage to the population growth rate (Caswell 1989, McPeek and Kalisz 1993, Silvertown et al. 1993), may offer further insights into the importance of each life stage to the persistence of a species in a particular habitat. Lefkovitch matrices have been used to predict the success of rare plants in different microhabitats (Kephart and Paladino 1997), but only rarely have they been used to project invasion potential for non-native woody plant species (I. Parker pers. com.).

Research objectives

This study seeks to determine not only the reproductive output of a potentially invasive pine, *Pinus nigra*, on the sand dunes of Lake Michigan, but also to evaluate its demographic potential in various receptor communities (foredunes, forest edges, wetpannes, and inland blowouts). Abiotic and biotic factors such as light, soil moisture, litter, understory cover, and species richness vary throughout the dune system and among different seral stages and may constrain the establishment of *P. nigra* in the dunes. Because the environmental conditions which regulate seed production vary among seral stages as well, individual trees may differ in their ability to produce seed, depending upon the seral stage into which they were introduced. Variable seed production, coupled with the differing array of microsites available for seedling establishment in these seral stages, may translate into differential invasion success among successional stages in the dunes.

The present time period is a critical one in which to study invasion of *P. nigra* into this system, because most of the 26,000 trees planted in the 1950's and 1960's have now reached maturity, and the oldest recruits (10 years of age) are not yet reproductive. Analysis of the current size structure of the population of recruits can give us an indication of future invasion patterns in different seral stages in the dunes.

The objectives of this study were document *P. nigra* reproduction, germination, seedling establishment, and subsequent transitions to larger size classes to project its invasive potential. In addition, seedling survivorship and density were examined in relation to a variety of biotic and abiotic factors to identify the environmental filters which regulate its survivorship and growth.

The following questions formed the basis for this study:

1) Does the reproductive output of *P. nigra*, as measured by seed production and germinability, vary among dune habitats and across years?

2) How do *P. nigra* population growth rates vary in different seral stages, and which stages of its life cycle contribute proportionally more to these population growth rates?

3) What are the key biotic and abiotic determinants of seedling survivorship and how do these vary among seral stages?

To answer these questions, reproductive output of *P. nigra* was monitored across two years in four different seral stages on the dunes. In addition, seedling survivorship and density were monitored in canopy and gap plots in three seral stages across three growing seasons. Biotic and abiotic variables were measured in each of these seral stages and correlated with successful seedling establishment.

Study species

Native to Europe and northern Africa, *P. nigra* grows to 30m in height and reaches 300 years of age (Vergos 1985, Vidakovic 1991). It typically reaches reproductive maturity by 15-20 years of age, but has been shown to produce cones as early as four years of age (Vidakovic 1974). Maximum cone production takes place from 60 to 90 years of age. Male cones produce copious pollen which is wind-dispersed in May and June (Burns and Honkala 1990). Female cones remain receptive to pollination for three days, but not all the new female cones on a tree are receptive at the same time. The window of time for successful pollination is quite brief, nonetheless, as is typical of pines. Fertilization takes place 13 months following pollination, and cones ripen the following fall.

Trees produce cones every year under normal conditions, but do so most abundantly every three to four years. Austrian pine cones each produce on average 30-40 sound (filled) seeds, approximately 50% of which are germinable. Poor cone or seed crops may be a result of bad weather during pollination or losses to insects and rodents during seed development (Vidakovic 1974).

METHODS

Study site

This investigation took place at Saugatuck Dunes State Park, as described in Chapter 2.

Reproductive output

Seed production in 1995.-- Austrian pine cones were counted and collected from trees in Fall 1995 upon ripening. Planted adult trees were randomly selected in five permanent sampling sites until five reproductive trees were located. All cones present on each of the five reproductive trees were counted in each of the four seral stages described in Chapter 1. Up to five second-year cones per reproductive tree were harvested for seed counting and laboratory germination trials. For trees with fewer than five cones, all available cones were harvested. Cones were oven dried at approximately 42°C for up to 48 hours. Intact seeds were removed from the open cones, counted, and stored at room temperature until germination trials began. Seed production per reproductive tree was determined by multiplying the average number of seeds per harvested cone by the number of cones per tree. These values were averaged for each site and multiplied by the proportion of reproductive trees in that site to give a mean number of seeds produced per tree in that site. Stand densities varied across seral stages (see Chapter 2), so it was important to compare seed production per unit area among seral stages as well. Stand density values (trees/m^2) were multiplied by seed production per tree to yield seed production/m^2. Values were compared across stages and years.

Laboratory germination trials.-- Seeds for germination trials were de-winged and soaked for 20 minutes in a 10% bleach solution to surface sterilize them, and then submersed for 20 minutes in distilled water to allow for seed imbibition. Half of the seeds from each cone were placed on moistened Whatman's 1 filter paper in petri plates using sterile technique and squirted with distilled water daily, or whenever condensation was no longer present in the petri plate. Germination trials were run for 14-18 days under constant light and temperature. Percent germination was calculated for each petri plate (representing a cone) and compared.

Seed production in 1994.-- In Fall 1994, cone and seed production as well as seed germinability were determined in a pilot study, similar to the 1995 study, but with a slightly altered sampling protocol. In 1994, all ten of the permanently marked trees in three of the established sampling sites in each of four seral stages were examined for the presence of cones (see Chapter 2 for experimental set-up). Because the foredune stands sampled contained as few as three trees, sample size was limited to three trees in foredunes. Cones were counted for each tree and up to five second-year cones were collected from each reproductive tree, as previously described. Seed counting and germination trials were performed as in 1995, except that all, rather than half of the seeds from each cone were placed in individual petri plates for germination trials.

Demography of naturally regenerating Pinus nigra at SDSP

Pinus nigra is currently regenerating in the foredune, wetpanne, and inland blowout seral stages at SDSP, but very little regeneration was evident under pine canopy and in adjacent native deciduous forest vegetation in the forest edge sites. (Sampling was not conducted on the other side of forest edge pine stands, at the interface with inland blowout vegetation, however.) Therefore, intensive studies of seedling distribution and regeneration were concentrated in foredune, wetpanne, and inland blowout sites. In each of these three seral stages, the extent of *P. nigra* regeneration was determined in open areas and under *P. nigra* canopy cover. Twenty 1m X 1m quadrats were randomly located in plots with <50% *P. nigra* overstory (classified as "gap plots"), bordered by *P. nigra*, and in adjacent plots under *P. nigra* canopy, where overstory cover was >85% (classified as "canopy plots"). Three replicates each of gap and canopy plots were sampled within each of the three seral stages. In inland blowout sites, however, no true gaps surrounded by *P. nigra* were available for sampling. Alternatively, the open areas bordering pine stands were sampled and hereafter referred to as "gap plots." Seedlings were too sparse in inland blowout "gap plots" for the selection of random quadrats, therefore entire populations of seedlings were inventoried at these three locations. Estimates of density for randomly located quatrats were based on the area sampled, and for inland blowout gaps, on the total area inventoried, and all comparisons were made on a per unit area basis. Number of Austrian pine seedlings and saplings <22 years old (offspring of the planted trees) was recorded for each quadrat, and age (as estimated by number of whorls with needles), crown area, and height was recorded for each seedling in each quadrat. Each individual was inconspicuously marked, and survivorship and growth were monitored at annual intervals in the growing seasons of 1995 and 1996. New seedlings were measured and marked each year.

Microsite variables

Biotic and abiotic variables were measured for each quadrat to determine which microsites were most conducive to establishment and growth of naturally regenerated *P. nigra* individuals. Biotic variables included species richness (number of species per m^2 plot) and ocular estimates of percent understory cover, and both were recorded for each quadrat in July 1994. The proportion of quadrat area covered by needle and/or deciduous litter was also recorded at this time, as was litter depth.

The abiotic variables, including light intensity, canopy openness, soil moisture, and soil pH were measured for each quadrat or a sub-sample of the quadrats in 1996. On a clear day in July, between 11:30 A.M. and 2:30 P.M., measurements of light intensity were taken in each quadrat with a Dekagon Ceptometer. Spherical densiometer readings were also taken in four cardinal directions for each quadrat, as a measure of canopy openness.

Soil moisture was measured gravimetrically at depths of 0-5cm and 10-15cm in 10-15 quadrats in canopy and gap plots within each of the three foredune and three wetpanne sites in July. Up to five quadrats of each of three *P. nigra* seedling density categories were selected in each plot for soil moisture measurements: L designated no seedlings, M 1-2 seedlings, and H, >2 seedlings. Soil samples were collected with a soil core or a trowel between 6:30 A.M. and 9 A.M., before significant plant transpiration and drying had taken place and soil moisture content was determined gravimetrically.

Soil pH was determined in the laboratory with an Oakton pH meter, for each of the soil samples taken for the soil moisture readings, above. Three readings were taken for each soil sample and minimum values for each sample were compared.

Mean values for each of the above microsite variables were calculated and compared for canopy and gap plots in each seral stage.

ANALYSIS

Reproductive output

To compare seed production per tree across seral stages and among years, mean seed production values for 1994 and 1995 were log transformed to normality and analyzed with a one-way ANOVA where the seed production in each of the eight combinations of year and seral stage were compared. Year was not treated as a separate effect since the limited sample sizes of the 1994 pilot study precluded such a comparison. Multiple comparisons were performed with Tukey's all-pairs comparisons. Seed production per unit area was compared in the same manner.

Seed germination values were arcsine transformed (arcsine*square root of germinability) to normality, and were compared separately for 1994 and 1995. A multi-level nesting design was used for 1995 arcsine transformed data to determine the source of the greatest variation in germinability. Trees were nested within site, sites were nested within stages, and stage was treated as the main effect. All the nested effects were modelled as random effects, while stage was modelled as a fixed effect, because it was not selected at random by the researcher. Data for each year were also pooled by stage and compared with a one-way ANOVA. Multiple comparisons (Tukey's all pairs comparisons) were examined for 1995 data.

Demography

Seedling density.-- To determine which seral stages and light levels were most conducive to the establishment and growth of Austrian pine seedlings and saplings, the density of seedlings (#/m^2) in three seral stages and in gap and canopy plots was analyzed across three years (1994-1996) with a Repeated Measure MANOVA. Each year was treated as a response variable (y), and stage, light, and stage*light interactions were modelled as fixed treatments. To further determine the effect of light and seral stage upon seedling establishment, density of seedlings older than two years of age were separated from the total density of seedlings and tested across three years with a Repeated Measure MANOVA in the same manner.

Repeated measure MANOVA compares three characteristics of the profiles of seedling density across the three sampling dates: "parallelism", "levels", and "flatness" (von Ende 1993). Parallelism is determined by examining the time*stage and time*light interactions, and significant differences of these interaction terms would indicate that density does not change in a parallel fashion across time among stages, or alternatively, among canopy and gap plots across time. If the time*stage interaction is significant, the significance of stage effects and stage*light interactions must be interpreted with caution (von Ende 1993). In similar fashion, if the time*light interaction is significant, all light main effects and interactions must be interpreted with caution. "Levels" are the differences in magnitude of the main effects of both stage and light treatments. The significance of these main effects would suggest that seedling densities vary among stages or among light treatments across years. Finally, the time effect tests for "flatness" (von Ende 1993), or the change in density across time.

Seedling height and survivorship.-- Mean height of juveniles (>1year old) was compared across seral stages in 1996. Height data from all three sites within each seral stage were log transformed to normality and compared using a nested two-way ANOVA, where stage, light, and stage*light interactions were modelled as fixed effects, and site(stage) was modelled as a random effect. The same nested ANOVA model was used to compare arcsine transformed seedling survivorship data for two transition periods (1994-1995 and 1995-1996).

