

STRUCTURE AND DYNAMICS OF A COASTAL DUNE FOREST
AT HUMBOLDT BAY, CALIFORNIA

by

Shayne Green

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Shayne Green

We certify that we have read this study and that it conforms to acceptable standards of scholarly presentation and is fully acceptable, in scope and quality, as a thesis for the degree of Master of Arts.

Approved by the Master's Thesis Committee:

[Redacted]	12-13-99
John O. Sawyer, Major Professor	Date
[Redacted]	12-13-99
Kenneth L. Lang	Date
[Redacted]	12/13/99
Andrea Pickart	Date
[Redacted]	12-13-99
John B. Stuart	Date
[Redacted]	12-13-99
Dale T. Thornburgh	Date
[Redacted]	15 Dec 99
Milton J. Boyd, Graduate Coordinator	Date
[Redacted]	20 Dec 1999
Ronald A. Fritzsche	Date
Dean of Research and Graduate Studies	

ABSTRACT

Forest stands occurring on coastal dunes along the western margin of Humboldt Bay, California are isolated fragments of a regional forest type that stretches discontinuously along the Pacific Coast from northern California to Alaska. I used aerial photographs to stratify the forest at Lanphere Dunes into 3 stand types. Using fixed-radius (13.2 m) circular plots, I sampled these types to determine their composition (overstory and understory), size structure (basal area, height, and sapling, seedling, snag and tree density), and age structure.

Beach pine, Sitka spruce, and mixed-species types exhibit significant compositional and structural differences. The beach pine type is distinguished not only by the importance of beach pine in the overstory, but by high stem density, low basal area, and the overall importance of bearberry in the understory. The Sitka spruce type is characterized by the importance of Sitka spruce in the overstory, low stem density, high basal area, and the importance of twinberry and wax myrtle in the understory. In the mixed-species type, beach pine and Sitka spruce are almost equally important among an overstory layer that often includes grand fir. This type exhibits stem density and basal area values intermediate to those of the other two types.

Age structure differences among the types are non-significant, suggesting that each type has a similar disturbance history as the others. Within each type, beach pine and/or Sitka spruce populations consist of numerous age classes that are normally distributed. Age class chronologies correspond (in part) among types and among spatially disjunct plots of the pine type.

Small patches of forest (<0.04 ha) typically include trees representing numerous age classes, and age class distributions (i.e. number and size) vary over larger areas. Patch dynamics are apparently complex and affect forest development at a variety of spatial and temporal scales.

These age and spatial patterns support the hypothesis that small-scale windfall events have been the most important disturbance factor underlying seedling establishment over the last 150 years. Though regeneration levels are currently low, beach pine stands generally appear to be self-replacing over a period of many decades.

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INTRODUCTION

Distinctive forests involving beach pine (*Pinus contorta* ssp. *contorta*)¹ and Sitka spruce (*Picea sitchensis*) occupy sand dunes along the western margin of North America, from Cape Mendocino in the south to the Straits of Juan de Fuca in the north (Wiedemann 1984). These dune forests are usually located near river mouths, bays, or on broad sea-cut terraces. Generally, they are part of a diverse coastal habitat complex that includes estuaries, dunes, and ocean. Dune forests are among the more interesting and less understood plant assemblages characterizing the coastal zone in the Pacific Northwest.

Forests inhabiting coastal dunes are subject to a harsh set of conditions that include a low-nutrient substrate, air-borne salt spray, desiccating summer winds and gale force winter gusts, fluctuating water tables, and episodic disturbance by sand inundation and fire (Wiedemann 1984). The severe conditions and complex disturbance processes that characterize coastal dunes habitat create a unique context for studying the dynamics of change in forest stands over time.

In the Pacific Northwest, many dune forests are dominated by Sitka spruce (Franklin and Dyrness 1973). Stands in California are recognized as disjunct fragments of this regional forest (Sawyer and Keeler-Wolf 1995). Sitka spruce is the largest of the world's spruces (Harris 1990), and it extends from Point Arena in California northward

¹ All common and scientific plant names follow Hickman (1993) unless otherwise noted.

into Alaska (Franklin and Dyrness 1973). Along its extent, it is commonly associated with beach pine or western hemlock (*Tsuga heterophylla*).

Pacific Northwest dune forests may also be dominated by beach pine (Franklin and Dyrness 1973), including disjunct fragments occurring in northern California (Sawyer and Keeler-Wolf 1995). Beach pine primarily inhabits nutrient-limited or otherwise marginal sites along the coast from Mendocino County, California to southern Alaska. It is one of four ecologically distinct subspecies (Lotan and Critchfield 1990) of lodgepole pine (*Pinus contorta*), which also includes a highly isolated Mendocino white plains race (ssp. *bolanderi*), a Rocky Mountain race (ssp. *latifolia*), and a Sierra-Cascade race (ssp. *murrayana*).

Beach pine and associated Sitka spruce stands are uncommon along the southern Oregon and northern California coast. These forests are considered rare in California (California Natural Diversity Data Base 1997), and intact stands are increasingly threatened by development elsewhere. In northern California, large stands are located near the mouth of Smith River, and between the mouth of Humboldt Bay and the Mad River. Forests here support exceptional lichen, moss, and mushroom floras (Lindsay 1973, VanHook 1985, cited in U.S. Fish and Wildlife 1998).

Although life history and stand characteristics of other lodgepole pine subspecies are well documented (see Lotan and Critchfield 1990 for a review), and geographic and genetic variation well studied (Critchfield 1957, Critchfield 1980, Wheeler 1981), relatively little is known about the stand dynamics of beach pine. Past research has focused on density/yield relationships in small beach pine plantations (Xie et al. 1995) or on responses to dwarf mistletoe infestations (Smith and Wass 1976, Wass 1976).

Ecological studies addressing beach pine have been either narrowly concerned with ectomycorrhizal associations (Sugihara 1980) or broadly focused on dune vegetation in general (Egler 1934, Byrd 1950, Hanneson 1962, Johnson 1963, Wiedemann 1966, Wiedemann 1984). Consequently, quantitative information regarding the size structure, age structure, species composition, and stand development patterns of mature beach pine stands is lacking, particularly in the southern portion of the beach pine's range.

Egler (1934) provided an early description of Oregon dune forest composition and proposed successional trajectories at the Coos Bay sand dunes. According to his accounts, important overstory species include beach pine, Douglas-fir (*Pseudotsuga menziesii*), Port Orford-cedar (*Chamaecyparis lawsoniana*), Sitka spruce, western hemlock, and western red cedar (*Thuja plicata*). He concluded that understories of bearberry (*Arctostaphylos uva-ursi*) and hairy manzanita (*Arctostaphylos columbiana*) are typical of young stands, while evergreen huckleberry (*Vaccinium ovatum*), rhododendron (*Rhododendron macrophyllum*), salal (*Gaultheria shallon*), and wax myrtle (*Myrica californica*) characterize older stands.

Johnson (1963) provided a qualitative description of north coastal California dune forests in his ecological study of the dune flora at Humboldt Bay. He argued for a climax forest here consisting of beach pine, Douglas-fir, grand fir (*Abies grandis*), and Sitka spruce in the overstory, and bearberry, evergreen huckleberry, coyote brush (*Baccharis pilularis*), salal, silk tassel (*Garrya elliptica*), and wax myrtle in the understory.

More recently, Wiedemann (1984) provided a description of coastal dune forest composition in his community profile of coastal sand dunes in the Pacific Northwest. He suggested that environmental gradients and successional pathways result in characteristic

species assemblages, and proposed seven distinct forest types based primarily on informal observations: 1) beach pine/rhododendron (*Pinus contorta* ssp. *contorta*/*Rhododendron macrophyllum*), 2) beach pine/hairy manzanita (*Pinus contorta* ssp. *contorta*/*Arctostaphylos columbiana*), 3) beach pine/slough sedge (*Pinus contorta*/*Carex obnupta*), 4) Douglas-fir/rhododendron (*Pseudotsuga menziesii*/*Rhododendron macrophyllum*), 5) Sitka spruce--beach pine/Hooker willow/Oregon beaked moss (*Picea sitchensis*--*Pinus contorta* ssp. *contorta*/*Salix hookeriana*/*Eurhynchium oreganum*), 6) western hemlock--Sitka spruce/salal/deer fern (*Tsuga heterophylla*--*Picea sitchensis*/*Gaultheria shallon*/*Blechnum spicant*), and 7) western red cedar/western labrador tea (*Thuja plicata*/*Ledum glandulosum*). Wiedemann named these communities after characteristic (or dominant) species of the tree, shrub, and herb layers, respectively.

Egler (1934) and Wiedemann (1966, 1984) inferred disturbance history in dune forests from empirical and historical evidence, and proposed stand development patterns for mature stands based on informal observations. Noting the charred remains of an extensive fire that swept along the Oregon coast 100 years prior to his study, Egler considered beach pine to be strictly a one-generation tree that was widespread along the Oregon coast as a result of fire. He maintained that beach pine is generally unable to reproduce in the shade of its own canopy and is therefore rapidly replaced by Sitka spruce as the dominant species. He considered Sitka spruce stands to represent the "aeolean subclimax" condition, which persists in the absence of fire because successive windfall events through centuries favor Sitka spruce over other species that reproduce less prolifically following such disturbances.

