Colonization constraints during primary succession on coastal Lake Michigan sand dunes

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Summary

1 Primary succession on coastal sand dunes has generally been presumed to be driven by autogenic environmental change associated with dune stabilization and gradual soil development.

2 An extensive chronosequence of dune-capped beach ridges is found adjacent to northern Lake Michigan and the youngest 13 ridges (aged 30–440 years old) show a clear pattern of primary succession and development of a forest ecosystem.

3 Seed-addition and seedling-transplant experiments indicated that colonization of young sand dunes by late-successional *Pinus* and *Quercus* species is constrained by limited seed dispersal, seed and seedling desiccation, and seed predation rather than seedling success being constrained by low soil nitrogen availability. Their establishment may therefore depend on coincidence of chance seed dispersal, favourable weather conditions and low rodent densities.

4 In addition, episodic burial by sand prevents most species from colonizing young dune ridges, while burial of seedlings by litter limits recruitment on older dune ridges with developing forest. The intensity of competition increases during succession.

5 Dune succession is better described as the transient dynamics of colonization and competitive displacement rather than the result of gradual soil development and competitive displacement.

Key-words: coastal sand dunes, colonization limitation, competition intensity, mechanism of succession, soil development

Journal of Ecology (2000) **88,** 825–839

Introduction

Plant succession on the coastal sand dunes of Lake Michigan has long been considered a classic example of primary succession (e.g. Cowles 1899; Olson 1958). Early successional species are presumed to facilitate the colonization of later-successional species by stabilizing the dune surface and by adding organic matter to the incipient soil, which increases the availability of both soil moisture and nitrogen (Olson 1958; Connell & Slatyer 1977). As soil organic matter gradually accumulates, larger species, which are hypothesized to be inferior competitors for soil resources but superior competitors for light, colonize and eventually outcompete earlier dominants by reducing the amount of available light (Tilman 1985, 1988). Succession is thus thought to be driven by gradual improvements in soil quality. This hypothesis, as formalized by Tilman (1985, 1988), assumes that species composition and abundance approach a quasi-equilibrium controlled by resource supply, and that succession occurs as resource availabilities change and different plant traits become favoured.

Recent experimental studies of primary succession and of secondary succession on nutrient-poor soils have, however, demonstrated transient dynamics associated with differences in plant life histories, growth rates, and colonization and competitive abilities (e.g. Walker & Chapin 1986; Walker *et al.* 1986; Gleeson & Tilman 1990; Tilman & Wedin 1991; Chapin *et al.* 1994). This non-equilibrium explanation of succession suggests that probabilistic colonization constraints limit the establishment of late-successional species, and that their slow growth rates

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delay competitive displacement of early successional species (e.g. Horn 1971; Werner & Platt 1976; Platt & Weis 1977; Gross & Werner 1982; Huston & Smith 1987; Tilman 1990, 1994). Probabilistic colonization constraints include chance seed arrival, seed and seedling desiccation associated with stochastic weather conditions, and seed and seedling predation.

These two hypotheses are not mutually exclusive. Amelioration of seed and seedling desiccation during succession is consistent with both hypotheses. Gradual accumulation of organic matter through time may improve the likelihood of plant colonization by retaining soil moisture, but the opportunities for colonization in sites without significant amounts of soil organic matter may also accrue through time, albeit infrequently, when weather conditions are favourable for colonization. Both mechanisms could produce the same pattern of gradual colonization and filling of the dune habitat by late-successional species. In the first case, soil development drives plant colonization, and in the second, plant colonization drives soil development.

This confounding of the hypotheses is not necessarily problematic. Field experiments can potentially determine if one or the other mechanism is of prevailing importance, while not wholly refuting the alternative. For example, if soil development drives succession by increasing the availability of soil moisture, then one would expect the performance of transplanted seeds or seedlings of late-successional trees to improve with increases in soil organic matter. Alternatively, if infrequent moist weather conditions occasionally permit colonization of late-successional species on undeveloped soils, then adding water to transplanted seeds or seedlings should promote establishment in sites with negligible soil development, and seed or seedling performance would not strongly conform to a gradient in soil

organic matter. However, despite the century-long interest in dune succession such experimental tests have not been conducted. In this study seeds and seedlings of species dominant during early, middle, and late succession were transplanted to replicated experimental plots both within and outside their distributions during a well-documented dune succession (Lichter 1998a), and treatments were implemented to determine the driving force of succession. The importance of competition as a limiting factor for colonization and regeneration, and the effects of sand movement on colonization were also examined. The experiments were conducted across the aggrading portion of an extensive dune chronosequence bordering northern Lake Michigan. Frequent formation of dune-capped beach ridges at this site resulted in clear patterns of primary succession, and of soil and ecosystem development (Lichter 1998a,b).

STUDY SITE

The dune chronosequence is located at Wilderness State Park in Emmet County of the lower Peninsula of Michigan. The proximity of the surrounding Great Lakes produces a semi-marine climate (Eichenlaub *et al.* 1990) with a mean annual temperature of 6.2 °C and mean annual precipitation of 772 mm (Nurnberger 1996). Over the past 3500 years, the prograding western shoreline of the park has accreted 108 dune-capped beach ridges, averaging a new ridge every 32 years (Lichter 1995, 1997). The surface of the dune ridge closest to the lake shore is still actively accreting sand, whereas the surfaces of the next two older dune ridges experience progressively less sand movement, and the surface of the 125 years-old dune ridge is essentially stable (Fig. 1), as are older ridges.
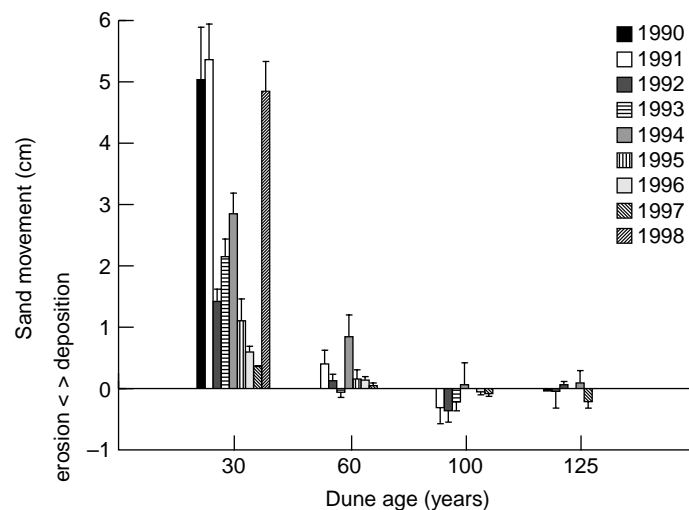
Fig. 1 Change in sand depth across the four dune ridges closest to the shore between 1990 and 1998. Data are annual means (± SE).