Transition matrices.-- Lefkovitch, or stage-based transition matrices were used to determine projected population growth rates in three seral stages. Matrices were constructed using age and height class data for three years under two light levels in three seral stages for a total of 12 matrices. *P. nigra* life history was categorized into five life stages: germinant (g), juvenile 1-3 (j1-j3) and adult (a) (Figure 4-1). The germinant life stage (g) was represented only by newly germinated individuals in their first growing season, while the juvenile life stages were determined by height ($j1<10$cm, $10\text{cm}\leq j2<25$cm, $j3>25$cm). None of the juveniles were reproducing. Adults (a) were defined as mature, reproductive trees and were lumped as one size category, because effects of planting density on seed production overshadowed any size based differences in fecundity. In this study, adults were represented only by planted trees, because none of the recruits had yet reached reproductive maturity. All individuals in g and j categories were naturally regenerated. Seeds of *P. nigra* are known to be viable in controlled conditions for up to 10 years (Burns and Honkala 1990), but data on seed bank survival of *P. nigra* in natural habitats were unavailable, so seed bank transition probabilities were not included in the model.

Several transitions were possible for each of the life history stages of *P. nigra* (Figure 4-2). Individuals in the g category could either die or transition to a j category. Although transitions from g to j1 were most common, transitions from g to j2 were also observed. Individuals in the j life stage could die, remain in the j life stage, or transition to the a life stage. Stasis or progression from small to large j's was most common, but burial by litter or tissue loss by herbivory could result in retrogression from larger to smaller j categories. Adults (a) could either die or remain as adults. They also produced seed each year .

Actual transition probabilities were determined from field plots in each seral stage. The fecundity estimate (F_{ag}) was determined by multiplying the mean per-tree seed production by the mean density of first-year seedlings in each seral stage and at each light level in each year of the study. This value was divided by the estimated mean seed production per square meter in each seral stage to yield a proportion of individuals that became germinants. The $(\#seedlings/m^2)*(\#seeds\ produced/m^2)^{-1}$ values were used in lieu of laboratory seed germination probabilities, because laboratory values ignore the filtering that takes place in the field with seed predation, moisture limitations, damping off, etc. Estimated seed production values, incorporated into the previous equation, were calculated from seed production data collected for each seral stage in 1994 and 1995. Because seed production values for trees in each seral stage were similar across years, they were averaged together and used in matrices for both 1994 to 1995 and 1995 to 1996 transitions.

P_{gj} and P_{jj} transition probabilities were determined by pooling data from all three replicates of each of the six possible combinations of light level, and seral stage in each year. The frequency of transition from one category to the next was divided by the total number of individuals in the first category at time one to yield its transition probability to the second category at time two. Because none of the recruits of the *P. nigra* population had yet reached reproductive maturity, an empirical transition probability from j3 to adult (P_{j3a}) was impossible to calculate. Instead, a probability of .04 (1/25) was used since j3 trees are typically at least seven years of age and will likely reach reproductive maturity within 25 years, suggesting that at least 1/25 of them are transitioning to the adult life stage annually. One percent mortality was included in the model for both the j3 life stage and the adult life stage, though these probabilities were also impossible to determine empirically. It is important to note that the transition from j3 to adult encompasses a large size range, and that stasis within the j3 category for up to 20 years would not be unexpected.

The population growth rates (lambda) were determined for each matrix, and elasticities, which describe the relative contribution of each life history stage to the population growth rate (Caswell 1989, Kephart and Paladino 1997) were also examined using RAMAS-Stage (Ferson 1991).

To project population sizes across time, initial population sizes for each life stage were needed. These values were simply the number of individuals in each category at the start of the simulation. The initial number of adults present in each seral stage was set at five, because this approximated stand density estimates in the sampling area. Initial seed input was determined by multiplying the seed production per tree by the initial number of adults in each seral stage, because the actual seed input was not known. These calculations assume that adult populations and seed inputs were the same in both canopy and gap plots, but this overestimates the initial adult populations in gaps. Since estimates of seed dispersal were not available, they were not included in the model, though they would clearly improve the accuracy of the resultant projections.

Microsite variables

To determine the differences in microsite variables in canopy and gap sites and among seral stages, each of the factors recorded was examined using a nested ANOVA, where stage, light, and stage*light were modelled as fixed effects and site(stage) was modelled as a random effect.

Nonparametric Spearman rank correlations between *P. nigra* seedling densities, survivorship, and the environmental variables of understory cover, species richness, needle and deciduous litter, litter depth, light intensity, canopy openness, soil moisture, and soil pH were also calculated.

All analyses were performed using JMP software (SAS 1995).

RESULTS

Reproductive output: seed production and laboratory germinability

Average seed production per tree in the foredunes was almost 10 times higher than that of wetpanne and inland blowout trees, and 20 to 40 times greater than that of forest edge trees, depending upon the year (Figure 4-3). Though log seed production varied significantly among stages, it did not differ across years.

On a per unit area basis, seed production in foredunes was only three times higher than that of the other seral stages in 1995 (Figure 4-4). Seed production did not vary among the remaining three seral stages in 1995. As a result of smaller sample sizes, 1994 seed production values did not vary statistically among seral stages.

Laboratory germinability was lowest for foredune seed in both 1994 and 1995 (Table 4-1), and while forest-edge seed had the highest germinability (89%) in 1994, wetpanne seed was most germinable in 1995 (18%). Differences in germinability across seral stages were not statistically significant in 1994 due, in part, to small sample sizes, but in 1995, foredune and inland-blowout seed was significantly less germinable than wetpanne and forest-edge seed. Germinability varied dramatically across years, with an average of 67% in 1994 and only 10% in 1995.

When 1995 data were pooled by seral stage and compared, germinabilities varied across seral stage of seed origin. A multi-level nested ANOVA indicated, however, that the greatest proportion of variation in germinability was among trees within sites (Table 4-2).

Table 4-1. Laboratory germinability for Austrian pine seed collected from four seral stages in 1994 and 1995. Germination trials performed with seeds from individual cones: n is the number of cones for which trials were run in each seral stage. Germinability per cone was significantly different across years, but also among seral stages in 1995.

		1994			1995		
Seral Stage	Mean (%)	S.E.	n	Mean (%)	S.E.	n	Significant difference
Foredune	59.8	5.2	30	8.1	1.3	98	b*
Forest Edge	88.9	6.6	3	4.5	3.0	30	ab
Wetpanne	67.6	4.4	38	18.2	3.3	58	a
Inland Blowout	69.6	5.2	33	6.0	1.4	78	b

*Means marked with different letters differ significant in germinability among stages in 1995 ($p=.05$, Tukey all pairs comparison HSD).

Table 4-2. ANOVA for 1995 arcsine transformed germination data. Germination values were determined for individual cones collected from trees in foredune, wetpanne, forest edge, and inland blowout seral stages.

Source	SS	MS	DF	F Ratio	p
Stage	0.95503	0.31834	3	1.9468	0.1563
Site(Stage)	2.31647	0.16546	14	1.1792	0.3248
Tree(Stage,Site)	6.03599	0.14037	43	2.6085	<.0001
Error	10.816385	0.053813	201		

Demography

Seedling density.-- Seedling densities were 1.5 - 4 times greater in foredune canopy plots than in those of other seral stages (Figure 4-5), depending on the year. Foredune gap seedling densities were also higher than those in other gaps (1.3 - 45 times more dense), except in 1996, when wetpanne gaps had the highest densities.

Repeated measure MANOVA indicated that total density did not change in a parallel fashion across time among stages, though it did have the same slope among light treatments across time (Figure 4-6, Table 4-3). The non-parallel nature of the profiles of seedling density in seral stages across time indicates that the significance of stage effects and stage*light interactions must be interpreted with caution (von Ende 1993). Stage effect was significant, however, suggesting that seedling densities varied among stages across years. Density did not differ among canopy and gap plots across years, but seedling density changed across time, as suggested by the significance of the time effect.

Table 4-3. Repeated measure MANOVA for density of all *P. nigra* seedlings in three sites within each of three seral stages and at each of two light levels across the growing seasons of 1994-1996.

Effect	Wilks Lambda	Exact F	DF Numerator	DF Denominator	p
Between subjects					
Stage	.493	6.16	2	12	.014
Light	.999	.0001	1	12	.992
Stage*Light	.921	0.52	2	12	.608
Within Subjects					
Time	.309	12.3	2	11	.002
Time*Stage	.272	5.04	4	22	.005
Time*Light	.766	1.68	2	11	.232
Time*Stage*Light	.743	0.88	4	22	.492

To examine the relationship between light and establishment of seedlings beyond the second growing season, a repeated measure MANOVA on older seedling densities (>2 years of age) was performed (Table 4-4). Profiles of seedling density in both seral stage and light treatments were not parallel across time, that is, densities did not change in the same direction and the same magnitude over three growing seasons (Figure 4-7). Neither stage nor light treatments, nor the interaction between them, differed significantly in seedling density. Contrary to the analysis of total density, densities of >2-year-old seedlings did not vary among stages, nor light treatments. But the mean densities were much less similar across canopy and gap plots than in the total density analysis. This would indicate that light levels play a more important role in the survivorship of seedlings beyond the second growing season than they play in the initial germination and recruitment of one to two year seedlings. Finally, the time effect on seedling density was highly significant, indicating that seedling densities varied across the three growing seasons. The direction of the time effect differed from that of total seedling density; the density of seedlings >2 years old increased with time, while total seedling density declined.

Table 4-4. Repeated measure MANOVA for density of *P. nigra* seedlings greater than two years of age within foredune, wetpanne and inland blowout seral stages and at each of two light levels (canopy and gap) across the growing seasons of 1994-1996.

Effect	Wilks Lambda	Exact F	DF Numerator	DF Denominator	p
Between subjects					
Stage	.648	3.26	2	12	.074
Light	.782	3.35	1	12	.092
Stage*Light	.849	1.07	2	12	.374
Within Subjects					
Time	.370	9.37	2	11	.004
Time*Stage	.342	3.90	4	22	.015
Time*Light	.919	0.48	2	11	.629
Time*Stage*Light	.757	0.76	4	22	.525

Seedling size.-- Juvenile seedlings (more than one season old) growing in wetpannes and inland blowouts in 1996 were two to four times taller in gap than canopy plots (Figure 4-8, Table 4-5). Log height of juvenile seedlings in foredunes did not differ across gap and canopy plots, however, nor did height vary with seral stage.

Table 4-5. ANOVA Table for log height of seedlings in foredune, wetpanne and inland blowout seral stages and in canopy and gap plots in established quadrats in 1996. 181 seedlings were measured.

Source	SS	MS Num	DF	F Ratio	p
Stage	0.47401	0.237	2	2.3318	0.1442
Site(Stage)	0.74141	0.12357	6	1.8501	0.0922
Light	3.05117	3.05117	1	45.6820	<.0001
Light*Stage	1.66273	0.83137	2	12.4472	<.0001
Error	11.28775	0.066791	169		

Survivorship.-- Seedling survivorship was two to three times higher in gap plots than under Austrian pine canopy (Figure 4-9, Table 4-6). In canopy plots, survivorship ranged from 19% to 46%, while survivorship in gaps was higher at 33% to 100%. Among seral stages, survivorship was highest in inland blowout gap plots (93-100%) and lowest in foredune canopy plots (19 - 36%).

Survivorship varied across years as well; a higher proportion of seedlings survived from 1995-1996 than from 1994-1995 in all but wetpanne gap plots. A nested ANOVA of arcsine transformed seedling survivorship for 1994-1995 indicated that seral stage and light effects and their interactions were significantly different (Table 4-7). Survivorship did not vary significantly among stages in 1995-1996 (Table 4-8). The pattern of interactions differed across the two time periods as well. In 1994 - 1995, survivorship in canopy and gap plots in foredunes did not differ, but by 1995-1996 survivorship in foredune canopy plots was significantly lower than in gap plots. Wetpanne canopy and gap survivorship were not statistically different in 1995-1996, but they were in 1994-1995. This indicates that the conditions in 1994-1995 were more conducive to survivorship in wetpanne gaps, and less so in foredune gaps than were the 1995-1996 conditions.