Wiedemann (1966) noted the presence of charcoal and burned wood within exposed old forest soil profiles, and summarized additional evidence from the literature implicating fire as an important factor shaping historic and pre-historic coastal dune forest stands in Oregon. However, in the absence of fire during the 140-160 years preceding his study, Wiedemann concluded that wind had become the most important active disturbance agent affecting coastal dune forests.

Wiedemann agreed with Egler that Sitka spruce eventually replaces beach pine as the dominant species in most dune forest stands. However, he observed that pure stands of both beach pine and Sitka spruce were found that showed no signs of compositional change and which had probably been pure stands since initiation. He concluded that, “the classical concept of succession whereby a mature forest is replaced by another growing up through it is not completely valid for the sand dune pine and spruce forests” (Wiedemann 1966).

Johnson (1963) hypothesized that succession occurs differently on wet and dry sites, and that the development of forest stands is accompanied by an increase in humus, plant competition, shade, soil litter, and water capacity. He suggested that major factors propelling succession included competition for light, nutrients, and water, and all factors affecting the suitability for seed germination and seedling survival.

OBJECTIVES OF THIS STUDY

Authors of past dune forest studies inferred ecological process largely from casual observation, but did not test their ideas vigorously by describing mature forest stands in detail. Consequently, quantitative information regarding their age structure, size structure, species composition, and stand developmental patterns is lacking. Such information may answer many important questions regarding the character of coastal dune forests in northern California. For example, what is the origin and history of the forest at Humboldt Bay? How does its composition compare with forests farther north? What is the age structure, and what does that suggest about the developmental patterns and disturbances of the coastal dune forest at Humboldt Bay?

In order to answer these questions, I developed three objectives

- 1) to identify and characterize distinct stand types,
- 2) to describe the size and age structures and species composition of selected stands, and
- 3) to characterize the disturbance regime and infer patterns of stand development

to guide my investigation of coastal dune forest stands near Humboldt Bay, California.

DESCRIPTION OF THE STUDY AREA

Location

Humboldt Bay is located along the Pacific coast of extreme northwestern California, in Humboldt County. Active and stabilized dunes extend from the mouth of Humboldt Bay northward for approximately 30 km. This strip of dunes is between 0.5 and 1.5 km wide. In addition to sand dunes, the stretch of coast known as Lanphere Dunes includes salt marsh and the Mad River Slough, a tidally influenced arm of Humboldt Bay. Lanphere Dunes was owned by The Nature Conservancy and managed as a preserve prior to its acquisition by the U.S. Fish and Wildlife Service in 1997. The study area consists of upland forested areas occupying dunes within the boundaries of what is now known as the Lanphere Dunes Unit of the Humboldt Bay National Wildlife Refuge (Figure 1). Riparian forest stands within the area were not studied.

Climate

The temperate maritime climate of the Humboldt Bay region is characterized by cool wet winters and mild dry summers. Mean annual temperature ranges between 10.0° and 11.7° C, and there is less than 7° C difference between lowest and highest monthly means (Miles and Goudey 1997). The area receives approximately 91 cm of rain per year, ranging from over 15 cm per month for November, December, and January to less than 1.5 cm per month for June, July, and August (National Weather Service 1998). Although most rainfall occurs from October through April, some precipitation occurs in the form of



Figure 1. North spit forests of Humboldt Bay, with the Lanphere Dunes study area shown in the north (map courtesy of USFWS, 1998).

Geomorphology and soils

The study area is included in the Humboldt Bay Flats and Terraces subsection of the Northern California Coast, a section of the Coast Ranges Geomorphic Province (Miles and Goudey 1997). Lanphere Dunes is part of a beach and dune complex that occurs on a low coastal plain near Humboldt Bay. Sediments carried by the Mad and Eel rivers are deposited in the ocean, transported by currents, washed ashore by waves, and blown overland by wind to form sand dunes. Lanphere Dunes consists of a younger system of active or recently stabilized dunes, and an older system of stabilized paleodunes (Cooper 1967, Pacific Watershed Associates 1991). This study included only upland conifer forests occupying stabilized paleodunes.

The topography of Lanphere Dunes is generally of low-relief, and the highest point rises less than 50 m in elevation. Topographic features include hollows, ravines, marginal and transverse ridges, and stabilized sand plains. Some low-lying areas, usually hollows and ravines, are filled with standing water during much of the rainy season, while higher areas drain quickly and remain relatively dry year-round. Soils are sandy with little horizontal development (U.S. Fish and Wildlife Service 1998).

Vegetation

Vegetation within the study area includes broadleaf riparian and conifer forest stands, though only conifer stands were included in this study. Beach pine and Sitka spruce dominated stands comprise an extensive forest stratum, with isolated stands of Douglas-fir and grand fir occurring at a fine scale. The beach pine dominated stands have been described as consisting of beach pine, Douglas-fir, and occasionally madrone

(*Arbutus menziesii*) in the overstory, and bearberry, evergreen huckleberry, salal, and silk tassel in the understory (Pickart, unpublished data, U.S. Fish and Wildlife Service 1998). Isolated Sitka spruce stands are interspersed throughout the broader expanse of beach pine forest. Broadleaf riparian forests dominated by Hooker willow (*Salix hookeriana*) and red alder (*Alnus rubra*) occupy drainage areas and wet hollows.

Land-use history

Wiyot Indians inhabited the Humboldt Bay region long before Europeans arrived in the mid-1800's. Several Wiyot villages and encampments are known to have existed both within and near Lanphere Dunes (Loud 1918). Most encampments in the immediate vicinity of the study area occurred along the western margin of Humboldt Bay and the Mad River Slough. Others were located closer to the ocean on the lee side of foredunes.

Most Wiyots were either killed or forced to leave the area shortly after the arrival of European settlers starting in about 1850 (Summerly 1967, Irvine 1915). Although the area was never heavily settled, several homes were established along the eastern margin of Lanphere Dunes in ensuing years. While there is no historical record of logging within forested areas of the Humboldt Bay dunes (including Lanphere Dunes), it is possible that some trees were cut as fuel wood. Limited grazing is also known to have occurred at some sites within the study area in the past (J.O. Sawyer 1997, pers. comm.).

METHODS

Stand selection

I used 1:2400 scale color aerial photographs obtained from Humboldt State University to partition the dunes forest into polygons based on canopy characteristics reflecting similarities in species composition, tree size, and canopy cover. I visited polygons to determine the dominant canopy tree species (as measured by cover), and then stratified polygons into five types¹: 1) pine, 2) spruce, 3) mixed-species, 4) Douglas-fir, and 5) grand fir. I sampled pine, spruce, and mixed-species stands in order to describe their size and age structures and species composition. Douglas-fir and grand fir stands were extremely limited in extent, and therefore not included in the sampling design and analysis.

Sampling design

Plot location and number

Pine, the most extensive type, consisted of three large polygons. To ensure even sampling across the type, I divided each polygon into six, seven, or eight (depending on polygon area) geographic sub-units of about equal area, and randomly placed plots in each. Spruce, the second-most extensive type, consisted of scattered stands interspersed among pine forest. I sampled all but the smallest stands of this type. The mixed-species type, co-dominated by beach pine and Sitka spruce, was even more limited in extent. It

¹ Types are listed in order of decreasing aerial extent.

consisted of two large polygons, which were intensively sampled, and several very small ones, only one of which was sampled (one plot).

I conducted a preliminary study to determine an adequate sample size for the pine and spruce types. Eight circular plots with a fixed radius of 13.2 m were established in randomly chosen polygons representing the pine and spruce types, respectively. I measured total density by tallying conifer trees greater than 7.62 cm in diameter at breast height (d.b.h.) on each plot. These density data were used to determine the number of plots needed in each type to ensure that sample population densities adequately represented true population densities. I used the sample adequacy formula:

$$n = t^2 s^2 / (k\bar{X})^2$$

where t is a t -distribution table value ($p=.90$), s^2 equals the variance, k =the proportion of the sample mean that is equal to the true difference between the sample mean and the population mean, and \bar{X} equals the mean density, to determine the number of plots (n) needed to achieve a sampling adequacy of approximately 80% (Bonham 1989). I determined that a sample size of 39 plots in the beach pine type, and 37 plots in the Sitka spruce type, would be adequate for the purposes of this study. The mixed-species type was area-limited and sample size equaled 9 plots total.