Vegetation surveys show successional changes across the dune chronosequence similar to the classic pattern described by Cowles (1899) and Olson (1958) at the Indiana Dunes. *Ammophila breviligulata* dominates the active dune ridge, but *Prunus pumila* and *Salix* spp. are also present. These species are replaced by the evergreen shrubs, *Juniperus communis* and *Arctostaphylos uva-ursi*, and by the prairie bunchgrass, *Schizachyrium scoparium*, within 100 years. Conifers including *Pinus strobus*, *Pinus resinosa*, *Larix laricina*, *Picea glauca*, *Picea mariana* and *Thuja occidentalis* colonize the margins of all of the interdunal swales but do not begin colonizing the crests of dune ridges until 150 years. A mixed coniferous forest dominated by *Pinus strobus* and *Pinus resinosa* develops between 225 and 400 years. *Betula papyrifera* also colonizes along the margins of the young interdunal swales, but other deciduous trees such as *Quercus rubra* and *Acer rubrum* do not enter the succession until 225 years, and do not become important components of the forest canopy until 440 years.

The experiments were conducted on four dune ridges chosen to represent early, middle and late succession. The first dune ridge, approximately 30 years old, is still accreting sand annually and is inhabited by few species (Fig. 2a). The adjacent dune ridge, which is 60 years old, has less sand movement but is otherwise similar to the 30-year-old dune ridge. The 150-year-old dune ridge (fifth from the shoreline) has a stable surface and supports an evergreen shrub and bunchgrass community with some pioneer trees (Fig. 2b). The 400-year-old dune ridge (eleventh from the shoreline) has a stable surface and supports mixed coniferous forest (Fig. 2c).

Materials and methods

On each dune ridge, a factorial experiments were laid out at three sites separated by at least 75 m to provide statistical replication. Although this design clearly represents pseudoreplication (Hurlburt 1984), the uniqueness of the chronosequence and logistical realities prevented inclusion of additional sites for true replication. The three experimental sites on each dune ridge encompassed much of the within-ridge variability in initial soil properties and vegetation.

Water-addition treatments were imposed in both seed-addition and seedling-transplant experiments. Water was obtained from shallow wells (2.4 m deep) installed between the 30- and 60-year-old dune ridges (to serve experimental sites on both ridges), and along the 150- and 400-year-old dune ridges. A small gasoline-powered centrifugal pump and garden hoses were used to saturate the surface soils of experimental plots.

SEED-ADDITION EXPERIMENTS

In November 1992, approximately 25 seeds of each of *Ammophila breviligulata*, *Schizachyrium scoparium*, *Arctostaphylos uva-ursi*, *Juniperus communis*, *Pinus strobus* and *Pinus resinosa*, and 10 seeds of *Quercus rubra* were dispersed to each of 24 randomly chosen locations on each of the four dune ridges. Natural rates of seed germination and seedling emergence were measured at a further 24 randomly chosen but unseeded locations on each dune ridge. Seed viability tests were conducted under a greenhouse mist bench. In April 1993, the proportion of seed-dispersal locations with seeds remaining was determined, and signs of seed predation such as opened seed hulls were noted. The seed-dispersal locations were revisited several times during the spring and early summer to check for seed germination and seedling emergence.

In May 1996, water-addition and seed-predator exclosure treatments were included in a factorial design. Seed addition sites ($n = 3$ on each ridge) were located near the water wells, each consisting of four 1-m^2 plots, randomly assigned to water-addition and seed-predator exclosure treatments. Exclosure plots were surrounded and covered with wire mesh (1.3 cm^2 of hardware cloth), which was also buried to least 20 cm to prevent tunneling, and with the top tied tightly to the sides. Between 200 and 300 seeds of each of *Ammophila breviligulata*, *Schizachyrium scoparium*, *Pinus strobus* and *Pinus resinosa* were distributed, each species to one of the four quarters within each plot. *Quercus rubra* seeds could not be obtained in sufficient quantity to be included in the experiment. The seeds were cold-stratified in wet sand at $-4\,°C$ for 4 months prior to the experiment. No seeds were placed in the centre (i.e. 25×25 cm) of the plot to allow quantification of the emergence of naturally dispersed seeds. *Ammophila* seeds were collected from the site while seeds of the other species were purchased commercially. Seed viability was determined in greenhouse germination tests. Seeds on the 30-year-old dune ridge were subsequently covered with approximately 1 cm of sand to mimic sand accretion during the preceding winter (i.e. using the 1996 measurements shown in Fig. 1). Water-addition plots were watered daily throughout the period of seed germination and seedling emergence, and twice per week thereafter until the end of the first growing season after which it was discontinued. Survival of the emerged seedlings was quantified each May and September over the next three growing seasons.