Table 4-6. Seedling survivorship in two growing seasons in three seral stages and in canopy and gap plots. N represents the number of quadrats which contained seedlings for which survivorship was determined across the time period. Contrasts between arcsine transformed seedling survivorship within each seral stage were performed within each time period to determine significant differences. Means marked with an asterisk were significantly different among light treatments within seral stage ($p<0.05$).

		1994 - 1995			1995 - 1996		
Seral Stage	Light	Mean	S.E.	n	Mean	S.E.	n
Foredune	Canopy	0.185	0.034	39	0.358*	0.093	23
	Gap	0.328	0.070	28	0.638*	0.087	18
Wetpanne	Canopy	0.255*	0.075	31	0.462	0.132	13
	Gap	0.889*	0.048	27	0.554	0.075	27
Inland	Canopy	0.285*	00.073	33	0.417*	0.149	12
Blowout	Gap	0.933*	0.040	30	1.000*	0	30

Table 4-7. ANOVA Table for 1994-1995 arcsine transformed survivorship of seedlings in foredune, wetpanne and inland blowout seral stages growing in canopy and plots (light) in established quadrats. Survivorship was calculated for 188 quadrats.

Source	SS	MS	DF	F Ratio	p
Stage	9.007	4.503	2	10.940	0.009
Site(Stage)	2.495	0.416	6	1.673	0.130
Light	23.518	23.518	1	94.611	<.0001
Light*Stage	6.256	3.128	2	12.585	<.0001
Error	43.749	0.249	176		

Structure and dynamics.-- Population size structure of the new recruits was very similar in canopy plots of all seral stages; structure of foredune gap populations was also similar to canopy plots (Figure 4-10, population sizes (n) in Table 4-9). In 1994, the highest proportion of individuals in the population were germinants, but in the two successive years the population shifted to a majority of individuals in the smallest juvenile size class (<10cm in height). No seedlings greater than 10cm in height were found in any of the canopy plots, though a small percentage of individuals (0.6% - 6.8%) exceeded 10cm in the foredune gaps.

The population was much more evenly distributed among life history stages in wetpanne and inland blowout sites. Nearly equal proportions of individuals were found in j2 and j3 classes in 1995 and 1996 in these sites. In addition, the proportion of individuals >25cm in height was highest in these gap plots (1.5% - 22.7% of the population). The proportion of germinants was 1.6 to 46 times higher in 1994 than in any successive year, indicating that 1994 was a relatively high recruitment year for *P. nigra*.

Table 4-8. ANOVA Table for 1995-1996 arcsine transformed survivorship of seedlings in foredune, wetpanne and inland blowout seral stages and in canopy and gap plots in established quadrats. Survivorship was calculated for 123 quadrats.

Source	SS	MS	DF	F Ratio	p
Stage	2.723	1.363	2	3.882	0.070
Site(Stage)	2.120	0.353	6	1.063	0.389
Light	5.707	5.707	1	17.168	<.0001
Light*Stage	2.424	1.212	2	3.646	<0.030
Error	36.897	0.332	111		

Table 4-9. Population size of regenerating *P. nigra* in three years in three seral stages in gap and canopy plots. No adults were included.

	1994		1995		1996		Area sampled (m^2)	
Seral Stage	Gap	Canopy	Gap	Canopy	Gap	Canopy	Gap	Canopy
Foredune	147	155	57	37	51	18	56	55
Wetpanne	61	55	51	10	32	11	61	60
Inland Blowout	36	65	35	13	36	6	620*	60

*** Total inventories were taken for entire blowout gap plots due to low seedling densities.**

Projection matrices.-- Transition matrices for 94-95 and 95-96 *P. nigra* populations in canopy plots indicated that no transitions beyond the j1 life stage had yet occurred (Table

4-10 and 4-11). Matrices for gap plots showed that survivorship of seedlings increased with size. For example, survivorship of germinants in wetpanne gaps was 73%, but was 100% for j1's. In addition, inland-blowout-gap individuals had the highest survivorship.

Projected population growth rates (lambda) varied with seral stage and with year where the probability of remaining an adult was 99% (Table 4-12) and yielded values that would indicate rapidly increasing populations (1.201) to slightly declining populations (0.997). These values were calculated only for gap plots because seedlings never grew taller than 10cm in canopy plots. From 1994 to 1995, all populations were increasing (lambda >1), and wetpanne sites had the highest population growth rates. In 1995-1996, however, population growth rates indicated that the populations were in decline. Growth rates could not be calculated in 1995-1996 for inland blowout populations because no germinants were present in 1996, thereby blocking the future population growth.

Population growth rates were approximately 0.02 lower for projections in which $P_{aa} = 0.95$. In the transition from 1994 to 1995, wetpannes still had the highest population growth rate, but foredune and inland blowout populations were increasing as well (1.028 and 1.022). From 1995-1996, growth rates in foredune and wetpanne were nearly equal and indicated that the population was declining.

A comparison of projected population sizes among seral stages in 1994-1995 indicated that if conditions remained as they were during this time period, the population of wetpanne sites would exceed their initial population sizes by 10,850 times in 50 years (Table 4-13). Foredune populations were projected to increase only 27 times in 50 years, while inland blowouts were projected to increase five-fold. If conditions from the 1995-1996 growing season were to continue, populations were projected to increase by 8% in 50

Table 4-10. 1994-1995 transition matrices for regenerating *Pinus nigra* populations in three seral stages in canopy and gap plots.

Foredune Canopy

	g	j1	j2	j3	a
g	-	-	-	-	95.883
j1	0.177	0.857	-	-	-
j2	-	-	-	-	-
j3	-	-	-	-	-
a	-	-	-	-	0.990
Tot Surv	0.177	0.857	0	0	0.990
Initial	141	14	0	0	5*

Foredune Gap

	g	j1	j2	j3	a
g	-	-	-	-	77.325
j1	0.27	0.647	0.900	-	-
j2	-	0.059	0.050	-	-
j3	-	-	0.040	0.950	-
a	-	-	-	0.040	0.990
Tot Surv	0.270	0.706	0.990	0.990	0.990
Initial	111	24	1	1	5

Wetpanne Canopy

	g	j1	j2	j3	a
g	-	-	-	-	5.373
j1	0.027	0.5	-	-	-
j2	-	-	-	-	-
j3	-	-	-	-	-
a	-	-	-	-	0.990
Tot Surv	0.027	0.500	0	0	0.990
Initial	37	18	0	0	5

Wetpanne Gap

	g	j1	j2	j3	a
g	-	-	-	-	5.012
j1	0.7	0.667	0.048	-	-
j2	0.033	0.333	0.714	-	-
j3	-	-	0.190	0.950	-
a	-	-	-	0.040	0.990
Tot Surv	0.733	1.000	0.942	0.990	0.990
Initial	30	9	21	1	5

Inland Blowout Canopy

	g	j1	j2	j3	a
g	-	-	-	-	14.018
j1	0.138	0.714	-	-	-
j2	-	-	-	-	-
j3	-	-	-	-	-
a	-	-	-	-	0.990
Tot Surv	0.138	0.714	0	0	0.990
Initial	58	7	0	0	5

Inland Blowout Gap

	g	j1	j2	j3	a
g	-	-	-	-	0.260
j1	0.889	0.615	0.083	0	-
j2	-	0.385	0.583	0.470	-
j3	-	-	0.333	0.480	-
a	-	-	-	0.040	0.990
Tot Surv	0.889	1.000	1.000	0.990	0.990
Initial	9	13	12	2	5

*Initial adult values are all set at n=5 since the mean stand density of trees is approximately five for the area sampled to determine these transition probabilities.

Table 4-11. 1995-1996 transition matrices for regenerating *Pinus nigra* populations in three seral stages in canopy and gap plots.

Foredune Canopy

	g	j1	j2	j3	a
g	-	-	-	-	16.496
j1	-	0.419	-	-	-
j2	-	-	-	-	-
j3	-	-	-	-	-
a	-	-	-	-	0.990
Tot Surv	0	0.419	0	0	0.990
Initial	0	43	0	0	5*

Foredune Gap

	g	j1	j2	j3	a
g	-	-	-	-	17.527
j1	0.087	0.629	0.900	-	-
j2	-	0.043	0.050	-	-
j3	-	-	0.040	0.950	-
a	-	-	-	0.040	0.990
Tot Surv	0.087	0.672	0.990	0.990	0.990
Initial	23	70	1	1	5

Wetpanne Canopy

	g	j1	j2	j3	a
g	-	-	-	-	5.91
j1	-	0.579	-	-	-
j2	-	-	-	-	-
j3	-	-	-	-	-
a	-	-	-	-	-
Tot Surv	0	0.579	0	0	0.990
Initial	0	19	0	0	5

Wetpanne Gap

	g	j1	j2	j3	a
g	-	-	-	-	0.143
j1	1	0.25	-	-	-
j2	-	0.15	0.5	-	-
j3	-	-	0.167	0.950	-
a	-	-	-	0.040	0.990
Tot Surv	1	0.400	0.667	0	0.990
Initial	1	40	18	3	5

Inland Blowout Canopy

	g	j1	j2	j3	a
g	-	-	-	-	0.519
j1	-	0.333	-	-	-
j2	-	-	-	-	-
j3	-	-	-	-	-
a	-	-	-	-	0.990
Tot Surv	0	0.579	0	0	0.990
Initial	0	18	0	0	5

Inland Blowout Gap

	g	j1	j2	j3	a
g	-	-	-	-	-
j1	-	0.526	-	-	-
j2	-	0.421	0.538	0.200	-
j3	-	-	0.462	0.760	-
a	-	-	-	0.040	-
Tot Surv	0	0.947	1.000	1.000	0.990
Initial	0	19	13	5	5

*Initial adult values are all set at n=5 since the mean stand density of trees is approximately five for the area sampled to determine these transition probabilities.

years in foredune sites and decrease to 1/4 of their initial size in wetpanne sites. If the projection was run for a longer period in foredunes, however, population size would decrease, since lambda <1.

Table 4-12. *P. nigra* population growth rates in gap plots in three seral stages as calculated from projection matrices from 1994-1995 and 1995-1996 transitions. Inland blowout population growth rates were inestimable for the second time period because none of the seeds transitioned to juveniles during this time.

	1994-1995		1995-1996	
Seral Stage	where P_{aa}=.99	where P_{aa}=.95	where P_{aa}=.99	where P_{aa}=.95
Foredune	1.047	1.028	0.997	0.970
Wetpanne	1.201	1.190	0.998	0.971
Inland Blowout	1.038	1.022	-	-

Table 4-13. Projected population size in three seral stages calculated from transition matrices for 1994-1995 and 1995-1996, where P_{aa}=0.99.

		1994-1995		1995-1996	
Years Elapsed Since Start	Foredune	Wetpanne	Inland Blowout	Foredune	Wetpanne
Initial	151	66	41	100	67
5	675	196	46	123	19
15	876	1152	62	116	18
25	1289	7270	88	114	18
50	4029	716000	221	108	18
Population Growth Rate	1.046	1.201	1.038	0.997	0.998

Elasticities indicated that the greatest proportional contribution to the growth rate in all seral stages is derived from the transitions in the j3 and adult life stages (Table 4-14). In the time period from 1995-1996 when survivorship in the earlier life history stages was lower, transitions in the j3 and adult life stages contributed to more than 90% of the population growth rate. In the 1994-1995 period in wetpanne and inland blowout sites,

Table 4-14. Elasticities* for 1994-1995 and 1995-1996 transition matrices for regenerating *pinus nigra* populations in three seral stages in gap plots, where P_{aa}=0.99.