Structure and composition

Circular plots with a fixed radius of 13.2 m were used to sample trees equal to or greater than 7.6 cm d.b.h (3.8 cm d.b.h. for beach pine), seedlings and saplings less than 7.6 cm (3.8 cm d.b.h. for beach pine), and to estimate understory tree, shrub, and herb

cover. At each plot I: 1) identified and tallied each tree by species, 2) estimated diameter at breast height for each tree, 3) determined height for at least one representative tree of the tallest species on the plot, 4) tallied all snags greater than 7.6 cm d.b.h. and 2 m tall, 5) tallied each sapling and seedling by species, 6) estimated total cover for each tree and shrub species, and for the most common herbaceous species. The total number (n) of samples taken from each type were as follows:

pine: $n = 39$

spruce: $n = 37$

mixed-species: $n = 9$

These sample data allowed me to quantitatively describe and compare size structure, species composition, and regeneration patterns for selected stands.

Age structure

I cored trees on a subsample of 17 pine plots, 10 spruce plots, and 2 mixed species plots in order to assess their age structure. The number of trees cored per plot varied according to type. In general, the number of trees cored per type was proportional to the mean tree density for that type. I chose to minimize the proportion of cored individuals to reduce stress to the population of trees comprising sampled stands.

I cored 9-11 trees per plot in the pine type, 3-4 trees per plot in the spruce type, and 15 trees total in the mixed species type. Beach pine trees were cored at 35 cm above ground level on the upslope side whenever possible. Other species, often larger in diameter and flared at the base, were cored at breast height (83.2 cm) to ensure that cores

consistently reached to the pith. I purposely sampled across size classes at all plots, but did not core trees below the 6.2 cm d.b.h. size class so as not to damage small trees.

Tree rings were removed from the field intact, mounted on wooden blocks, razor trimmed, and hand-sanded with successively finer sandpaper down to 600 grit. The age of each tree was determined by counting growth-rings under a binocular dissecting microscope in the laboratory. Ages were documented for those trees with cores exhibiting growth-rings that could be counted from the pith to the cambium layer. Two cores representing large diameter spruce trees with widely spaced growth rings did not reach the pith. In those cases I estimated age using the following formula (USDA Forest Service 1995):

$$\text{Age} = (\text{DBH}/2 - \text{Bark thickness} - \text{Core length}) \times \text{Number of rings on innermost } 2.54 \text{ cm of core} + \text{Number of rings on core}$$

Some estimate was needed to account for the number of years it took each tree to reach coring height. I estimated that three and seven years, for trees cored at 35 cm and breast height, respectively, constituted reasonable assumptions. These estimates were derived in part by using the distance between branch whorls on saplings of various heights within the study area as a measure of height growth rates. Additionally, I cored two Sitka spruce individuals twice each, once at breast height and once at 35 cm. Cores differed by an average of four rings at those heights.

DATA ANALYSIS

Structure and composition

I calculated and compared tree basal area, density, and understory composition among the pine, spruce, and mixed-species types. Basal area and density comparisons among types were conducted for all tree species combined, as well as for individual tree species. Comparisons were made using either a one-way analysis of variance (ANOVA) or the Kruskal-Wallis one-way ANOVA on ranks when normality and equal variance assumptions were not met. When significant differences among types were found using the one-way ANOVA test, the Tukey-Kramer multiple comparison procedure was used to determine which types differed from one another with respect to the parameter of concern. The Kruskal-Wallis Z-test was used to compare types to one another when the Kruskal-Wallis one-way ANOVA on ranks found significant differences to exist among them (Hintze 1995). Snag densities and tree heights were described using simple statistics.

I calculated mean cover for the ground cover, shrub, and tree layer in each type. ANOVA and multiple comparison procedures were used to compare common understory species cover values among types. Comparisons were made only for species having a mean cover value of greater than three percent in at least one type. For the pine type, I also calculated the Spearman rank correlation coefficient and R^2 value to measure the relationship between stand age (mean age per plot) and various shrub cover values.

I calculated the importance of each dominant overstory and understory species (by type) and expressed it as a percentage. In the overstory, this statistic represents the

frequency values (Mueller-Dombois and Ellenberg 1974). The importance of each tree species in the regeneration layer of the pine type was calculated using relative sapling and seedling density and frequency values. Relative frequency and cover values were used to calculate the importance of individual species in the understory layer of each type.

Age structure

While age distribution patterns were analyzed for each of the three dominant stand types, pine was subjected to a more thorough analysis because: 1) pine is the most extensive type, 2) the population dynamics of beach pine are the least understood, and 3) small sample sizes in the spruce and mixed-species types constrained the potential for detailed age structure analyses.

I tested for significant differences in mean age among types. I divided beach pine plots into groups based on the mean age of sampled trees, tested for significant differences among those groups, and compared and contrasted age distribution data among groups using graphical displays and simple statistics.

I used histograms to depict age distribution patterns for the pine, spruce, and mixed-species types, and utilized density traces (Hintze 1995) to resolve age distribution patterns at a fine temporal scale. Density traces are smoothed histograms that reflect the relative frequency of trees along the data range. Subjective decisions that have a high impact on the look of histograms, such as the choice of a particular bin width and number, are eliminated by the use of density traces. I also used violin plots, which display density traces for multiple sample populations side by side, to compare age distribution

patterns among types. Thus, this unconventional tool helped to resolve age distribution patterns that may otherwise have been overlooked.

Since I purposely cored trees across size classes rather than selecting them entirely at random, I decided to assess how well the size class distribution of cored trees represented that of the larger subsample population in both pine and spruce stands. To do this, I calculated the relative proportion of trees within each of several size classes for both the cored and subsampled populations, respectively. I then compared the resulting percentage values for each population to determine how the size class distribution of cored trees compared to subsample size class distributions.

I tested the tree age data for each type to determine if they were normally distributed. I tested for normality at the five-percent significance level using the Martinez-Iglewicz normality test. Sample sizes were large enough in the spruce and mixed-species types to reject normality, but too small to accept it based on this test alone (Hintze 1995). I therefore relied upon both the Martinez-Iglewicz normality test and visual graphics to assess normality for those types.

Size/age relationships

I assessed the relationship between tree age and diameter by calculating the Spearman rank correlation coefficients and linear regression models for beach pine and Sitka spruce trees in pine and spruce stands.

Regeneration

I described stand regeneration using simple statistics to summarize the density and distribution of conifer saplings and seedlings for each type. I explored the relationship between sapling and seedling density and bearberry cover values in the pine type by calculating the Spearman rank correlation coefficient and regression equations for the two parameters.

RESULTS

Overstory structure and composition

Total basal area is significantly lower in the pine type than in either the spruce or mixed-species type (one-way ANOVA on log-transformed data, $p < 0.0001$). Total overstory tree density differs significantly among all types (Kruskal-Wallis one-way ANOVA on ranks, $p < 0.0001$), with density values highest in pine, lowest in spruce, and intermediate in the mixed-species type. Mean values for tree basal area and density (total and by species) are summarized for each type in Tables 1 and 2, respectively.

Beach pine basal area and stem density values differ significantly among types (Kruskal-Wallis one-way ANOVA on ranks, $p < 0.0001$ in both cases). The pine type exhibits the highest values, followed by mixed-species and spruce, respectively.

Sitka spruce basal area differs significantly among types (Kruskal-Wallis one-way ANOVA on ranks, $p < 0.0001$), with the highest values occurring in the spruce type, followed by mixed-species, and then pine. Mean Sitka spruce stem density is significantly lower in the pine type (Kruskal-Wallis one-way ANOVA on ranks, $p < 0.0001$) than in either spruce or mixed-species.

Neither Douglas-fir basal area (Kruskal-Wallis one-way ANOVA on ranks, $p = 0.7570$) nor stem density (Kruskal-Wallis one-way ANOVA on ranks, $p = 0.7797$) differs significantly among types. Mean grand fir basal area (Kruskal-Wallis one-way ANOVA on ranks, $p < 0.0001$) and stem density values (Kruskal-Wallis one-way ANOVA on ranks, $p = 0.0011$) were both significantly higher in the mixed-species type than in pine or spruce.

Table 1. Mean basal area (m²/ha) of conifer species by stand type, with one standard deviation in parentheses.

	Pine type	Spruce type	Mixed-species type
Beach pine	24.23 (10.17)	1.26 (2.34)	12.50 (5.17)
Douglas-fir	0.09 (0.52)	0.51 (2.22)	0.0 (0.0)
Grand fir	0.03 (0.20)	0.49 (1.98)	2.53 (4.18)
Sitka spruce	0.59 (2.06)	39.75 (20.41)	19.56 (5.12)
Totals	24.94 (9.88)	42.01 (16.64)	34.59 (7.59)

Table 2. Mean density (stems/plot, stems/ha) of conifer species by stand type, with one standard deviation in parentheses.