SEEDLING-TRANSPLANT EXPERIMENT

At each of the three experimental locations on the 30-, 150- and 400-year-old dune ridges, five pairs of plots, 2×2 m, separated by a 1-m access zone, were

Fig. 2 Plant communities on (a) the 30-year-old dune ridge, (b) the 150-year-old dune ridge, and (c) the 400-year-old dune ridge.

laid out for seedling transplants. The existing vegetation in one plot of each pair was clipped and roots were severed to 30-cm depth around the outer plot boundary and along lines dividing each plot into four 1-m^2 subplots (neighbour removal, compared with intact neighbours-present plots). The 400-year-old dune ridge is forested and neighbours-removed plots were placed in recent windthrow gaps (approximately 15 m in diameter), and the complementary neighbours-present plots were placed

Fig. 2 *Continued*

nearby under forest canopy. Light competition from the surrounding forest was not completely eliminated but light levels in the 400-year-old neighbours-removed plots were significantly higher than average values for the coniferous forest (66.3% vs. 13.1% of full sunlight in the two plot types, as measured with a Sunflect ceptometer (Decagon Devices, Pullman, WA, USA) 1-m above the ground on a cloudless day in June 1991; Kruskal–Wallis one-way ANOVA on ranks, $H = 39.997$, 1 d.f., $P < 0.001$).

Factorial nitrogen-fertilization and water-addition treatments were applied to four 1-m^2 subplots within each plot. Addition of a small amount (approximately 0.5 g) of dry NH_4NO_3 fertilizer (33–0-0) directly to the dune surface every other week during each growing season of the 3-year experiment, supplied $3.5 \, \mathrm{g \, N \, m^{-2} \, year^{-1}}$ to fertilized plots while minimizing leaching losses. Ion exchange resin techniques (see Lichter 1998a for methods) indicate that availability of NO_3^- and NH_4^+ to transplanted seedlings receiving the fertilization treatment increased approximately 12-fold and 6-fold, respectively.

Water was applied directly to the appropriate subplots two or three times per week throughout each growing season of the experiment. Although the surface soils of non-forested dunes dry extremely rapidly (Lichter 1998a), soil moisture levels were returned to field capacity at each watering and this should have eliminated water stress for seedlings receiving the treatment.

Dominant plant species from each of the three dune ridges were chosen for the transplant experiment. Rhizomes of *Ammophila breviligulata* and cuttings of *Arctostaphylos uva-ursi* and *Juniperus communis* were collected from the site and rooted under a greenhouse mist bench. Two-year-old *Pinus strobus* and *Quercus rubra* seedlings were purchased from a commercial nursery located in Michigan. Each species was randomly assigned to a pair of plots at each site and seedlings were randomized to each treatment combination. A subsample of seedlings and cuttings was dried and weighed for estimates of initial biomass. In May of 1992, nine ramets of *Ammophila*, eight rooted cuttings of *Arctostaphylos*, nine seedlings of *Pinus* and eight seedlings of *Quercus* were transplanted (bare root) to each treatment in the designated paired plots, but an insufficient quantity of *Juniperus* cuttings had rooted successfully. *Juniperus* was therefore replaced in the experiment with *Schizachyrium scoparium*, using seedlings generated from seed over winter in a greenhouse. *Schizachyrium* is a co-dominant with *Arctostaphylos* and *Juniperus* on open (i.e. non-forested) dune ridges. All plots were watered daily

for an initial period of 3 weeks, after which, only those subplots assigned to the water-addition treatment were watered.

At the beginning of each June, July, August and September between 1992 and 1994, the survival and heights of transplanted seedlings were recorded, and any regrowth of neighbours was removed. The seedling-transplant experiment was terminated in June 1995 and surviving seedlings were harvested, dried and weighed to determine their above-ground biomass.

STATISTICAL ANALYSES

Both ANOVA and survival analysis were used. For the factorial seed-addition experiment, the effects of dune age, experimental treatment and species identity on seedling emergence were analysed with ANOVA using the arcsin square-root transformation with proportion data (Sokal & Rohlf 1995). The effects of dune age, experimental treatment and species identity on survival of emerged seedlings were tested with survival analysis using the non-parametric log-rank test to determine significant differences among groups. Survival analysis is the proper statistical procedure for data describing time until an event (i.e. death) occurs (Allison 1995; Kleinbaum 1996).

For the seedling-transplant experiment, the effects of dune age, experimental treatment and species identity on seedling survival were tested with survival analysis, and effects of these factors on seedling growth were tested with ANOVA. Time-until-death of individual seedlings was the response variable for survival analysis, whereas mean above-ground biomass per surviving seedling per 1-m^2 treatment subplot was the response variable for ANOVA. Several parametric models were fitted to hazard functions to test for significant covariates of seedling survival among dune age, experimental treatment, seedling age and species identity. The log-normal model provided the best fit based on the log-likelihood criterion. For multiple comparisons among groups, the non-parametric log-rank test was used. For ANOVA, the final above-ground biomass of seedlings was log transformed to increase the reality of the model assumptions (Sokal & Rohlf 1995). All statistical analyses were performed with SAS version 6.11, SAS Institute 1989–96.

Results

SEED-ADDITION EXPERIMENTS

The first seed-dispersal experiment revealed intense predation of seeds of both *Pinus* species and of seeds of *Quercus* across the succession, whereas seeds of early and mid-successional species were not preyed upon (Table 1). Most dispersal locations had

no remaining *Pinus* and *Quercus* seeds but occasional empty hulls implicated rodent predators, notably *Peromyscus leucopus* (M. Spritzer, unpublished data, E. Du Val, unpublished data), a voracious predator of pine and oak seeds (De Steven 1991; Gill & Marks 1991; Ostfeld *et al.* 1997). There was negligible germination of any species on the open dune ridges but both experimentally and naturally dispersed pine seeds germinated on the forested dune ridge (Table 1).

The subsequent factorial seed-addition experiment revealed statistically significant differences in seedling emergence among dune age, species and both water-addition and seed-predator exclosure treatments (Table 2). Several interactions were statistically significant among group and treatment effects. Overall seedling emergence was greatest on the 30-year-old dune ridge (Fig. 3), probably because the *c.* 1 cm of sand burial provided some protection from desiccation and predation. Seeds of both species of *Pinus* generally germinated as well as or better than seeds of open-dune species. However, few seeds of any species germinated unless the plots were watered (Fig. 4a & b), except for a few *Pinus* seeds on the relatively moist and shaded forested dune ridge. Seeds were preyed upon across all four dune ridges (Fig. 4c), but this was due to almost all *Pinus* seed being removed while grass seeds were apparently ignored (Fig. 4d). A significant water-addition by seed-predator exclosure treatment interaction suggests that successful *Pinus* seedling establishment requires the removal of both constraints (Table 2; Fig. 5).