<u>1994-1995</u>

Foredune Gap

	g	j1	j2	j3	a
g	-	-	-	-	0.029
j1	0.029	0.054	0.004	-	-
j2	-	0.033	0.002	-	-
j3	-	-	0.029	0.284	-
a	-	-	-	0.029	0.506

Wetpanne Gap

	g	j1	j2	j3	a
g	-	-	-	-	0.051
j1	0.048	0.107	0.038	-	-
j2	0.008	0.086	0.131	-	-
j3	-	-	0.051	0.194	-
a	-	-	-	0.051	0.240

Inland Blowout Gap

	g	j1	j2	j3	a
g	-	-	-	-	0.023
j1	0.023	0.058	0.017	-	-
j2	-	0.040	0.132	0.064	-
j3	-	-	0.086	0.074	-
a	-	-	-	0.023	0.462

<u>1995-1996</u>

Foredune Gap

	g	j1	j2	j3	a
g	-	-	-	-	0.006
j1	0.006	0.012	0.001	-	-
j2	-	0.007	0.0004	-	-
j3	-	-	0.006	0.122	-
a	-	-	-	0.006	0.834

Wetpanne Gap

	g	j1	j2	j3	a
g	-	-	-	-	0.007
j1	0.007	0.002	-	-	-
j2	-	0.007	0.007	-	-
j3	-	-	0.007	0.132	-
a	-	-	-	0.007	0.825

Inland Blowout Gap

*All elasticities reflect transitions from Table 4-10 and 4-11, where the probability of remaining an adult = 0.99.
Calculation of elasticities was not possible for the 1995-1996 Inland Blowout Gap matrix, since there were no transitions to the germinant life stage during that time period.

Table 4-15. Elasticities* for 1994-1995 and 1995-1996 transition matrices for regenerating *Pinus nigra* populations in three seral stages in gap plots where P_{aa}=0.95.

1994-1995

Foredune Gap

	g	j1	j2	j3	a
g	-	-	-	-	0.005
j1	0.031	0.062	0.005	-	-
j2	-	0.037	0.002	-	-
j3	-	-	0.031	0.384	-
a	-	-	-	0.031	0.384

Wetpanne Gap

	g	j1	j2	j3	a
g	-	-	-	-	0.052
j1	0.048	0.114	0.041	-	-
j2	0.004	0.090	0.140	-	-
j3	-	-	0.052	0.204	-
a	-	-	-	0.052	0.204

Inland Blowout Gap

	g	j1	j2	j3	a
g	-	-	-	-	0.023
j1	0.023	0.072	0.025	-	-
j2	-	0.047	0.184	0.091	-
j3	-	-	0.114	0.101	-
a	-	-	-	0.023	0.299

1995-1996

Foredune Gap

	g	j1	j2	j3	a
g	-	-	-	-	0.010
j1	0.010	0.020	0.001	-	-
j2	-	0.011	0.0006	-	-
j3	-	-	0.010	0.464	-
a	-	-	-	0.010	0.464

Wetpanne Gap

	g	j1	j2	j3	a
g	-	-	-	-	0.010
j1	0.010	0.004	-	-	-
j2	-	0.010	0.011	-	-
j3	-	-	0.010	0.467	-
a	-	-	-	0.010	0.467

Inland Blowout Gap

*All elasticities reflect transitions from Table 4-10 and 4-11, except that here the probability of remaining an adult = 0.95. Calculation of elasticities was not possible for the 1995-1996 Inland Blowout Gap matrix, since there were no transitions from seed to germinant during that time period.

transitions in the j3 and adult life stages contributed less than half to the population growth rate. When the probability of remaining an adult was decreased to 95%, the proportional contribution of the j3 and adult life stages were 2-10% less than when P_{aa} =99% (Table 4-15).

Microsite variability

Community attributes.-- Quadrats located within canopy plots in all three seral stages had a high percentage of needle litter cover (87-88%), very little deciduous litter cover (0.1-7%), and a low percentage of bare soil (0.7- 2.7%) (Table 4-16). Gap quadrats varied across seral stages in litter attributes. Foredune-gap quadrats had 11 times more needle litter cover than inland blowouts, while wetpanne-deciduous-litter cover was three times that of foredunes and seven times higher than inland-blowout deciduous-litter cover. Bare soil was most prevalent in inland-blowout-gap quadrats (85%), and very low in both foredune and wetpanne gap quadrats (5-6%).

Table 4-16. Average % needle and deciduous litter cover, and % bare soil in canopy and gap plots in three seral stages. N refers to the number of m^2 quadrats sampled. Significant ANOVA results for Stage, Site(Stage), Light and Light*Stage interactions are listed as w=stage effect, x=site(stage) effect, y=light effect, and z=light*stage effect.

Ground Cover	Needle Litter (%)		Deciduous Litter (%)		Bare Soil (%)	
	Canopy	Gap	Canopy	Gap	Canopy	Gap
Foredune	85.2	64.8	0.7	22.3	2.67	4.82
Wetpanne	83.1	17.9	7.1	71.3	2.69	6.45
Inland Blowout	87.1	5.9	0.1	7.6	0.69	84.67
n	174	145	174	145	174	134
Significance	w y z		w x y z		w x y z	

Soil moisture and pH measurements were taken only in foredune and wetpanne sites (Table 4-17). Soil moisture ranged from 0.72 to 1.43% in canopy plots in wetpannes and foredunes, similar to values in foredune gap plots (0.72 - 0.74%). Wetpanne soil moisture in gap plots was 10-19 times higher than that of canopy and foredune gap plots (11 - 13%). In the top 5cm of soil, pH was .3 to .4 units lower in canopy than gap plots and 0.2 to 0.8 units lower than at a depth of 10-15cm. Additionally, foredune soil was 0.4 to 0.6 pH units more basic than wetpanne soil.

Table 4-17. Average soil moisture and soil pH at two depths (0-5cm and 10-15cm) in canopy and gap plots in foredune and wetpanne seral stages. N refers to the number of m^2 quadrats sampled. Significant ANOVA results for Stage, Site(Stage), Light and Light*Stage interactions are listed as w=stage effect, x=site(stage) effect, y=light effect, and z=light*stage effect.

Soil Factors	Soil Moisture at 0-5cm (%)		Soil Moisture at 10-15cm (%)		Soil pH at 0-5cm		Soil pH at 10-15cm	
	Canopy	Gap	Canopy	Gap	Canopy	Gap	Canopy	Gap
Foredune	1.16	0.74	0.72	0.72	5.65	5.92	6.44	6.51
Wetpanne	1.43	13.48	0.91	10.52	5.11	5.56	5.89	5.91
n	75	75	75	73	77	74	77	74
Significance	x y z		x y z		w y		NS	

Light intensity and canopy openness were higher in gaps than canopy plots, but differed across stages in gap plots (Table 4-18). Foredune gap quadrats received the lowest light intensities and had the least open space in the canopy, while wetpannes were characterized by intermediate light intensities and canopy openness. Inland blowout gaps had three times the light intensity of foredune gaps and 2.5 times the canopy openness.

Biotic factors varied across canopy and gap plots and also among stages (Table 4-19). Species richness was lowest in canopy plots, but wetpanne canopy quadrats contained three times more species than inland blowouts. Wetpanne gap species richness was four times higher than both foredune and inland blowout gap quadrats which averaged 2.5 species per m^2. Understory cover was low in canopy plots (0.4 - 5.2%), but foredune canopy plots had more vegetative cover than did wetpannes. Inland blowout gap cover was minimal (8%), but foredune and inland blowout cover was high (52 - 80%).

Table 4-18. Average light intensity and canopy openness in canopy and gap plots in three seral stages. N refers to the number of m^2 quadrats sampled. Significant ANOVA results for Stage, Site(Stage), Light and Light*Stage interactions are listed as w=stage effect, x=site(stage) effect, y=light effect, and z=light*stage effect.

Light Factors	Light Intensity (microeinsteins*m^{-2}s)		Canopy Openness (%)	
	Canopy	Gap	Canopy	Gap
Foredune	116.62	464.58	8.08	33.04
Wetpanne	80.88	773.90	4.83	56.10
Inland Blowout	84.83	1456.43	6.69	85.12
n	172	146	174	147
Significance	w x y z		w x y z	

Community correlates with survivorship.-- Strong correlations suggested that litter and light were both important to the survivorship of *P. nigra* seedlings during 1994-1995, but that the amount of bare ground in the plot was most important in regulating survivorship during the period of 1995-1996 (Table 4-20). From 1994-1995, survival was strongly negatively correlated (-0.624) with the amount of needle litter in the plot and positively correlated with light-related factors (light intensity (0.523) and canopy openness (0.611)). These same factors were also significantly correlated with survivorship the following year (95-96), but the association was not as strong. Deciduous litter, litter depth and soil factors (pH and soil moisture) were not significantly correlated with 1995-96 survivorship, and were only weakly so in 1994-95.

Table 4-19. Average species richness and understory cover in canopy and gap plots in three seral stages. N refers to the number of m^2 quadrats sampled. Significant ANOVA results for Stage, Site(Stage), Light and Light*Stage interactions are listed as w=stage effect, x=site(stage) effect, y=light effect, and z=light*stage effect.

Vegetation	Species Richness (#species/m^2)		Understory Cover (%)	
	Canopy	Gap	Canopy	Gap
Foredune	0.95	2.64	5.20	52.35
Wetpanne	1.63	8.80	3.89	80.41
Inland Blowout	0.44	2.23	0.35	8.17
n	174	147	163	145
Significance	w y z		w x y z	

Table 4-20. Spearman rank correlations between Austrian pine seedling survivorship and abiotic and biotic variables. Soil moisture and pH values were taken for a subsample of quadrats in only foredune and inland blowout sites, therefore sample sizes are smaller for these correlations. n indicates the number of quadrats used for the correlation analysis.

	Survivorship	1994-	1995	Survivorship	1995-	1996
Variable	Spearman Rho	p	n	Spearman Rho	p	n
Needle Litter	-0.6242	***	169	-0.4096	***	111
Deciduous Litter	0.4704	***	169	0.1073	NS	111
Litter Depth	-0.2430	**	96	-0.2330	NS	56
Bare Ground	0.4156	***	169	0.5960	***	111
Species Richness	0.4295	***	169	-0.0503	NS	111
Understory Cover	0.4104	***	169	-0.0329	NS	111
Canopy Openness	0.6111	***	169	0.4734	***	111
Light Intensity	0.5246	***	186	0.4219	***	122
Soil Moisture (0-5cm)	0.3607	**	88	0.2036	NS	51
Soil Moisture (10-15cm)	0.4275	***	88	0.2280	NS	51
Soil pH (0-5cm)	0.0744	NS	88	0.0152	NS	51
Soil pH (10-15cm)	-0.0783	NS	88	0.0607	NS	51

** $0.001 \le p < 0.01$
*** $p < 0.001$

Correlations between the number of seedlings present in each plot and environmental factors were also examined, and were found to be much weaker than those with survivorship. In 1994, seedling counts were weakly positively correlated with needle litter (rho = 0.20) and negatively correlated with deciduous litter (rho = -0.23). None of the other correlations with 1994 seedling counts were statistically significant. Weak correlations (rho = -0.29 to 0.369) were evident between both 1995 and 1996 counts and all environmental factors excepting soil moisture and soil pH. The strongest correlations in 1995 were with canopy openness (rho = 0.338) and light intensity (rho = 0.249), and in 1996 with light intensity (rho = 0.369), needle litter (rho = -0.296) and bare ground (rho = 0.297).

DISCUSSION

Assuming tree seedlings were planted after two or three years of growth, introduced *P. nigra* individuals at SDSP were between 25 and 42 years of age during the time of this study, and the older trees were approaching the peak of reproductive maturity (60-90 years of age). Though many barriers separated seed production from actual germination and establishment of young *P. nigra* individuals, many seeds were germinating, and some seedlings were becoming established.