	Pine type	Spruce type	Mixed-species type
Beach pine			
plot	21.1 (8.5)	0.6 (1.1)	6.1 (3.6)
ha	521.00 (209.9)	14.8 (27.2)	150.6 (88.9)
Douglas-fir			
plot	0.05 (0.2)	0.01 (0.4)	0.0 (0.0)
ha	1.2 (4.9)	0.3 (9.9)	0.0 (0.0)
Grand fir			
plot	0.03 (0.2)	0.2 (0.4)	1.2 (1.6)
ha	0.7 (4.9)	4.9 (9.9)	29.6 (39.5)
Sitka spruce			
plot	0.3 (0.8)	5.6 (2.8)	5.6 (1.5)
ha	7.4 (19.8)	138.3 (69.1)	138.3 (37.0)
Totals			
plot	21.5 (8.4)	6.5 (3.2)	12.9 (3.5)
ha	530.3 (207.0)	160.2 (80.0)	318.3 (3121.1)

Beach pine (90%) and Sitka spruce (81%) were the most important overstory species in the pine and spruce types, respectively. The two species were of nearly equal importance in the mixed-species types (beach pine = 41% and Sitka spruce = 46%). Complete importance results for overstory conifers are presented in Table 3.

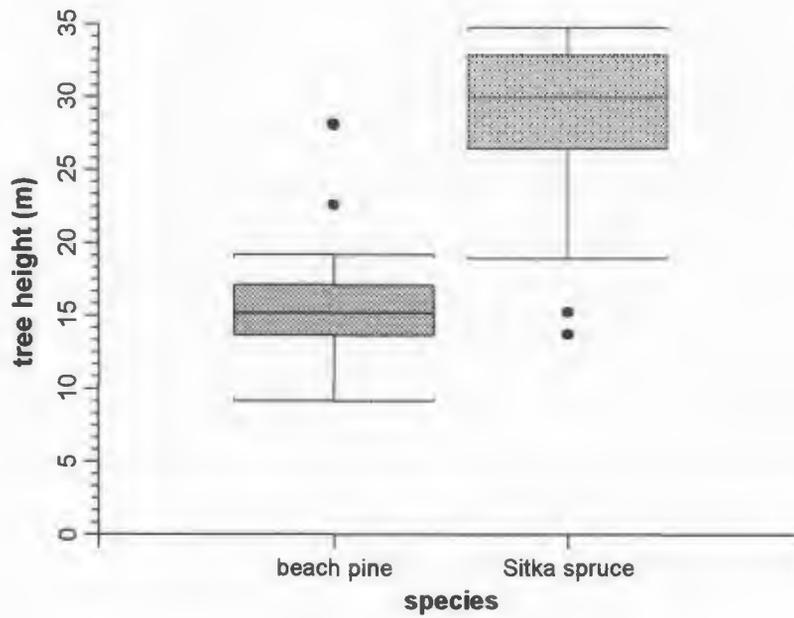
The mean tree height of sampled beach pine individuals occupying the upper canopy layer of pine stands is 15.4 m (STD = ± 3.2 m), while Sitka spruce individuals in spruce stands averaged 29.8 m (STD = ± 6.3 m). Based on this measure, the canopy layer is significantly taller in the spruce type than in pine (Kruskal-Wallis one-way ANOVA on ranks, $p < 0.0001$). While height differences between beach pine (mean = 17.5 m, STD = ± 3.6 m) and Sitka spruce (mean = 25.4 m, STD = ± 4.2 m) are less pronounced in the overstory of the mixed-species type, Sitka spruce is still significantly taller (Kruskal-Wallis one-way ANOVA on ranks, $p < 0.0001$). Comparisons between beach pine and Sitka spruce height are shown in Figure 2.

Mean snag density is presented for each species by type in Table 4. There were an average of 2.7 snags per pine plot (STD = ± 2.0), 1.2 snags per spruce plot (STD = ± 1.4), and 3.1 snags per mixed-species plot (STD = ± 2.4). Snags occurred with a high frequency (87.2%) on pine plots, and density varied little among them (STD = ± 1.96 snags per plot).

Table 3. Importance ((relative basal area + relative density + relative frequency)/3) of overstory conifer species by stand type.

	Beach pine	Douglas-fir	Grand fir	Sitka spruce
Pine type				
Importance (%)	92.2	1.6	0.7	5.4
Importance rank	1	3	4	2
Spruce type				
Importance (%)	12.0	1.9	4.8	81.3
Importance rank	2	4	3	1
Mixed-species type				
Importance (%)	40.9	0.0	12.8	46.3
Importance rank	2	4	3	1

a)



b)

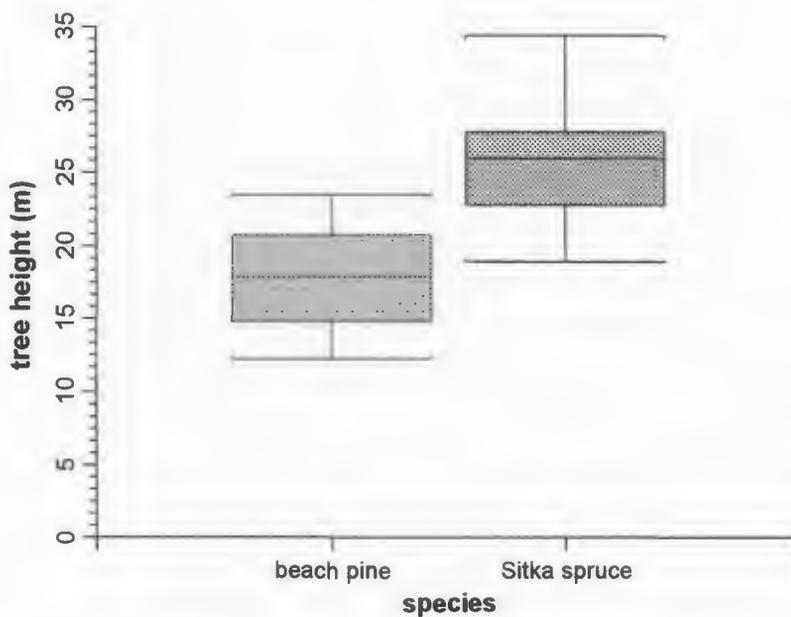


Figure 2. Boxplots comparing beach pine and Sitka spruce tree heights in a) the pine and spruce types, and b) the mixed-species type. Boxes represent the interquartile range with the median shown as a crossbar. Upper and lower adjacent values are displayed as T-shaped lines, and outliers appear as solid circles.

Table 4. Mean snag density (snags/plot) of conifer species by stand type, with one standard deviation in parentheses.

	Pine type	Spruce type	Mixed-species type
Beach pine	2.67 (1.96)	0.62 (1.09)	2.56 (2.19)
Douglas-fir	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Grand fir	0.0 (0.0)	0.08 (0.36)	0.22 (0.44)
Sitka spruce	0.0 (0.0)	0.54 (0.73)	0.33 (0.71)
Totals	2.67 (1.96)	1.24 (1.40)	3.11 (2.42)

Understory composition and cover

Mean ground cover, shrub, and tree layer cover values are presented for each stand type in Table 5. Importance values and rankings are presented for individual understory species (at least 3% important) in Table 6. In the pine type, the four most important species are evergreen huckleberry (46.7%), salal (9.4%), bearberry (8.6%), and wax myrtle (7.5%). In the spruce type, evergreen huckleberry (39.8%), wax myrtle (17.3%), and twinberry (6.3%) are most important. Evergreen huckleberry (50.6%) and salal (20.7%) dominate the understory of the mixed-species type, with no other understory species having an importance percentage greater than 5%.

Bearberry cover is significantly higher in pine than in other types (Kruskal-Wallis one-way ANOVA on ranks, $p = 0.0001$). Evergreen huckleberry cover is significantly lower (Kruskal-Wallis one-way ANOVA on ranks, $p = 0.0275$) and wax myrtle cover higher (Kruskal-Wallis one-way ANOVA on ranks, $p = 0.0011$) in spruce than in other types. Salal cover differs significantly among types (Kruskal-Wallis one-way ANOVA on ranks, $p = 0.0001$), with mixed-species having the highest cover, followed by pine and spruce, respectively. Silk tassel cover does not significantly differ among types (Kruskal-Wallis one-way ANOVA on ranks, $p = 0.8503$). Twinberry (*Lonicera involucrata*) and red flowering currant (*Ribes sanguineum*) cover values are significantly lower in the pine type than in spruce (Kruskal-Wallis one-way ANOVA on ranks, $p = 0.0431$ and $p = 0.0183$, respectively).

Table 5. Cover values of ground cover, shrub, and tree layers by stand type, with one standard deviation in parentheses.

	Ground cover	Shrub	Tree¹	Other²
Pine type:				
Cover (%)	16.9 (24.8)	74.0 (26.6)	6.3 (9.8)	2.6 (3.6)
Spruce type:				
Cover (%)	8.9 (20.1)	66.2 (27.6)	17.8 (22.1)	7.0 (4.6)
Mixed-species type:				
Cover (%)	0.6 (1.7)	90.0 (9.7)	3.3 (10.0)	6.1 (7.0)

¹ This category includes wax myrtle, which may be considered either a tall shrub or small tree.

² This category consists primarily of downed logs, needles, sand, paths and paths, but in some cases also includes sparsely distributed herbaceous species.

Table 6. Importance ((percent cover + relative frequency)/2) of understory species by stand type¹.