Survival curves for the emerged seedlings showed that most mortality occurred during the first year after germination. Within 2 years, *Ammophila* seedlings suffered 100% mortality across the succession, but *Schizachyrium*, *Pinus strobus*, and *Pinus resinosa* seedlings generally fared better during this period (Fig. 6). *Schizachyrium* seedlings died under forest cover but had high survival rates on the open dune ridges (Fig. 6). Sand accumulation was high on the active 30-year-old dune ridge during the third winter (see Fig. 1) and buried seedlings of all species (Fig. 6). *Pinus strobus* seedlings showed the opposite pattern to *Schizachyrium*, i.e. high survival rates on the forested dune ridge but lower survival rates on the open dunes (Fig. 6). *Pinus resinosa* seedlings did not survive as well as *Pinus strobus* on the forested dune ridge but performed comparably on the open dune ridges (Fig. 6).

SEEDLING-TRANSPLANT EXPERIMENT

Mortality among the transplants was highest during the first month of the experiment, lower during the second month, high again during the third month, and low thereafter (Table 3). High initial mortality was assumed to be due to transplant loss and these

Table 1 Results of the 1992–93 seed-dispersal experiment. Proportion of locations where seeds of each species dispersed in autumn were still present the following spring, with the proportion of dispersal locations with germinating seed given in parentheses. Control data refer to locations without dispersed seeds. Low values for seed presence implies seed predation

| Species	30 years	60 years	150 years	400 years	Means
Ammophila breviligulata.	0.92 (0.04)	0.96 (0.00)	0.87 (0.00)	1.00 (0.00)	0.94 (0.01)
Schizachyrium scoparium	0.92 (0.00)	0.83 (0.00)	0.83 (0.00)	0.96 (0.00)	0.89 (0.00)
Arctostaphylos uva-ursi	0.96 (0.00)	0.75 (0.00)	1.00 (0.00)	0.92 (0.00)	0.91 (0.00)
Juniperus communis	0.92 (0.00)	0.67 (0.00)	0.92 (0.00)	0.79 (0.00)	0.83 (0.00)
Pinus resinos	0.21 (0.04)	0.08 (0.00)	0.08 (0.00)	0.25 (0.25)	0.16 (0.07)
Pinus strobus	0.13 (0.00)	0.00 (0.00)	0.00 (0.00)	0.25 (0.25)	0.10 (0.06)
Quercus rubra	0.00 (0.00)	0.08 (0.00)	0.21 (0.00)	0.17 (0.00)	0.12 (0.00)
Control (all species)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.33 (0.33)*	0.08 (0.08)

* Mainly *Pinus resinosa* and *P. strobus*. Values for these species were subtracted from observed frequencies for plots containing their dispersed seeds on this ridge.

Table 2 Results of factorial seed-addition experiment using ANOVA with arcsin square-root transformed proportions of viable seed that germinated per treatment plot as the response variable

Source	d.f.	MS	F	P
Sites (S)	2	0.041	0.51	0.626
Age (A)	3	0.394	4.82	0.049
Error I: S × A	6	0.082		
Water addition (W)	1	4.594	155.39	< 0.0001
Predator exclosure (P)	1	1.320	44.65	< 0.0001
W × P	3	0.467	15.78	< 0.0001
A × P	3	0.037	1.26	0.311
W × P	1	0.935	31.63	< 0.0001
A × W × P	3	0.013	0.44	0.729
Error II: S × A × W × P	24	0.030		
Species (Sp)	3	0.234	15.99	< 0.0001
A × Sp	9	0.162	11.09	< 0.0001
W × Sp	3	0.120	8.19	< 0.0001
P × Sp	3	0.399	27.30	< 0.0001
A × W × Sp	9	0.112	7.67	< 0.0001
A × P × Sp	9	0.017	1.18	0.3165
W × P × Sp	3	0.259	17.68	< 0.0001
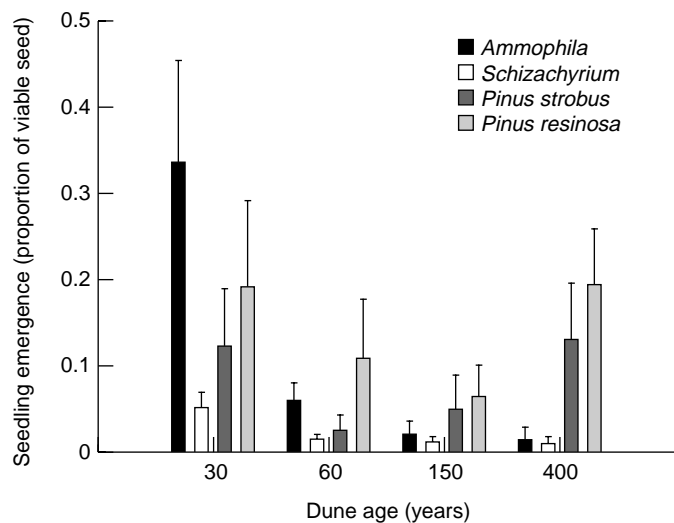
Fig. 3 Seedling emergence from added seeds as a function of dune age and species. Data (means ± SE) are combined from all treatments in a factorial experiment.
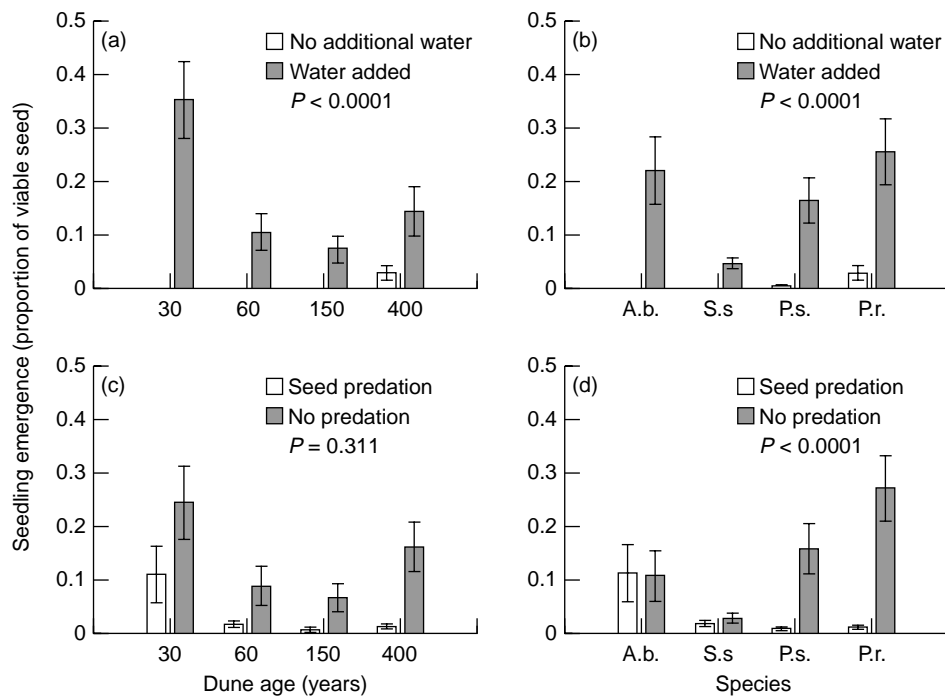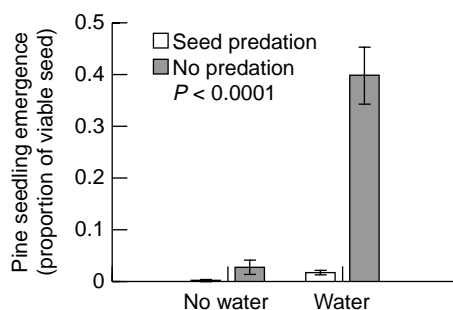
Fig. 4 Effects of water supply and predator exclusion on germination of added seeds in the factorial experiment. Data are observed means ($\pm$ SE), analysed by dune age or species identity.