Reproductive output

The earliest filter in pine regeneration is at the level of seed production, which can be constrained by cone set, pollination, and embryo abortion. Cone set has been shown to be limited by environmental factors including light intensity, temperature, water stress and nutrient availability (Owens 1995), all of which vary among successional stages in the dunes. Pines with fewer actively growing branch tips will produce fewer cones. Foredune *P. nigra* stand densities were significantly less than those of wetpanne and forest edge stands (Chapter 2), and the shading that occurs in the denser stands may limit the number of growing branch tips and inhibit cone initiation (Table 4-18). This may begin to account for the 10 to 40-fold greater per-tree seed production in foredune stands relative to wetpannes and forest edges (Figure 4-3).

Because P. *nigra* seed production did not differ across years, it is assumed that neither 1994 or 1995 was a mast year. Heavy cone crops are typically produced every three to four years in *P. nigra.* (Vidakovic 1991).

Pollination limitation can occur following cone set, but does not become evident until the germination phase of the life cycle. Unpollinated ovules may develop normally until the date of fertilization, but the seeds that develop will not be filled and will not germinate (Owens 1995). Cold, wet weather during the short time window of pollen receptivity in the spring (three days) may inhibit pollen cloud formation which is essential for significant seed set to occur in pines (Vidakovic 1974). Climatic differences may be the cause of the differences in seed germinability across years in the dunes (Table 4-1), although an examination of monthly precipitation and temperature records for May and June of 1993 and 1994, indicates that weather patterns were quite similar in these years during the time at which pollination would have taken place for the 1994- and 1995-collected cones. The majority of ungerminated seeds from both 1994 and 1995 were hollow (Leege personal observation), however, which suggests that pollination was unsuccessful for ungerminated seeds in these years. Perhaps other as yet unidentified factors are acting to influence these differences in seed germinablity across years.

If pollination does occur, the next constraint to seed production in conifers is embryo abortion, which may occur as a result of self-inviability (Owens 1995). Multiple fertilizations may occur in pines, but most self-fertilizations result in post-zygotic abortions. Seeds with aborted embryos will be filled but will not germinate. In foredunes where the *P. nigra* individuals are distributed in small groups and located in the path of the westerly winds off the lake, pollination limitation is likely severe. The only pollen source for these individuals is the small stands which they inhabit. If pollination does occur, the probability of selfing is much higher, which may result in the abortion of embryos following fertilization. The combination of pollination limitation and embryo abortion may be responsible for the significantly lower germinabilities of foredune seed (Table 4-1). Wetpanne and forest-edge seeds were most germinable and because stand densities in these seral stages are much greater, pollination limitation and the likelihood of selfing are probably much less.

The greatest source of variation in germinability was among trees within sites (Table 4-2). This may reflect genetic differences among trees, or differential pollination success as a result of location in the stand. Trees on the windward side of the stand are less likely to experience successful pollination than those on the leeward, since pollen will be dispersed in the direction of the prevailing wind.

Demography

Population structure and demography give a picture of past events which have shaped the population, but can also give an indication of its demographic future (Bullock et al. 1996). This information can be used in predicting invasion potential of *P. nigra* in the dune system.

Seedling density and survivorship.-- ***Pinus nigra*** seedling densities varied among successional stages and were highest in foredunes (Figure 4-5). This variation across stage is likely in response to the higher seed input from the foredune trees, but also reflects microsite differences in conditions conducive to germination and survivorship. Total seedling densities did not vary between canopy and gap plots, but densities of established seedlings greater than two years of age tended to be higher in gap plots (Figure 4-5), though this result was not statistically significant (Table 4-4). Seedling height and survivorship, which are both higher in gaps (Figure 4-8, Table 4-6), corroborate this finding and suggest that the "gap" classification encapsulates characteristics which are conducive to successful *P. nigra* regeneration. The comparison of total seedling densities with densities of older seedlings suggest that gap and canopy plots are equally conducive to dispersal and germination, but that gaps, due to their differing environmental conditions, are more likely to allow establishment of the pine seedlings over time.

The higher seedling densities in foredunes are not due to higher survial; survivorship was lowest in this seral stage for both 1994-1995 and 1995-1996 (Table 4-6). Foredunes have a greater average canopy cover than either of the other two seral stages, and lower average light intensity, as well as more needle litter (Tables 4-16 - 4-19), and these characteristics may negatively impact young seedlings.

Pinus nigra seedling survivorship was significantly higher in gaps than in canopy plots (Table 4-6 to 4-8). Gaps generally provide high light intensities, but low soil moisture, while plots under pine canopy provide low light intensities, but high moisture due to cooler temperatures and a deep layer of needle litter. Soil moisture is likely particularly important to germination and survivorship through the first season, but light availability may be more important in regulating establishment and growth in subsequent years. Additionally, seedling roots may be unable to penetrate the deep litter layer (subject to drying) to reach the soil under pine canopy and are consequently unable to become established after the first year.

Wetpanne gaps present a departure from the traditional forest gap, in that soil moisture levels are more than ten times that of other gap plots (Table 4-17). Therefore moisture limitation is not a consequence of occurrence in wetpanne gaps. Alternatively, wetpanne gaps are inundated for a period of time each growing season and survivorship may instead be inhibited by waterlogged and anaerobic soils in the early stages of growth.

Size structure.-- Population size-structure data suggest that all canopy plots were alike, regardless of the seral stage in which they were located, but that populations in foredune gaps were most similar to those in canopy plots (Figure 4-10). The even size structure of wetpanne and inland blowout gap populations suggests higher survivorship and stronger recruitment into larger size categories than that of foredune populations. These data indicate that the formation of gaps is essential to the regeneration of this species, but that in foredune sites, regeneration within gaps may be limited. In addition, the non-forested areas around the pine stands are very likely vulnerable to invasion, because they possess characteristics similar to those of gap plots.

Also of importance was the variation in the proportion of the population in the germinant life history category across years (Figure 4-10). The proportion of germinants was high in all seral stages in 1994, but was reduced to a small proportion of the population in successive years. This may be due to differences in seed input or germinability across years, but is most likely a response to differing climatic conditions during the critical time period during which germination took place. Water availability through the germinant life stage is well known to be a limiting factor in successful establishment. The conditions in 1994 were very wet at the beginning of the summer, while the two successive years were drier and not as conducive to germination and early survival of young pine seedlings. In 1995, seeds were highly germinable but the climatic conditions were not supportive of early survival. In 1996, the early summer conditions were very wet, but germinablity of seed was much lower, therefore limiting successful recruitment into the germinant life history stage. Regeneration of *P. nigra* appears to be constrained at different stages of its life history in different years.

Matrix projections indicate that population growth rates were highly variable across years but that those of wetpanne *P. nigra* populations were always highest (Table 4-12). Foredune and inland blowout growth rates were similar, but because initial population sizes were lower in inland blowouts, projected population sizes in 50 years were also much less (Table 4-13). Kephart and Paladino (1997) found significant spatiotemporal variation in growth rates of a rare perennial in two microhabitats and suggested that long term monitoring must be an essential part of a successful management strategy. Long-term projections of population size of *P. nigra* in the dunes, however, must be modified by the effects of successional change as well as by density dependent effects.

Because *P. nigra* population growth rates were so variable during the two transition periods for which they were determined, it is important to examine the relationship between climatic variables and population fluctuations. Based upon weather data from the years examined, it is hypothesized that June precipitation > 12.4cm (high) is too high for successful wind pollination, while June precipitation < 7.8cm (low) is too low for successful germination and seedling establishment. Successful recruitment and survivorship, and consequent population growth of *P. nigra* (lambda >1) would be expected to be associated with low June precipitation during pollination followed in two years by high June precipitation during germination and establishment of seedlings. Alternatively, unsuccessful recruitment and population decline would be expected to be associated with high June precipitation during pollination followed in two years by low

June precipitation during germination and establishment of seedlings. Climate data for the period of 1955-1997 for the Holland weather station, 13 km from SDSP, indicate that 12% of these series of years met the previously established criteria for poor conditions, and 16%, the criteria for good conditions for *P. nigra* population growth. If past weather patterns are predictive of the future, a net increase in *P. nigra* population size will be expected over time.

Elasticities indicate that the rate of transition from the largest juvenile (j3) to the adult life stage contributed the most to growth rates in these populations (Table 4-14 -4-15). This is in concordance with many other woody species (Silvertown et. al 1993) where stasis and progression in larger size categories contributes proportionally most to the growth rate. A hypothetical four percent reduction in survivorship for adults shifted the highest elasticities from the adult life stage to the j3 life stage and decreased the growth rate in all seral stages (Table 4-15). This can be interpreted to suggest that the adult stage is the most sensitive life history stage for *P. nigra* in the dunes and thereby the most important stage to control. The gradual removal of adults from the population is projected to slow population growth and may stem the invasion of this species in the dunes. Adult removal will increase light intensity, however, and may create conditions more conducive to pine seedling germination and growth.

Microsite variables

As is common among conifers, *Pinus nigra* seedling survivorship was closely correlated with light (Table 4-16). Gray and Spies (1996) found a strong positive relationship between light and conifer seedling survivorship in the Pacific Northwest, but also found that high soil surface temperatures and high transpiration rates in the most exposed sites resulted in cambial death and seedling desiccation. This would suggest that survivorship would peak at moderate light levels, but this pattern was not evident at SDSP.

The importance of light to seedling survivorship varied with the year, however. In 1995-1996, bare soil was the environmental factor most highly correlated with survivorship of *P. nigra* seedlings in the dunes (Table 4-16). Light appeared to play a more important role in establishment during years of high recruitment of germinants, but in years of low germinant recruitment, the presence of bare soil may facilitate root penetration to available water, which is likely more limiting in these years. Allen and Lee (1989) found bare soil to be a favorable microsite for *P. nigra* invasion in tussock grassland in New Zealand, but Tilman (1997) found no significant effect of bare soil with respect to community invasiveness in a native oak savannah in Minnesota.

The relative unimportance of soil pH in *P. nigra* seedling survivorship indicated that the acidic needle litter input of the pines is not unfavorably altering conditions for pine regeneration. Reduction in soil pH may have negative impacts upon the native vegetation, however, and may act to leach available nutrients (Clough 1991). Soil pH was lower under canopy than in gap plots, and higher in foredunes than wetpannes (Table 4-17).

Despite their lower seed production, higher species richness and understory cover, wetpannes were most susceptible of all seral stages to *P. nigra* invasion in the three years studied. It has long been held that areas of low understory cover and low species richness would be most susceptible to invasion (Crawley 1986, Fox and Fox 1986, Orians 1986), but this study has established otherwise in the dune system. Tilman (1997) found that invasibility was limited by increased species richness in oak savannah. The highest number of species in a 1m^2 plot in this study was 14 (in dune wetpannes), and 296 of 321 plots studied in all seral stages had fewer than 10 species within them. The oak savannah study investigated a majority of plots with 12-25 species (Tilman 1997), and perhaps the narrow point of overlap in the range of species richness in the two studies represents a threshold value at which the effect of species richness upon community invasibility changes. In addition, high species richness is just one of a suite of characteristics unique to wetpannes in the dune system. The combination of factors that comprise this dune habitat are conducive to *P. nigra* success. Not coincidentally, perhaps, is the fact that *P. banksiana*, the only pine native to the three seral stages investigated in this portion of the study, is located almost exclusively in wetpanne sites in this dune system. Preliminary studies suggest that the success of this native pine in seral stages other than the wetpanne is limited by low soil moisture and seed predation (Lichter pers. com.).