	Evergreen huckleberry	Wax myrtle	Salal	Bearberry	Twinberry	Silk tassel
Pine type:						
Cover (%)	64.9	5.3	6.9	7.4	0.9	1.0
Frequency (n=39)	38.0	13.0	16.0	13.0	4.0	6.0
Importance (%)	46.7	7.5	9.4	8.6	2.0	2.8
Importance rank ²	1	4	2	3	-	6
Spruce type:						
Cover (%)	53.0	17.3	3.0	0.0	4.3	1.9
Frequency (n=37)	35.0	23.0	5.0	0.0	11.0	7.0
Importance (%)	39.8	17.3	3.4	0.0	6.3	3.6
Importance rank	1	2	6	-	3	5
Mixed-species type:						
Cover (%)	72.2	3.3	15.6	0.0	0.6	1.1
Frequency (n=9)	9.0	1.0	8.0	0.0	1.0	2.0
Importance (%)	50.6	3.3	20.7	0.0	1.9	3.8
Importance rank	1	4	2	-	-	3
Mean importance (%):	45.7	9.3	11.2	2.9	3.4	3.4
Importance rank for all types:	1	3	2	6	4 (tie)	4 (tie)

¹ Only includes species with either: 1) a mean cover value of greater than 5 percent in at least one stand type, or 2) a combined mean cover value of at least 2 percent for all types.

² Ranks calculated only for species 2.5% important or more.

Table 6 (cont'd). Importance ((percent cover + relative frequency)/2) of understory species by stand type¹.

	Red-flowering currant	Grasses (all species)	Slough sedge	Other²
Pine type:				
Cover (%)	0.0	5.3	3.0	5.3
Frequency (n=39)	0.0	3.0	2.0	38.0
Importance (%)	0.0	3.8	2.1	17.0
Importance rank ³	-	5	-	
Spruce type:				
Cover (%)	1.9	5.3	2.2	11.1
Frequency (n=37)	7.0	3.0	4.0	37.0
Importance (%)	3.6	3.8	2.6	19.6
Importance rank	5	4	7	
Mixed-species type:				
Cover (%)	0.6	0.0	0.0	6.6
Frequency (n=9)	1.0	0.0	0.0	9.0
Importance (%)	1.9	0.0	0.0	17.8
Importance rank	-	-	-	
Mean importance (%):	1.8	2.5	1.6	18.1
Importance rank for all types:	-	7	-	

¹ Only includes species with either: 1) a mean cover value of greater than 5 percent in at least one stand type, 2) a combined mean cover value of at least 2 percent for all types.

² Includes downed logs, needles, sand, trails, and sparsely distributed or uncommon herbaceous species.

³ Ranks calculated only for species 2.9% important or more.

Age structure

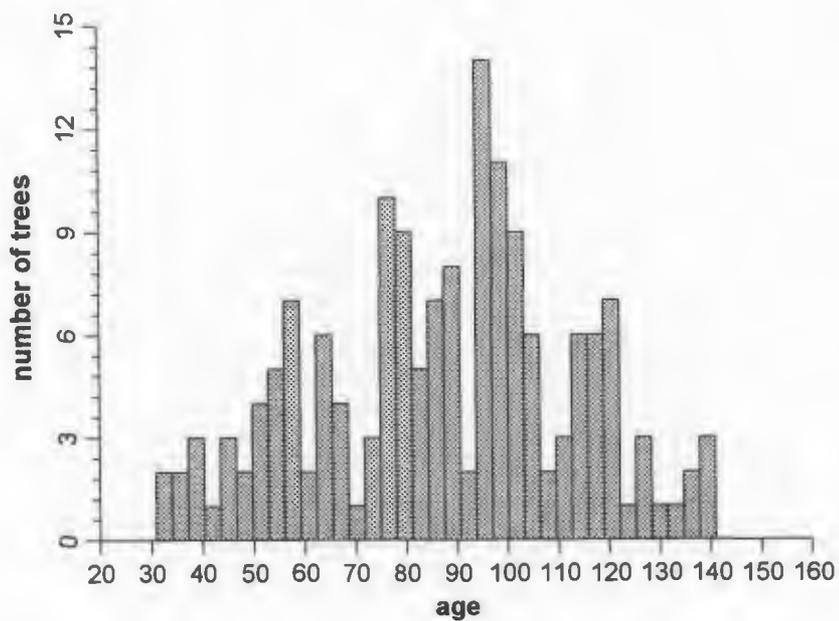
The pine type

Beach pine stands of the pine type are uneven-aged, exhibit a normal age distribution, and are comprised of multiple age classes (Figure 3). Most trees (55%) are between 70 and 110 years old, although many are either younger (26%) or older (19%). As many as 12 cohorts of trees have been established during the last 150 years (Figure 3b), although some of these are less apparent than others.

Pine plots can be divided into 3 groups exhibiting significant differences in mean tree age among them (one-way ANOVA, $p < 0.0001$; Figure 4a). I characterized the groups as: 1) young ($n = 3$), 2) intermediate ($n = 11$), and 3) old ($n = 3$). Many age classes correspond chronologically among the 3 groups, but vary in relative strength (Figure 4b). The young group is unique in that it includes many age classes, particularly the youngest ones, with no corresponding counterparts among the other two groups.

Individual 0.04 ha pine plots typically include trees representing numerous age classes (Figure 5a). Still, the range of tree ages on each plot is almost always less than about 65 years, with most trees being established within a time period of approximately 45 years (Figure 6a).

a)



b)

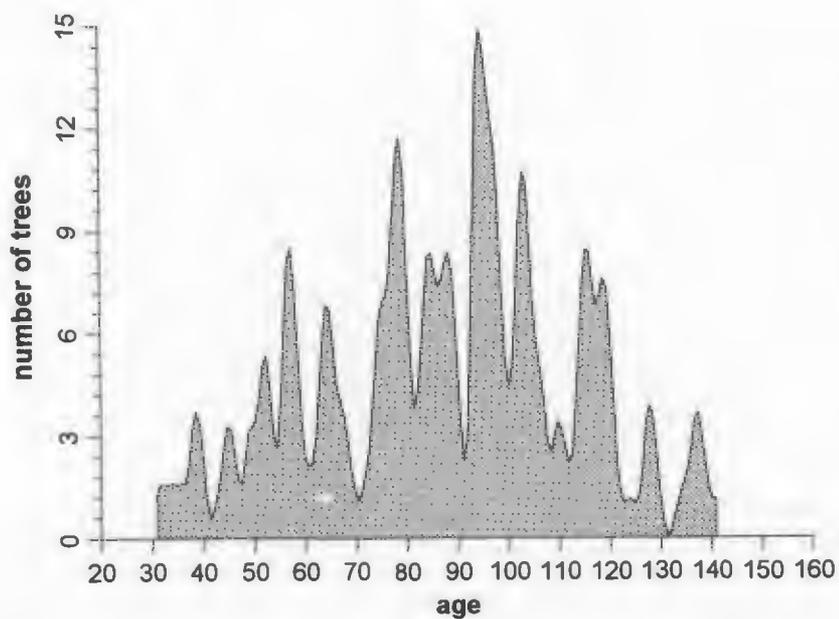
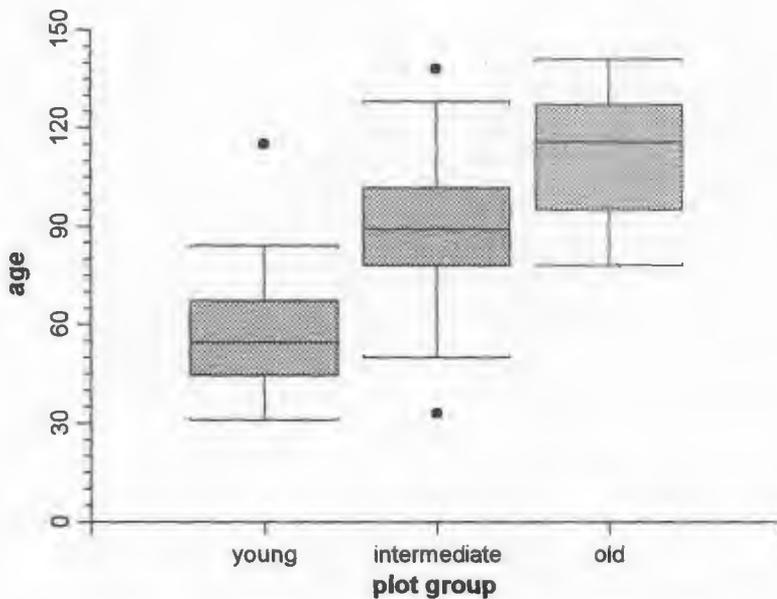


Figure 3. Age distribution for beach pine trees in the pine type, shown by a) histogram and b) density trace, which depicts the concentration of trees along the age range (Hintze 1995).

a)



b)