seedlings were therefore removed from the data set. There were no qualitative differences in results between the full data set and the abridged data set that excluded transplant loss. High mortality during the third month was probably associated with natural constraints on establishment imposed by the environment during the first growing season. Because *Schizachyrium* seedlings were not transplanted until the second year of the experiment, differences in survival between *Schizachrium* and the other four species might be related to temporal differences in establishment conditions or to differences in seedling age. I therefore included a covariate in

Fig. 5 Effect of water supply and predators on pine seedling emergence in the factorial experiment. Data are means ($\pm$ SE).

the analysis describing seedling age at the beginning of the second year of the experiment.
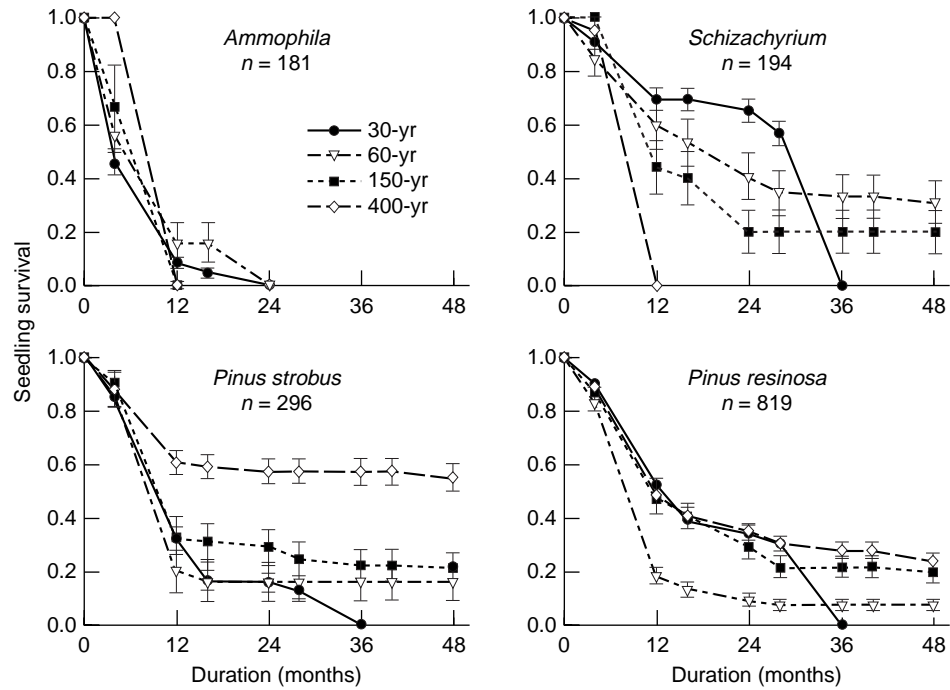
Transplant loss accounted for 755 (24.0%) of the initial 3145 seedlings (Table 3). The majority of seedlings (1262 out of 2390, 52.8%) that survived the first month of the experiment survived to the end of the 3-year-old experiment. There was little mortality after the end of the first winter. Seedling survival was significantly affected by dune age, species identity, seedling age and two of the treatments: only the fertilization treatment did not have a significant effect (Table 4). The dune age × species and dune age × neighbour–removal interactions were also significant. The net effect of existing vegetation on overall seedling survival and growth became more negative with increasing dune age (Fig. 7). Seedlings of open-dune species were more negatively affected by existing vegetation than were tree seedlings. The general results of the survival analysis are consistent with those of ANOVA using log-transformed mean seedling size per treatment subplot as the response variable (Table 5).

Comparisons of baseline survival (i.e. in unmanipulated plots with the neighbours-present but without addition of fertilizer or water) and growth among species on the active dune ridge test whether soil development is required for colonization of late-successional trees. Survival of *Pinus* and *Quercus* seedlings did not differ statistically from survival of *Ammophila* and *Arctostaphylos* seedlings (Fig. 8a),

Fig. 6 Seedling survival curves for germinated seeds of different species on different dune ages. Data are means (± SE).