Conclusion

This study suggests that the recruitment and spread of *P. nigra* at SDSP is limited by different factors in different years. Environmental factors play a different role in the filtering process depending upon the size of the pool of germinants and the climatic conditions. Light availability, composition and cover of litter, and biotic factors such as understory cover and species richness are more highly positively correlated with seedling survivorship in years of high recruitment, while the availability of bare ground is the highest positive correlate with survivorship in years of low recruitment. The variability of the effects of environmental factors upon *P. nigra* seedling survivorship across years emphasizes the importance of long term monitoring in attempting to predict the invasiveness of introduced plant species. Matrix elasticities indicate that changes in the transition probabilities in the adult and largest juvenile stages are the most likely to alter population growth rates. Consequently, control of these life history stages is of greater consequence than management of smaller size classes. Despite the fact that management efforts ought to focus on reducing the survivorship of the larger size classes, this study indicates that the eventual distribution of *P. nigra* will largely be determined by its interactions with the environment during the early stages of its life.

This study also documents the successful reproduction and recruitment of *P. nigra* in three seral stages on the dunes of Lake Michigan. The introduced pine is clearly gaining a foothold in its novel environment, though differentially so in foredunes, wetpannes and inland blowouts. High *P. nigra* population growth rates in wetpannes in 1994-1995 suggest that this seral stage is most prone to invasion by the pine. Foredunes and inland blowouts appear to be less invasible, though their populations were increasing in 1994-1995 as well. The indication of successful *P. nigra* proliferation in the dune environment presented in this chapter signals the transition from non-native species introduction to biological invasion.

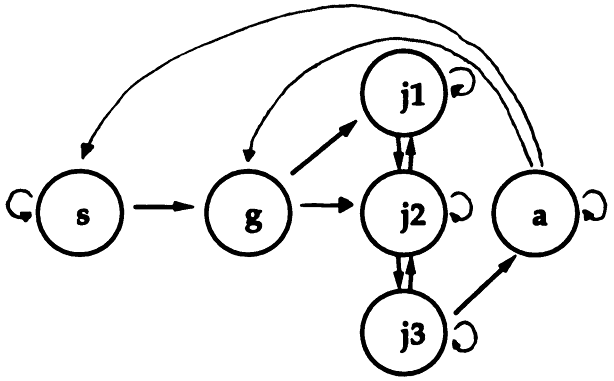


Figure 4-1. Life cycle for *Pinus nigra* where terms indicating the stages of the life cycle are defined as follows:

s = seed
g = germinant (first season seedling)
j1 = 0-10cm seedling
j2 = 10-25 cm seedling
j3 = >25 cm seedling
a = reproductive tree

Matrix Model

Stage at t

$$\begin{array}{llccccc}
 & & g & j1 & j2 & j3 & a \\
 & g & - & - & - & - & F_{ag} \\
\text{Stage at } t+1 & j1 & P_{gj1} & P_{j1j1} & P_{j2j1} & - & - \\
 & j2 & P_{gj2} & P_{j1j2} & P_{j2j2} & P_{j3j2} & - \\
 & j3 & - & - & P_{j2j3} & P_{j3j3} & - \\
 & a & - & - & - & P_{j3a} & P_{aa}
\end{array}$$

Figure 4-2. Matrix model for *P. nigra*. Life cycle terms are defined in Figure 4-1. P refers to the probability of transition from the life cycle stage at time t to the life cycle stage at time t +1. F is a fecundity coefficient that describes the adult contribution of offspring to time t + 1 during time t. The s stage was not included because seed bank transition probabilities were not known.

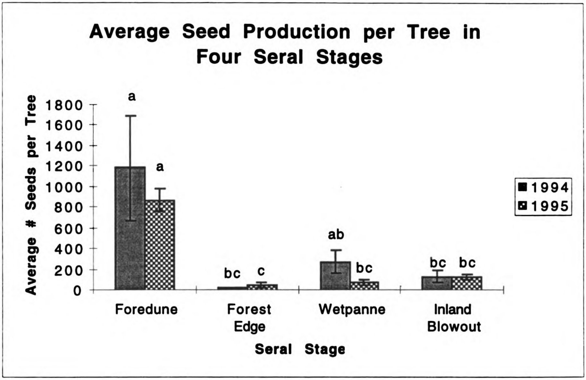


Figure 4-3. Mean 1994 and 1995 seed production per tree ±SE in Austrian pine stands in four seral stages. Means were calculated from cone counts from up to five reproductive trees, and seed counts in up to five cones per reproductive tree in five sites per seral stage, 1995 (n=5). Data taken from ten trees in each of three sites per seral stage in 1994 (n=3). Bars demarcated with different letters denote statistically significant differences in seed production among stages and across years (p=.05, Tukey all pairs comparison HSD).

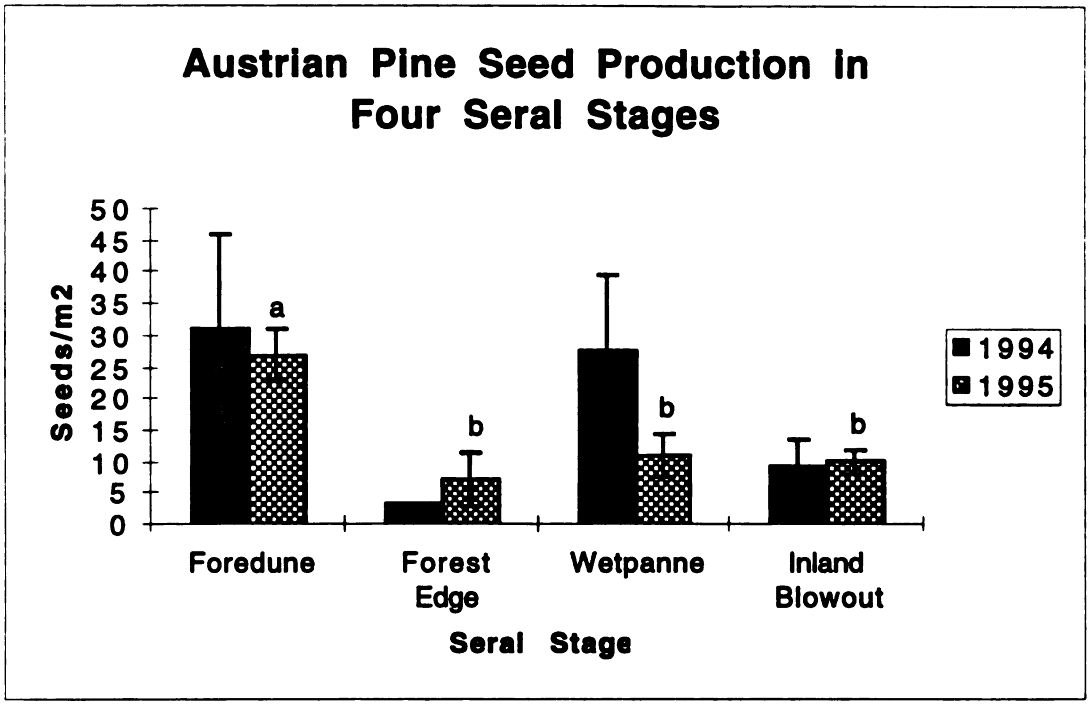


Figure 4-4. Mean seed production per unit area ±SE for 1994 and 1995 in Austrian pine stands in four seral stages. Means were calculated from cone counts from up to five reproductive trees, and seed counts in up to five cones per reproductive tree in five sites per seral stage, 1995 (n=5). Data taken from ten trees in each of three sites per seral stage in 1994 (n=3). Significance testing was done only for 1995 data. Bars demarcated with different letters denote statistically significant differences in 1995 seed production among stages (p=.05, Tukey all pairs comparison HSD).

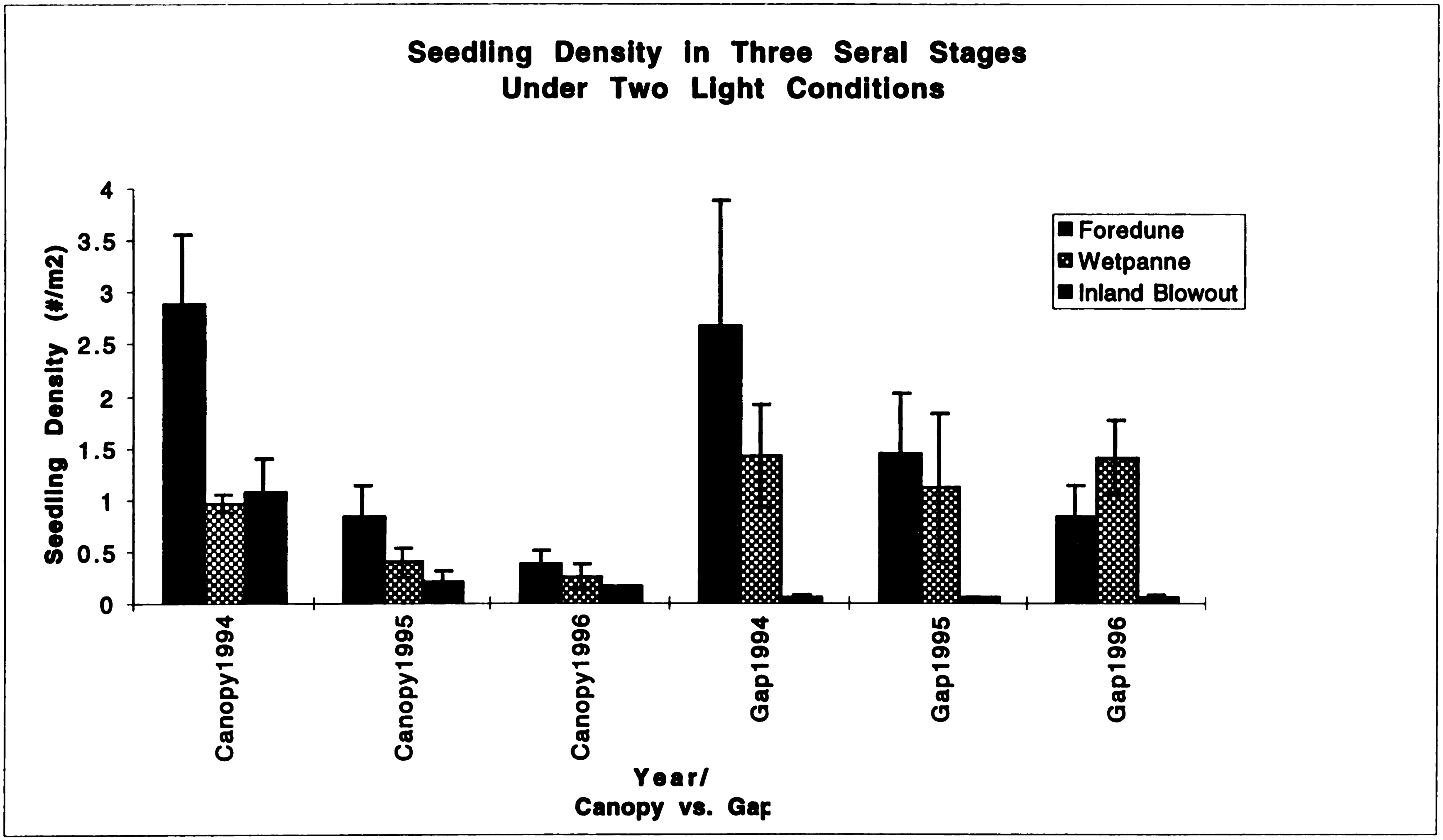
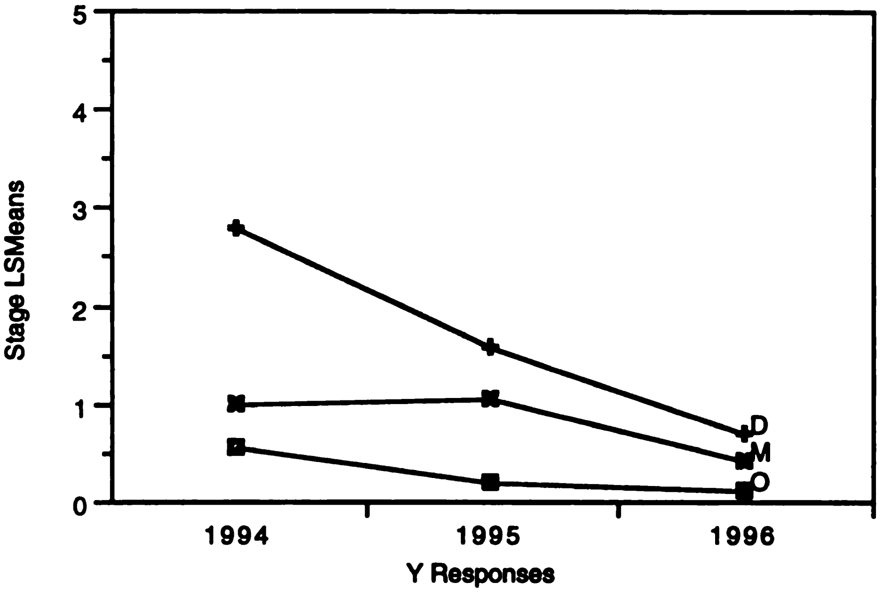