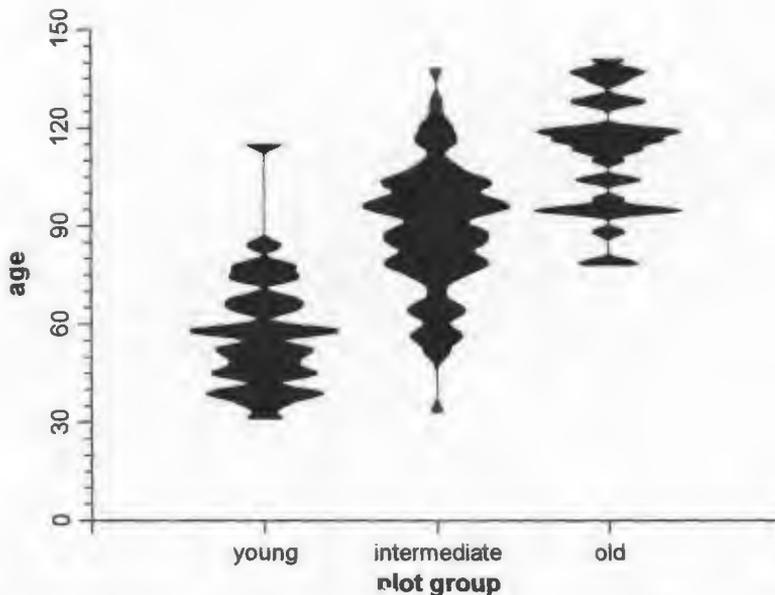
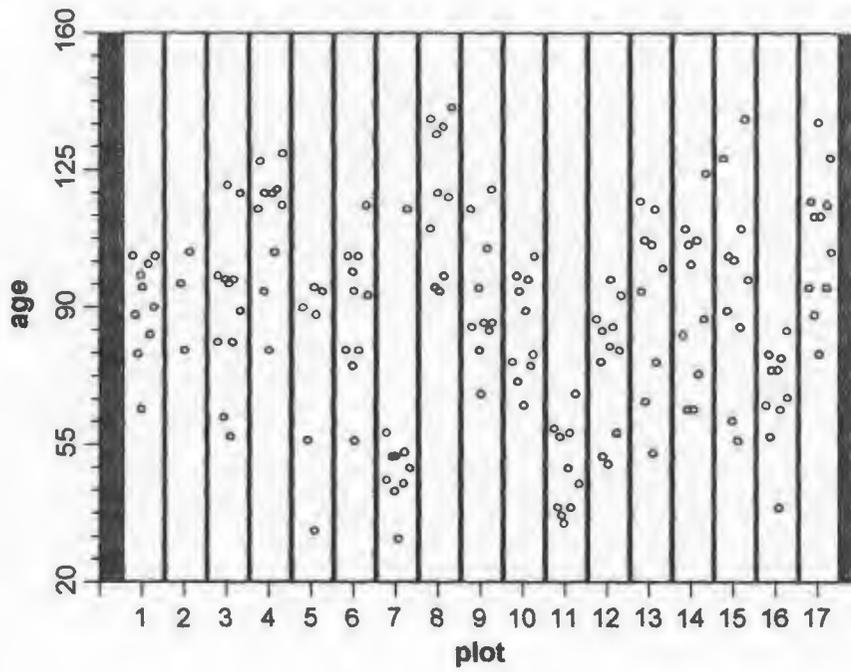


Figure 4. Comparison of age distributions for groups representing significant differences in mean age among pine plots. a) Boxplots represent the interquartile range with the median shown as a crossbar. Upper and lower adjacent values are displayed as T-shaped lines, and outliers are displayed as solid circles. b) Violin plots, each consisting of two identical density traces (for symmetry), one extending right and the other left of an invisible vertical axis (Hintze 1995). Violin plots highlight peaks and valleys in the age distribution of each group and help to identify corresponding cohorts among them.

a)



b)

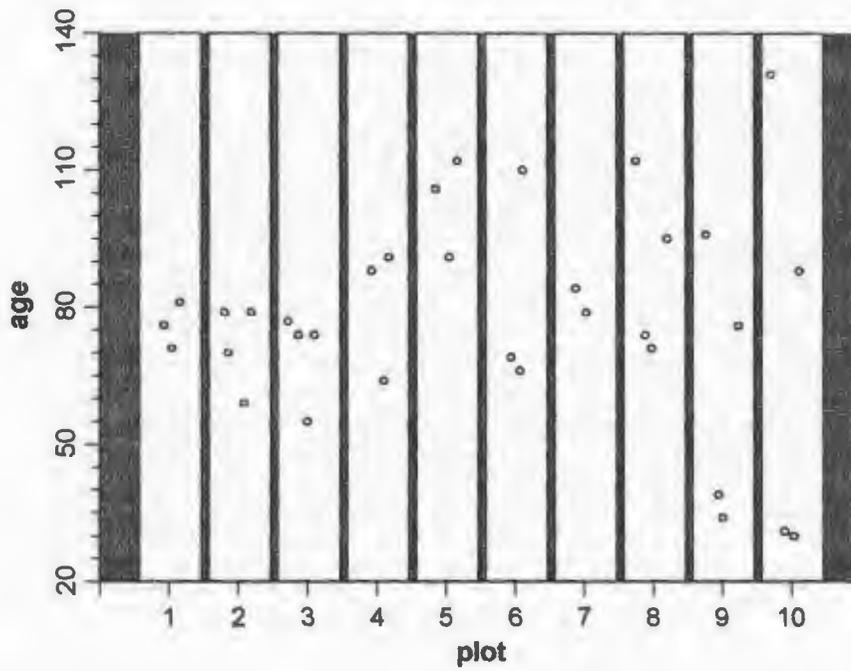
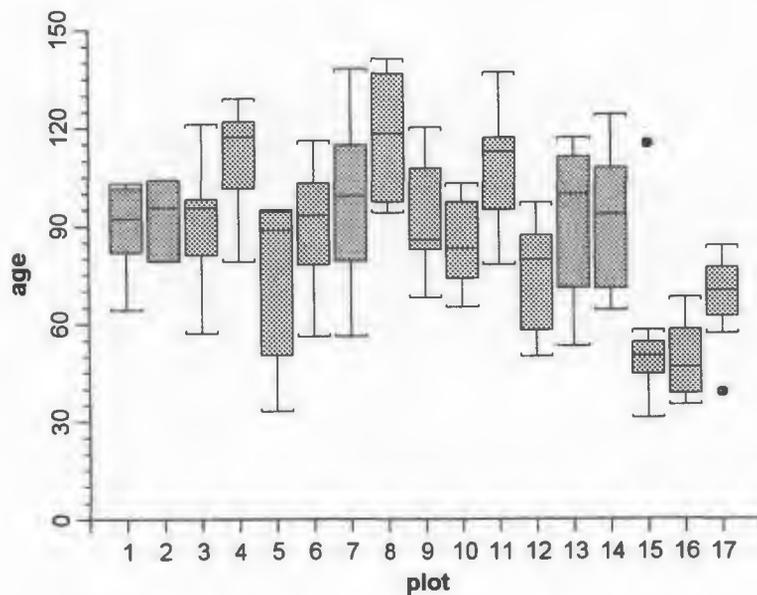


Figure 5. Age distribution of trees on individual 0.04 ha a) pine and b) spruce plots.

a)



b)

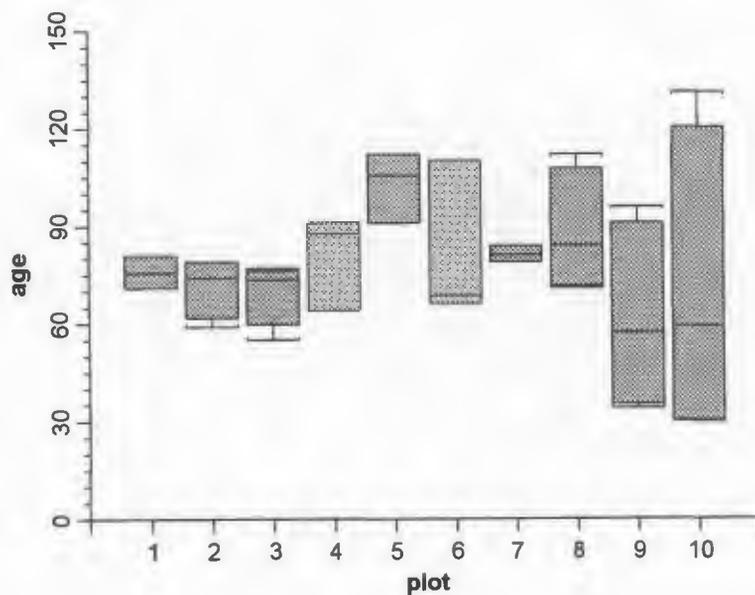


Figure 6. Boxplots of tree ages for individual a) pine and b) spruce plots. Boxes represent the interquartile range with the median shown as a crossbar. Upper and lower adjacent values are displayed as T-shaped lines, and outliers are displayed as solid circles.