Table 3 Life table survival estimates for seedling-transplant experiment. Estimates of conditional probability of seedling mortality, survival, and hazard are means (± SE)

Interval (month)	Deaths	Censored	Effective sample size	Conditional probability	Survival	Hazard
*0–1	755	0	3145	0.240 (0.008)	1.000 (0.000)	0.273 (0.010)
1–2	208	0	2390	0.087 (0.008)	0.760 (0.008)	0.091 (0.006)
2–3	291	0	2182	0.133 (0.007)	0.694 (0.008)	0.143 (0.008)
3–12	402	0	1891	0.213 (0.009)	0.610 (0.008)	0.026 (0.001)
12–13	12	0	1489	0.008 (0.002)	0.473 (0.009)	0.008 (0.002)
13–14	0	0	1477	0.000 (0.000)	0.473 (0.009)	0.000 (0.000)
14–15	44	0	1477	0.030 (0.004)	0.470 (0.009)	0.030 (0.005)
15–24	140	0	1433	0.100 (0.008)	0.456 (0.009)	0.011 (0.001)
24–25	0	175	1293	0.000 (0.000)	0.411 (0.009)	0.000 (0.000)
25–26	2	0	1118	0.002 (0.001)	0.411 (0.009)	0.002 (0.001)
26–27	2	0	1116	0.002 (0.001)	0.410 (0.009)	0.002 (0.001)

Table 4 Results of seedling-transplant experiment. Parameter estimates for log-normal model (± SE) and significance tests for covariates of seedling survival and for dune age–treatment interactions

| Variable	d.f.	Estimate	Chi-square	P
Intercept	1	7.363 (0.454)	262.6	< 0.0001
Dune age (A)	1	− 2.024 (0.189)	115.0	< 0.0001
Species identity (Sp)	1	− 1.377 (0.099)	193.7	< 0.0001
Seedling age (Age)	1	− 0.979 (0.182)	29.0	< 0.0001
Neighbour removal (NR)	1	− 0.669 (0.279)	5.7	0.015
Nitrogen fertilization (N)	1	0.113 (0.278)	0.2	0.633
Water addition (W)	1	1.043 (0.279)	14.0	< 0.0001
A × Sp	1	0.762 (0.046)	270.0	< 0.0001
A × NR	1	0.525 (0.128)	17.0	0.001
A × N	1	− 0.097 (0.127)	0.6	0.443
A × W	1	− 0.177 (0.127)	1.9	0.163
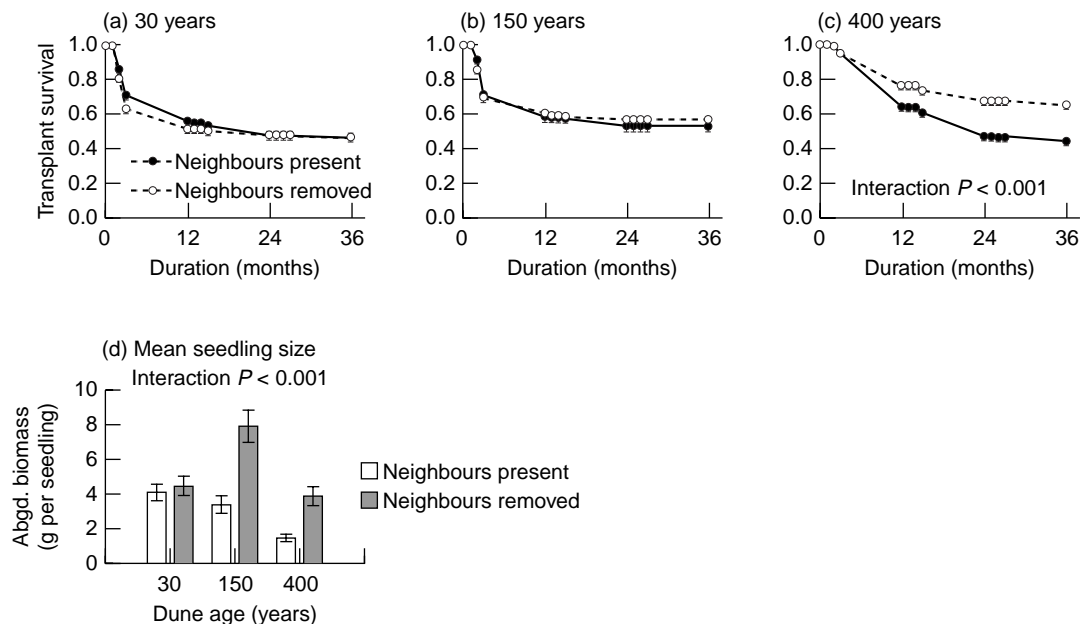
Fig. 7 Survival and growth of transplanted seedlings. Effect of dune age and neighbour removal on survival (a, b & c) and mean final size (d), summed over species identity, N-fertilization treatment, and water-addition treatment. Data are means (± SE).

Table 5 Results of seedling transplant experiment using ANOVA with log-transformed mean seedling above-ground biomass per treatment subplot as the response variable