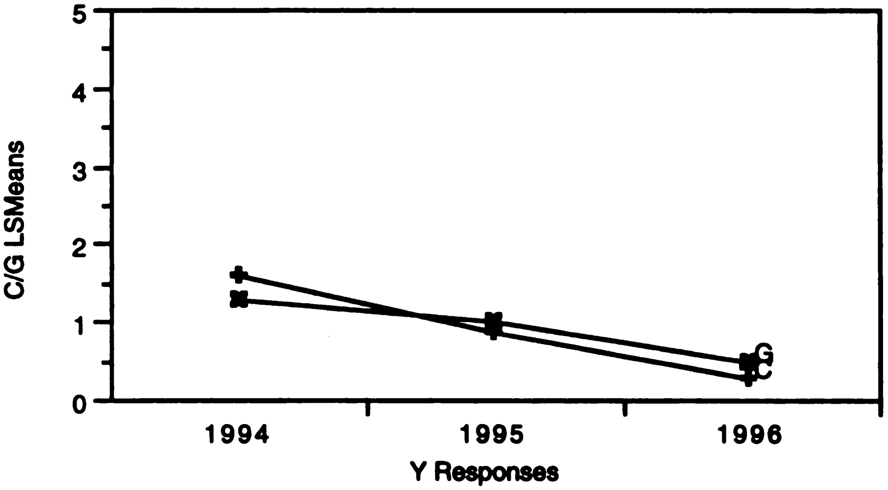
Figure 4-5. Seedling density ± SE in three seral stages in canopy and gap plots. Data are averages of densities of seedlings in three sites in each light level and in each seral stage in 1994-1996.

Stage



Stage	1994	1995	1996
D	2.79246032	1.57608605	0.69484127
M	1.00634921	1.06200919	0.43214286
O	0.57340153	0.1992155	0.11456638

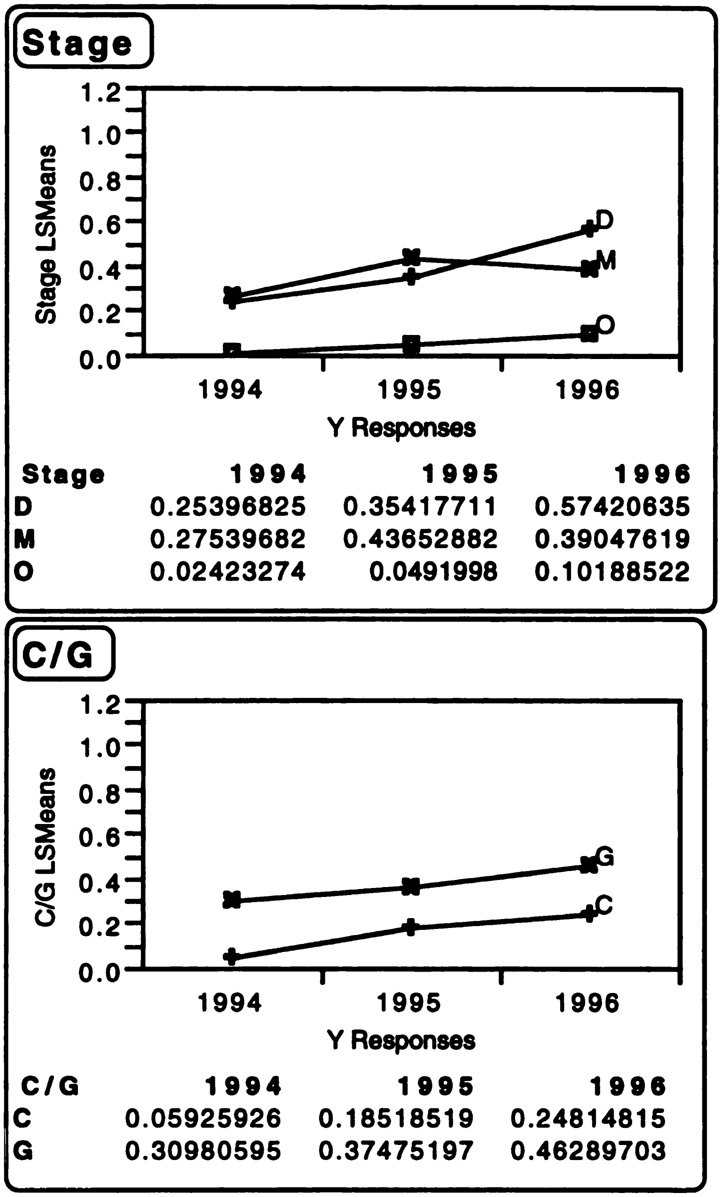
C/G



C/G	1994	1995	1996
C	1.62592593	0.87865497	0.30740741
G	1.28888145	1.01288552	0.52029293

Figure 4-6. a) Seedling density across three years in three seral stages: foredune (D), wetpanne (M) and inland blowout (O). Least square mean seedling densities are plotted against year.

b) Seedling density across three years in two light conditions: canopy (C) and gap (G). Least square mean seedling densities are plotted against year.



Stage	1994	1995	1996
D	0.25396825	0.35417711	0.57420635
M	0.27539682	0.43652882	0.39047619
O	0.02423274	0.0491998	0.10188522

C/G	1994	1995	1996
C	0.05925926	0.18518519	0.24814815
G	0.30980595	0.37475197	0.46289703

Figure 4-7. a) Density of >two-year-old seedlings across three years in three seral stages: foredune (D), wetpanne (M) and inland blowout (O). Least square mean seedling densities are plotted against year.
b) Density of >two-year-old seedlings across three years in two light conditions: canopy (C) and gap (G). Least square mean seedling densities are plotted against year.

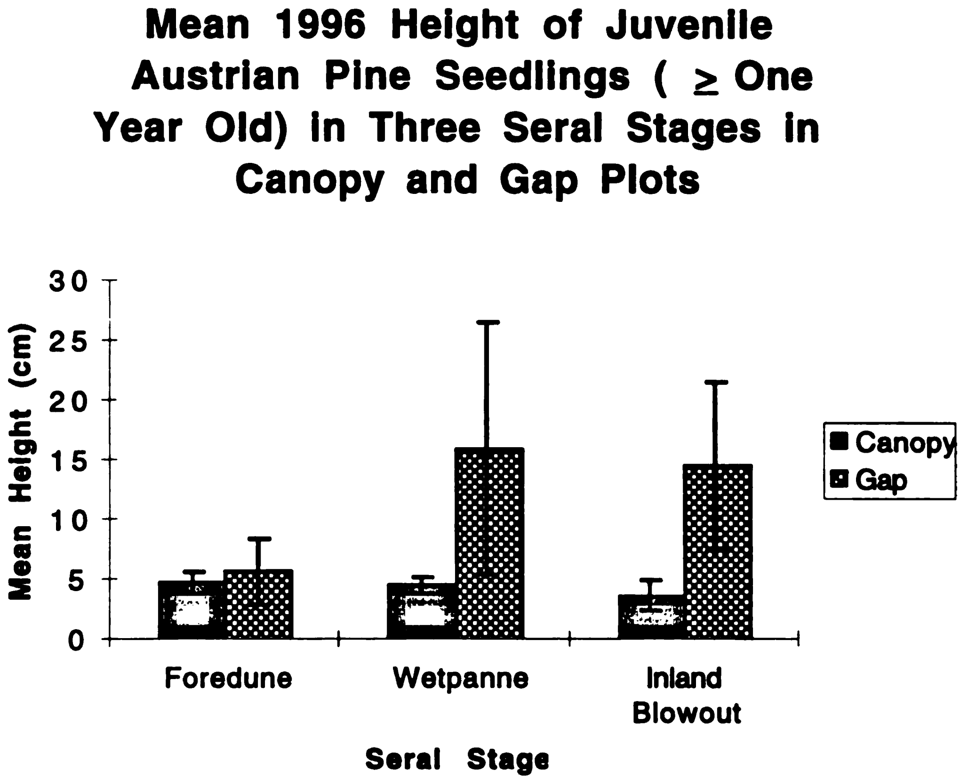


Figure 4-8. Mean height ± SE of juvenile Austrian pine seedlings (≥1y) in foredune, wetpanne and inland blowout seral stages in canopy and gap plots (n=3 sites). Seedlings measured in three sites in each seral stage in 1996.

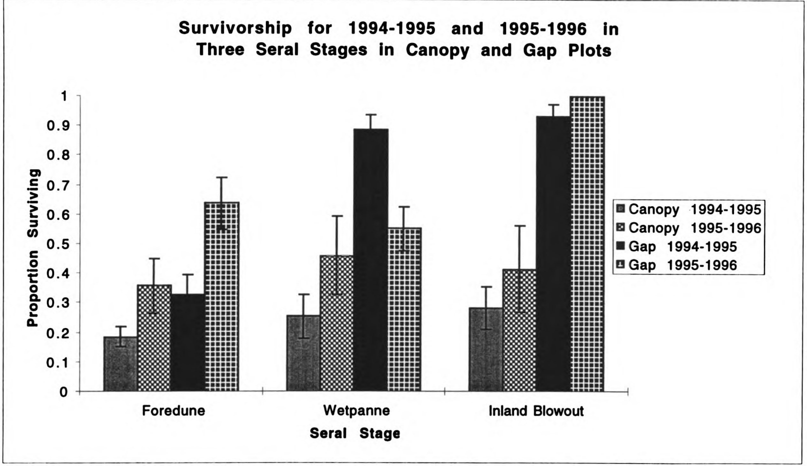


Figure 4-9. Seedling survivorship ± SE in three seral stages in canopy and gap plots over two growing seasons: 1994-1995 and 1995-1996.