The relationship between mean tree age and shrub (not including bearberry) cover is weak on sampled pine plots, with a Spearman rank correlation coefficient of only 0.2496 ($p = 0.3696$). The R^2 value of 0.14 indicates that mean tree age at a site explains little of the variation in shrub cover values. The correlation coefficient between stand age and bearberry cover is 0.0892 ($p = 0.7519$). The R^2 value of 0.0005 indicates that mean tree age at a given site explains almost none of the variation in total bearberry cover.

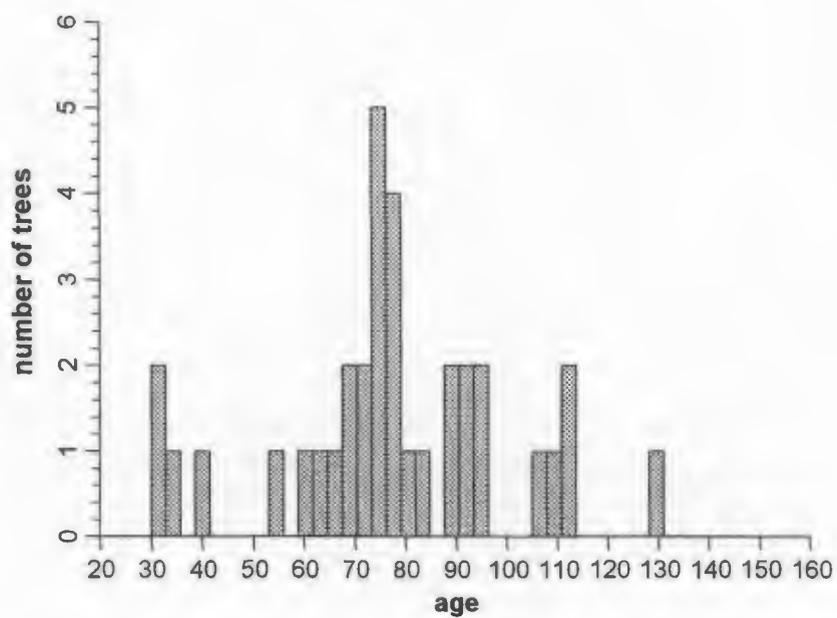
The spruce type

Sitka spruce stands of the spruce type are uneven-aged, exhibit a normal age distribution, and consist of multiple age classes (Figure 7). Distinct age classes are fewer and less easy to discern than in pine stands, but at least four are apparent in the age data (Figure 7a,b).

The chronology of spruce age classes corresponds closely to that of pine (Figure 8), except that those of spruce are consistently about five years younger their pine counterparts (compare Figures 3 and 7). This consistent discrepancy suggests either that seedling establishment of Sitka spruce is slower than that of beach pine following disturbance, or that the average number of years it takes a tree to reach coring height differs between species. If the latter is true, my seven-year estimate of Sitka spruce at d.b.h. may be low.

The mean age of sampled trees comprising spruce stands is significantly lower than that of pine and mixed-species stands (one-way ANOVA, $p = 0.0382$). Relative to groups representing age variation among pine plots, sampled spruce stands are

a)



b)

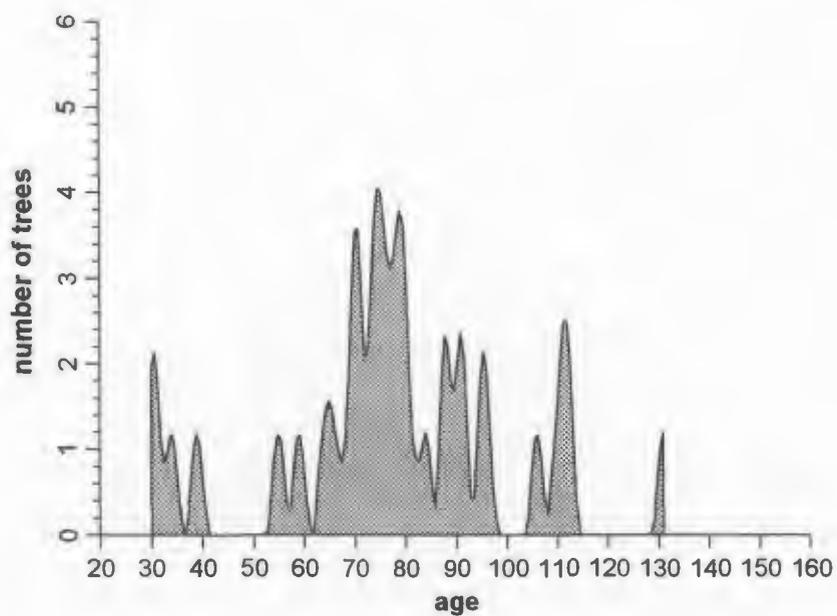


Figure 7. Age distribution for Sitka spruce trees in the spruce type, shown by a) histogram and b) density trace, which depicts the concentration of trees along the age range (Hintze 1995).

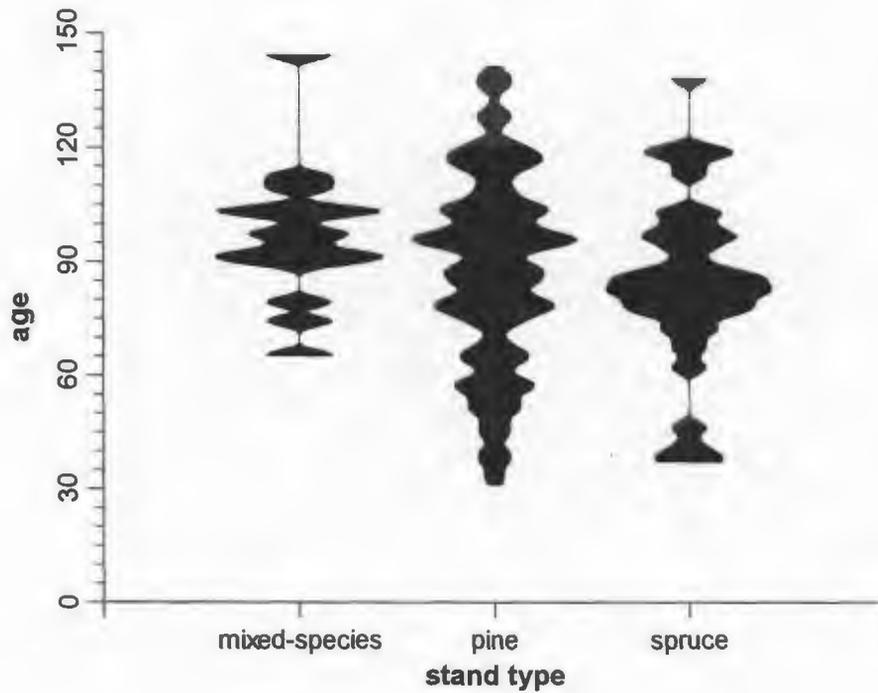


Figure 8. Violin plots comparing the age distributions of the mixed-species, pine, and spruce stand types. Violin plots consist of two identical density traces (for symmetry), one extending right and the other left of an invisible vertical axis (Hintze 1995). Here, violin plots help to identify corresponding cohorts among stand types by showing periods of high and low seedling establishment for each. Spruce tree ages have been adjusted by five years for the spruce type (see Results) to make comparisons easier.

significantly younger than pine plots characterized as either intermediate or old (one-way ANOVA, $p < 0.0001$ in both cases). Spruce stands are significantly older than pine plots characterized as young (one-way ANOVA, $p < 0.0001$).

The mixed-species type

Stands comprising the mixed-species type are uneven-aged and exhibit an approximately normal age distribution (Figure 9). Although the sample size is too small to confidently identify age classes, tree ages are consistent with the multi-cohort pattern exhibited by pine and spruce stands (Figure 8).

Mean tree age is significantly higher in sampled mixed-species stands than in spruce stands (one-way ANOVA; $p < 0.0001$), but does not differ significantly from that of pine stands. Both the oldest sampled tree, a 221 year old grand fir, and the oldest sampled beach pine (144 years), occur in this type.

Size/age relationships

The Spearman rank correlation coefficient for beach pine tree diameter and age is 0.3856 ($p < 0.0001$), and the regression equation ($p < 0.0001$) is:

$$\text{Age} = 63.94 + 0.89(\text{DBH})$$

The R^2 value for the regression equation is 0.13, indicating that diameter alone explains little of the variation among beach pine ages and therefore is a poor predictor of age.