Source	d.f.	MS	F	P
Sites (S)	2	0.11	0.04	0.715
Dune age (A)	2	1.65	11.32	0.022
Error I: S × A	4	0.14		
Sp	4	3.33	30.03	< 0.001
Sp × A	8	1.30	11.74	< 0.001
Error II: S × A × Sp	24	0.11		
Neighbour removal (NR)	1	3.15	37.56	< 0.001
A × NR	2	0.74	8.77	0.001
Sp × NR	4	0.04	0.43	0.786
A × Sp × NR	8	0.08	0.98	0.461
Error III: S × A × Sp × NR	30	0.08		
Nitrogen fertilization (N)	1	0.14	3.45	0.065
Water addition (W)	1	1.39	34.04	< 0.001
N × W	1	0.02	0.59	0.443
A × N	2	0.01	0.28	0.758
A × W	2	0.15	3.58	0.030
Sp × N	4	0.05	1.18	0.322
Sp × W	4	0.02	0.61	0.656
NR × N	1	0.01	0.09	0.760
NR × W	1	0.21	5.02	0.026
A × N × W	2	0.00	0.01	0.989
Sp × N × W	4	0.01	0.26	0.906
NR × N × W	1	0.01	0.25	0.620
A × Sp × N	8	0.01	0.34	0.948
A × Sp × W	8	0.10	2.36	0.018
A × NR × N	2	0.05	1.18	0.309
A × NR × W	2	0.03	0.66	0.520
Sp × NR × N	4	0.04	0.95	0.438
Sp × NR × W	4	0.12	2.99	0.020
Error IV: S × A × Sp × NR × N × W	218	0.04		
Total	360			

with 28% of tree seedlings surviving transplanting to unmanipulated plots on the active dune ridge. Similarly, on the 150-year-old dune ridge, tree and open-dune seedlings survived equally as well (Fig. 8b), but on the 400-year-old forested dune ridge, tree seedlings survived substantially better than seedlings of open-dune species (Fig. 8c). Surprisingly, *Arctostaphylos* seedlings performed poorly on the 150-year-old dune ridge where this species is a community dominant (Fig. 8b).
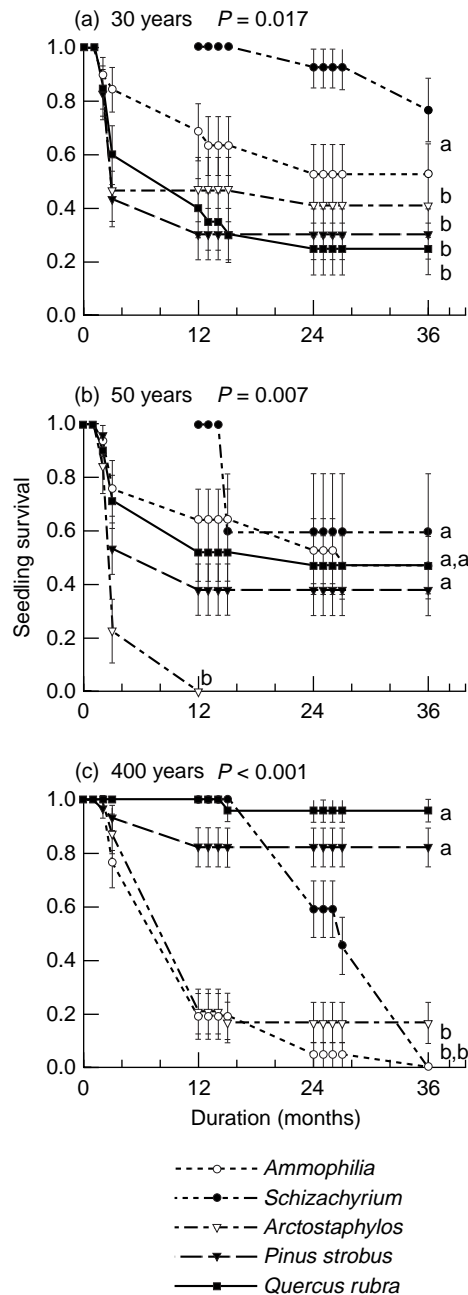
Fig. 8 Effects of dune age and species identity on base line survival (i.e. in unmanipulated plots) of transplants. Data are means (± SE). Letters denote statistically distinguishable species groups.
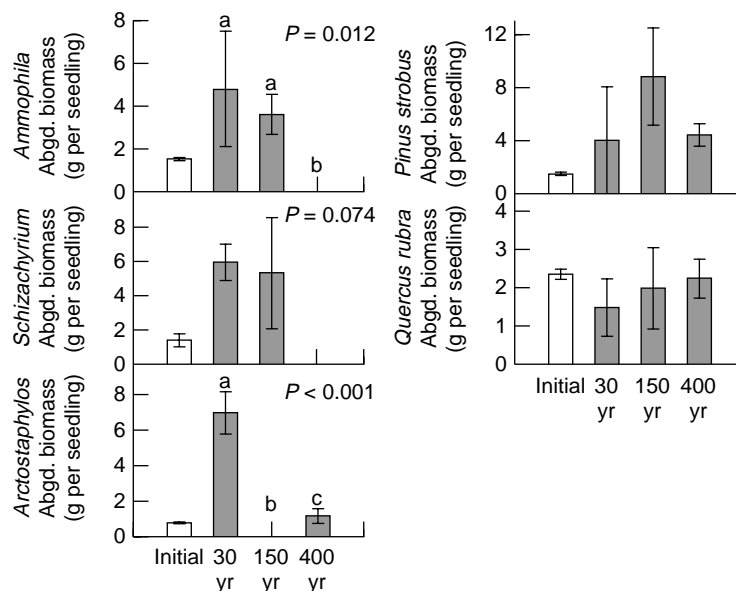
Comparisons of initial and final seedling size showed that seedling survival at a site was generally associated with growth and accumulation of above-ground biomass during the period of the experiment (Fig. 9). The final size of *Quercus rubra*, however, was approximately equal to its initial value in all three dune habitats.

Discussion

These experiments demonstrated that dune succession is primarily driven by transient dynamics associated with probabilistic colonization rather than environmental change associated with gradual soil development. Most of the late-successional pine and oak seeds that disperse to young exposed dune ridges will be lost to either seed and seedling desiccation or seed predation. Although trends in seedling survival and growth across the open dune ridges suggest that soil development may improve seedling performance, this effect is much less important than these severe constraints on colonization; constraints that soil development does not mitigate.