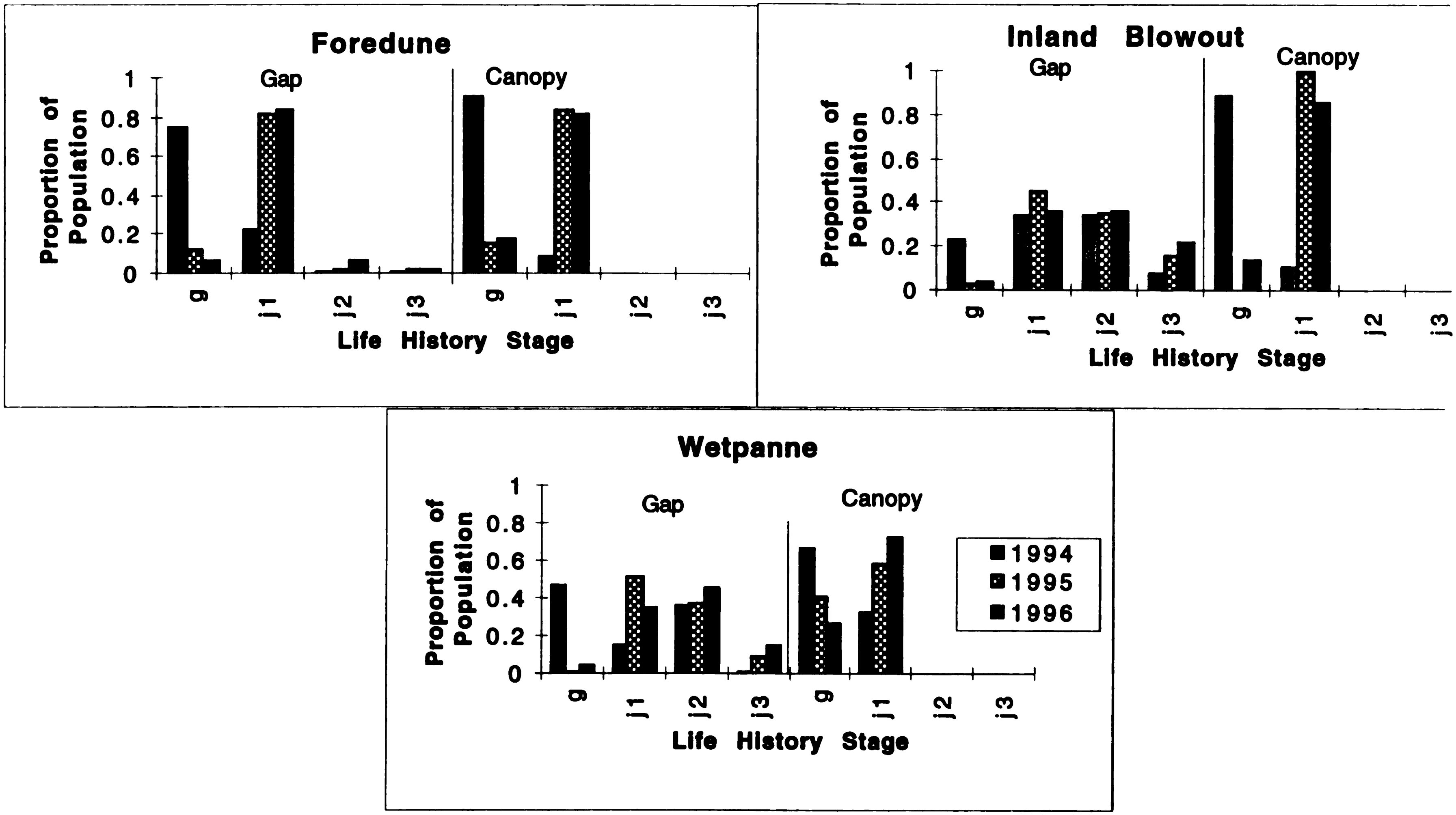


Figure 4-10. a)-c) Size structure in regenerating Austrian pine populations in three seral stages in gap and canopy plots. Data represent proportions of all individuals in four life history stages in each of three growing seasons (1994-1996). Life history stages are as follows: germinant (g), juvenile 1-3 (j1-j3) and where the germinant stage (g) was represented only by newly germinated individuals in their first growing season, and the juvenile stages were determined by height (j1<10cm, 10cm≤j2<25cm, 25cm<j3). None of the juveniles were reproducing.

CHAPTER 5

GENERAL CONCLUSIONS

This investigation provides an early diagnosis of a pine invasion on the sand dunes of Lake Michigan. The findings presented indicate that *P. nigra* clearly has the potential to threaten the ecological integrity of the dune system at SDSP. *Pinus nigra* has been successful in primary establishment, reproduction, and recruitment phases of the invasion process, and has therefore joined the ranks of the 10% of introduced species that escape cultivation and become naturalized (Williamson 1996).

Pinus nigra survived and grew equally well in foredunes, forest edges, wetpannes (ephemeral dune ponds), and inland blowouts and exhibited a broad ecological tolerance for diverse environmental conditions. The primary establishment phase of invasion did not exclude the pine from any of the dune habitats into which it has been planted, but established individuals appeared to be most growth limited by spring drought, even in wetpannes.

It is interesting to note that *P. nigra* exhibited ecological responses at different spatial scales in the different phases of early invasion. While primary establishment success did not correspond with the environmental differences among seral stages in the dunes, reproduction success clearly differed among seral stages. *Pinus nigra* seed production per tree and per unit area was highest in the foredunes and lowest in the forest edges, and appeared to be negatively correlated with stand density. The open-grown trees of the foredunes produced heavy crops of cones, whereas many of the densely planted forest edge trees did not reproduce at all. Seed germination varied from 10% to 67% across the two year period (1994-1995), perhaps as a response to weather conditions during pollination.

Pinus nigra seedling recruitment has also been successful in three of four seral stages at SDSP. Seedlings were extremely rare under pine canopy and in adjacent native forest in forest-edge sites, so this seral stage was not investigated further. Seedling densities were highest in foredune sites, most likely as a response to high seed input, but survivorship was lowest in this seral stage. Within stages, survivorship was positively associated with open or sparse canopy conditions, here referred to as gap plots, though environmental correlates with survivorship varied depending upon the size of the pool of new seedlings. In years with high numbers of germinants, light, understory cover, and species richness/m^2 were all positively correlated with survivorship, but in years of smaller germinant cohorts, the presence of bare soil was most highly associated with survivorship.

Pinus nigra had already significantly impacted native dune communities at SDSP, even though the second generation of individuals had not yet matured and the invasion was still in its earliest stages. Its effects were extensive; it reduced light intensity, increased soil development, and generally inhibited understory cover and species richness under its canopy. Composition of the pine understory community was often less than 20% similar to that of the adjacent dune community.

The population projection matrices suggest that *Pinus nigra* will persist on the dunes in foredune, wetpanne and inland blowout seral stages. Population growth rates varied across the years of 1944-95 and 1995-96, from rapidly increasing (1.201) to decreasing (0.970), but were always highest in wetpannes. At the very least, *Pinus nigra* populations are expected to remain stable in foredunes and inland blowouts; at most, they are expected to increase rapidly in wetpannes, expanding to 17 times their original numbers within 15 years.

The wetpanne habitat appeared to be most threatened by the invading pine.

Evidence of more successful primary establishment in this seral stage, as measured by height growth, suggested that wetpanne conditions were more conducive to pine growth than those in other seral stages. Reproduction was intermediate, but seedling survivorship was high, and matrix projections indicated that population growth rates were highest in wetpannes as well. The conditions conducive to the survivorship and growth of the parent trees appeared to aid in recruitment as well.

Wetpanne communities were already heavily impacted by the presence of the invader. Low light intensity, understory cover and species richness were evident under *P. nigra* canopy, but the environmental effects of *P. nigra* extended even into the wetpannes themselves. *Pinus nigra* threatened to alter the character of wetpannes by driving a conversion to a more terrestrial community, as suggested by the increased woody component in the flora, and by drying the soil, though present soil moisture content may reflect intrinsic differences between *P. nigra* and *P. banksiana* wetpannes. If these trends continue, the unique flora of the wetpanne habitat may be lost beneath the shade of the growing *P. nigra* recruits and as a response to the continued drying of the soil by increased transpiration of the trees.

Pinus nigra did not appear to be recruiting in the forest edge seral stage. Though primary establishment, or growth of the planted trees was successful, the reproduction and recruitment phases of the invasion process were not. The impact of *P. nigra* on understory cover and species richness was less pronounced in this seral stage, in that they were least inhibited of any seral stage, relative to sites without *P. nigra*. The presence of the pine also appeared to facilitate succession by extending the abiotic conditions of the native forest into the adjacent blowout. Woody tree species had recruited into larger size classes under pine canopy, and in the absence of significant pine regeneration, were projected to eventually dominate and replace the pines.

The prospects for *P. nigra* invasion and impact in inland blowout and foredune seral stages were similar. Primary establishment was successful, and near-equilibrium population growth rates suggested that the pines present would replace themselves. Impacts on the native dune communities were extreme, in that understory communities were nearly absent relative to sites without *P. nigra*. The woody tree and shrub species present under pine canopy rarely grew larger than seedlings and were not expected to replace the pines without significant gap formation.

Analysis of projection matrix elasticities suggests that the large juvenile and adult life-stages contributed most to population growth rates. Any alteration in survivorship of particular life-stages will in turn influence population projections and may be used to manage invasive pine populations. For example, if the survivorship of adult and large juvenile life- stages was curtailed by girdling or tree removal, population growth rates would be expected to decrease. Tree removal would result in gap formation, however, and data from this study show that gap characteristics are highly correlated with seedling survivorship. Increased survivorship would feed back to increase population growth rates, potentially negating the consequences of the reduction in adult survivorship. Therefore control of *P. nigra* populations at SDSP must include reducing survivorship of both adults and juveniles.

Considering that *P. nigra* appears not to be playing an important role in dune stabilization, and that its removal from the dunes would likely not be harmful, the following management recommendations are advised. For additional information, please see the full management plan for *P. nigra* at SDSP, to be filed with the Parks and Recreation Division of the Michigan DNR in Fall 1997.

Gradual removal of the adult pines by girdling is recommended for foredune and blowout stands. Regenerating saplings around these stands should be clipped at ground level every five years to control the spread of the pines. As the girdled pines die and light penetrates the canopy, the dominant species from the adjacent vegetation should be planted under the former pine canopy to facilitate the successful restoration of the dunes to their original state.

The same recommendations apply for wetpannes, but because this seral stage is most threatened by the presence of *P. nigra*, removal of the adult pines is much more urgent. It is not known if *P. nigra* stands are altering the hydrology of the wetpannes, however. Therefore trees should be girdled rapidly in several wetpannes, but left untouched in several others. Water levels in girdled and ungirdled stands should be monitored to determine if *P. nigra* is responsible for the drying of the wetpannes. It may not be possible to reverse the trajectory of succession in these wetpannes, but it will be important to discern the role that *P. nigra* plays in their apparent drying. Regenerating saplings should be clipped at ground level every 3 years, as population growth rates in wetpannes are high. Other woody species in the wetpanne (abundant due to the presence of *P. nigra*) should also be thinned, to reduce transpiration levels and to begin to reverse the current successional trajectory .

Forest edges are least threatened by *P. nigra*. Because little pine regeneration is evident in the deciduous forest adjacent to *P. nigra* stands, and because deciduous woody species are recruiting under the pine canopy, these *P. nigra* stands should be left as they are. The blowout areas on the other side of the pine stands should be monitored every five years for evidence of pine regeneration and any new recruits clipped at ground level.

The success of these management practices should be monitored every three years. Permanent transects should be established in girdled locations to follow the response of the native vegetation to tree death. In addition, regenerating *P. nigra* population sizes should be monitored to determine the success of girdling and clipping in curtailing population growth.

Follow-up studies might include further analysis of the species that colonize pine sites but are absent from surrounding dune vegetation. This study suggested that animal dispersed species and those with clonal growth patterns were more successful in establishing in the presence of *P. nigra*. It would be interesting to further examine seed dispersal, germination and recruitment limitations of native woody species under pine canopy in all seral stages, and in so doing to begin to explain the mechanism of *P. nigra* impact and effect on the process of dune succession.

Knowledge of potential dispersal distances is essential for projecting the spread of an invader. It would be interesting to overlay projected seed shadows of *P. nigra* on actual seedling distributions, in order to examine patterns of seedling survivorship and growth and to predict the extent and direction of spread. Seed predation and herbivory may also be significant factors in the success of *P. nigra* on the dunes, and an examination of these interactions would further explain population dynamics of the invader.

It is ironic that the presumed stabilization advantage of the *P. nigra* introduction has not come to pass, yet at the same time, the non-native pines have become a major ecological force which threatens the integrity of the dune system. The pines have already altered native community composition, and with their continued proliferation, will have lasting and potentially irreversible effects. This study has clearly documented the transition from introduction to invasion, and has begun to identify the consequences of "biological pollution" in the sand dunes of the Great Lakes.

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