The rate of dune succession thus depends on interacting environmental constraints associated with chance seed dispersal, stochastic weather conditions and fluctuating populations of rodent seed predators. The significant interaction between the water-addition and predator-exclosure treatments in the seed-addition experiment suggests that pine colonization may be episodic. Although some seeds may escape predation even under high predator densities, significant rates of germination and establishment are most likely when moist weather conditions coincide with low predator abundances (Fig. 5). Conifer establishment in xeric habitats has been correlated with the frequency of precipitation (West *et al.* 1975; Richardson & Bond 1991; Miller & Halpern 1998), and populations of the principle seed predator, *Peromyscus leucopus*, are also known to fluctuate in cycles that may be influenced by weather (Sexton *et al.* 1982; Wolff 1985; Krohne *et al.* 1988; Ostfeld 1988; Kesner & Linzey 1997; Lewellen & Vessey 1998). Prolonged winters or stormy springs might synchronize moist soils and low population densities of *Peromyscus*, and thereby provide a window of opportunity for tree colonization.

Limited seed supply to young dune ridges must also restrict colonization. Both pine and oak have high year-to-year variability in seed production (Sharik *et al.* 1989; Sork *et al.* 1993; Koenig *et al.* 1994; Clark *et al.* 1998a). Although pine has a relatively narrow seed shadow (Greene & Johnson 1989; Clark *et al.* 1998a), those for oak are leptokurtic implying that while most seeds fall close to the parent tree, a few are widely dispersed by animals (Clark *et al.* 1998b). The presence of established pine seedlings along the margins of the interdunal swales indicates that seeds occasionally disperse to

Fig. 9 Effects of dune age on baseline growth (i.e. difference between initial and final seedling size in unmanipulated plots) of transplants. Data are means ($\pm$ SE). Letters denote statistically distinguishable differences among dune ages.

the adjacent upland dune ridges, although many that reach the exposed surfaces of young dunes will subsequently be transported into the adjacent interdunal swales as wind velocities capable of moving sand will also move seeds. Oak seed dispersal to young dune ridges must depend on animal vectors transporting acorns over several tens of metres; arboreal squirrels (Smith & Follmer 1972) or blue jays (Johnson & Adkisson 1985; Johnson & Webb 1989), which are capable of such transfer, but are not common on the open dune ridges.

In both experiments the survival curves of tree species flatten out after the first year, indicating that once naturally colonizing seedlings have survived their first year they are likely to persist. Seedlings would have a consistent source of water for transpiration once their roots have reached the shallow water table. Further tree establishment on young dunes would be facilitated by consistent seed supplies as pioneer trees begin producing seed, and by the moister dune surfaces produced by litter inputs and shading effects (e.g. Kellman & Kading 1992; Callaway 1995; Rousset & Lepart 2000).

The results are consistent with an extensive literature which similarly documents tree life histories with similar population bottlenecks at the seed germination and seedling establishment stages (e.g. Canham & Marks 1985; Clark *et al.* 1999; Rey & Alcantara 2000), and with experimental studies of other primary successions. Seed rain monitoring and seed-addition experiments indicated that seed supply limits colonization of mid- and late-successional species following deglaciation at Glacier Bay, Alaska (Chapin *et al.* 1994). For the same succession, tree-

ring reconstructions of local colonization histories showed that rates and pathways of succession depended on the distance to seed sources of late-successional spruce and hemlock (Fastie 1995). Similarly, distance to seed source was the best predictor of tree recruitment on reclaimed mine surfaces in central Florida (McClanahan 1986). Seed rain also influences floodplain succession (Walker & Chapin 1986; Walker *et al.* 1986; Johnson 1994), and colonization of volcanic slopes following eruptions at Mount St. Helens (Wood & del Moral 1987; del Moral & Bliss 1993) and Krakatau (Whittaker *et al.* 1989).

Episodic sand burial also limits colonization of mid- and late-successional species on active dunes. All experimental seedlings emerging from seed on the 30-year-old dune ridge were buried during the winter of 1998 when sand accretion rates were high. During the nine-year period that sand accretion has been monitored at the site, approximately 22 cm of sand accumulated on the 30-year-old dune ridge. This amount of sand accumulation would effectively prevent colonization of all species lacking special adaptations for withstanding burial.

Dune succession is best explained by differential colonization and competitive abilities of plants in the particular environments they experience across dune chronosequences. *Ammophila* generally colonizes new areas of beach and dune through horizontal rhizome growth and sprouting of new culms (Olson 1958). It is not dependent on seedling recruitment to maintain viable populations on active dunes, and therefore is not limited by the extreme desiccating conditions of stable dune surfaces.

However, other dune species must colonize and recruit from seed, and are vulnerable to desiccation. *Schizachyrium* and *Arctostaphylos* dominate young open dunes before forest develops. Although their rates of germination and seedling establishment on the open dune ridges were no greater than those of *Pinus strobus* and *Pinus resinosa*, their seeds were not preyed upon. Also, their shorter time to reproductive maturity gives them an advantage in supplying seeds to newly colonized dunes. These species are eventually competitively excluded as trees establish and grow, and the environment is profoundly altered (Lichter 1998a). Open-dune species generally inhabit high light environments and therefore are probably vulnerable to light competition, which is exacerbated by burial by litter in developing forest. Many of the seedlings of open-dune species transplanted to the forest became completely covered with conifer litter falling during the winter. Litter burial is frequently an important recruitment constraint during old-field succession (Sydes & Grime 1981; Monk & Gabrielson 1985; Bergelson 1990; Carson & Peterson 1990; Tilman & Wedin 1991; Tilman 1993).

In summary, coastal sand dunes represent complex environmental gradients along which colonization limitation and sand movement represent major environmental constraints during early succession, and competition and regeneration limitation represent major environmental constraints during later succession. There is little evidence that soil development and corresponding increases in availability of soil moisture and nitrogen drive succession. Soil development is more a consequence of tree colonization and growth than a factor driving tree colonization and succession. A more thorough understanding of dune succession might be achieved with experiments that further examine the mechanisms of colonization limitation and competitive exclusion, and that map plant allocation to traits that confer colonization and competitive abilities (e.g. Gleeson & Tilman 1990; Tilman & Wedin 1991). This study joins a growing list of theoretical and experimental studies suggesting that successional patterns are widely explained by a trade-off between plant colonization and competitive abilities.

Acknowledgements

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