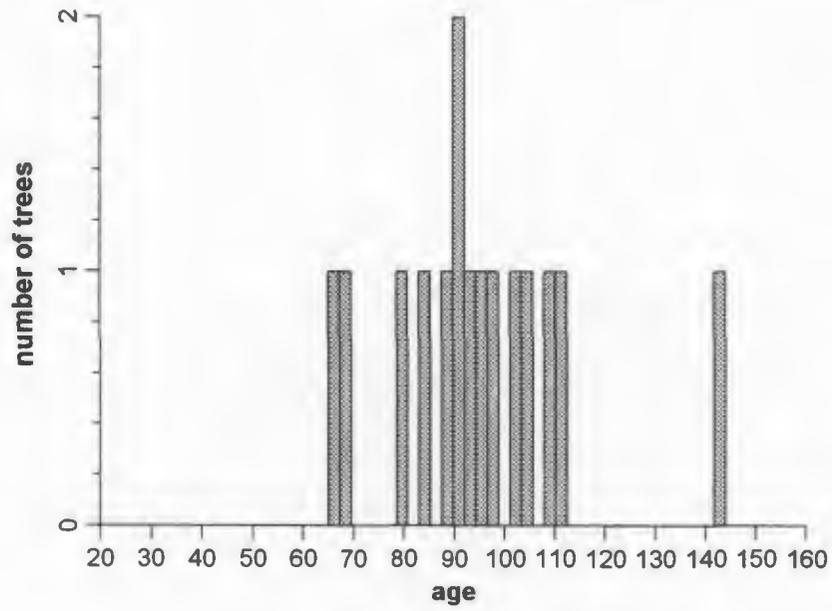


Figure 9. Histogram showing the age distribution of beach pine and Sitka spruce trees in the mixed-species type.

The Spearman rank correlation coefficient for Sitka spruce size and age is 0.5758 ($p = 0.0001$), and the regression equation ($p < 0.0001$) is:

$$\text{Age} = 52.61 + 0.50(\text{DBH})$$

The R^2 value for the regression equation is 0.40. That diameter alone explains less than half of the variation in age among Sitka spruce trees indicates that it is a poor predictor of age in the species. The size and age of beach pine and Sitka spruce trees are plotted in Figure 10.

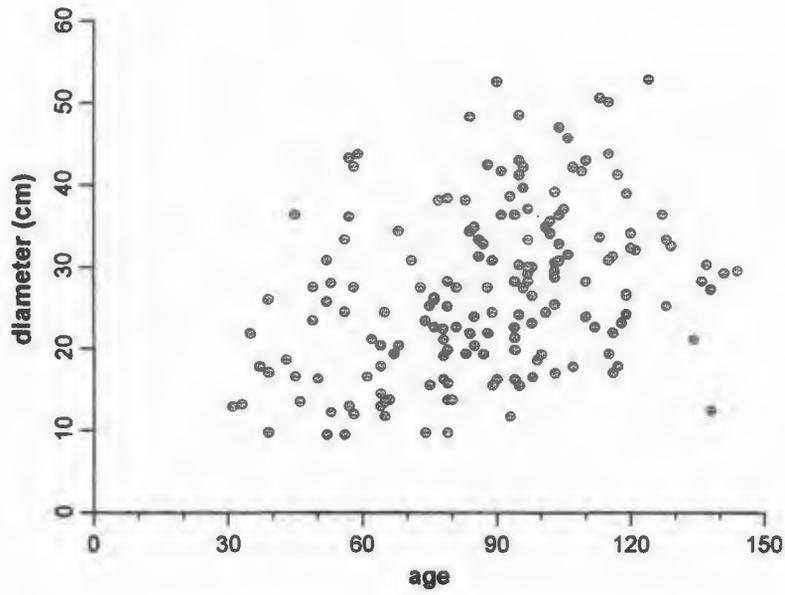
The results of my comparison between size-class distributions of cored trees and subsample populations are presented in Table 7. Based on the magnitude of these differences and the relatively weak relationship between size and age for both species, I conclude that my sampling across size classes had little bearing on age distribution results.

Regeneration

All stand types are characterized by a paucity of saplings and seedlings, particularly spruce and mixed-species. Beach pine plots averaged 3.2 saplings and seedlings per plot (STD = ± 7.18), while spruce (STD = ± 0.54) and mixed-species (STD = ± 0.44) each averaged only 0.2 per plot (Table 8).

Saplings and seedlings are unevenly distributed across the pine type, with only six plots (15.3% of the sample area) accounting for 87.8% of all regeneration age trees. Saplings and seedlings occurred on sample plots with a frequency of only 30.8%. Beach

a)



b)

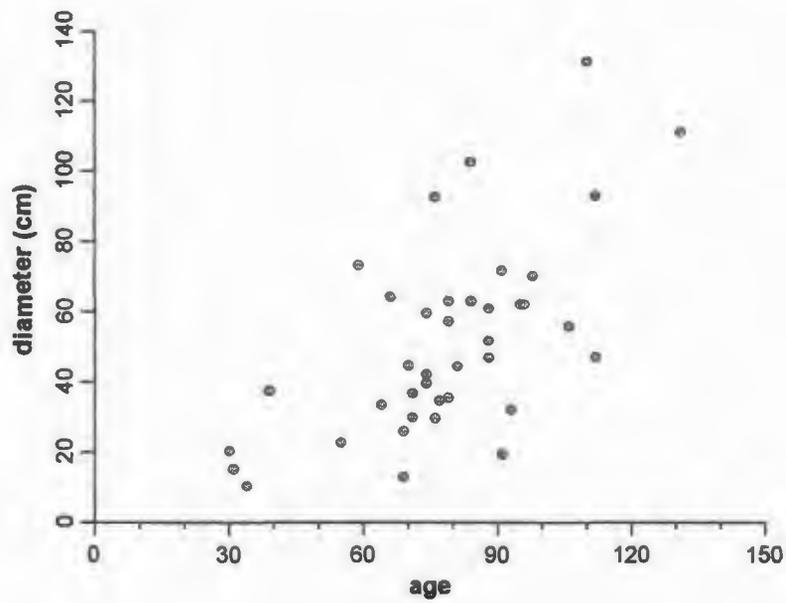


Figure 10. Scatter plots showing the size/age distribution of individual a) beach pine and b) Sitka spruce trees.

Table 7. Comparison of size class distributions of cored trees and tallied trees on a) pine and b) spruce subsample plots.

a)

Size class (d.b.h. in cm)	7.2-17.9	18.0-27.9	28.0-37.9	>38.0
Tallied trees	26%	45%	20%	9%
Cored trees	24%	33%	29%	14%
Difference	2%	12%	9%	5%

b)

Size class (d.b.h. in cm)	0.0-39.9	40.0-80.0	>80.0
Tallied trees	32%	52%	16%
Cored trees	41%	44%	15%
Difference	9%	8%	1%

Table 8. Mean sapling and seedling density (individuals/plot) of conifer species by stand type, with one standard deviation in parentheses.

	Pine type	Spruce type	Mixed-species type
Beach pine	2.51 (5.99)	0.0 (0.0)	0.0 (0.0)
Douglas-fir	0.18 (.60)	0.16 (0.54)	0.22 (0.44)
Grand fir	0.03 (0.16)	0.0 (0.0)	0.0 (0.0)
Sitka spruce	0.51 (2.0)	0.16 (0.54)	0.22 (0.44)
Totals	3.23 (7.18)	0.16 (0.54)	0.22 (0.44)

pine (59.0%) is the most important species in the regeneration layer of the pine type, followed by Sitka spruce (25.5%) and Douglas-fir (13.0%)(Table 9).

The Spearman rank correlation co-efficient for sapling and seedling density and bearberry cover values is 0.7220 ($p < 0.0001$), indicating a strong correlation between the two variables on pine plots. The R^2 value is 0.75, indicating that bearberry cover explains most of the variation in sapling and seedling density in the pine type.

Mean sapling and seedling density in the pine type (3.23/plot) approximates that of snags (2.67/plot). However, saplings and seedlings are present on pine plots much less frequently (31%) than are snags (87%), and their density values exhibit a higher degree of variation (STD = ± 7.2 and ± 2.0 , respectively).

Table 9. Importance $((\text{relative density} + \text{relative frequency})/2)$ of conifer species in the understory layer of the pine type.

	Beach pine	Douglas-fir	Grand fir	Sitka spruce
Total density (saplings and seedlings/plot)	98	7	1	20
Frequency (n=39)	8	4	1	7
Relative density	78	6	(<0.5)	16
Relative frequency	40	20	5	35
Importance percentage	59.0	13.0	2.5	25.5

DISCUSSION

Structure and composition

The results of my sampling support the original forest stratification into three distinct stand types: 1) pine, 2) spruce, and 3) mixed-species. A summary of structural and compositional characteristics for each type is included in Table 10. Also, informal observations indicate that Douglas-fir and grand fir are included among the more important overstory species in only small, isolated forest patches.

The conifer forest at Lanphere Dunes is structurally complex. It involves an overstory canopy layer that is vertically and horizontally heterogeneous. Canopy tree height varies considerably between the pine and spruce types and within the mixed-species type (Figure 2). Although I did not formally analyze variation within the pine and spruce types, I often found it difficult to discern a distinct canopy layer on individual plots because of the diversity of tree heights at that scale.

Distinct understory layers also contribute to the forest's structural complexity. The spruce type includes a distinct understory tree layer consisting primarily of wax myrtle (Tables 5 and 6). However, the understory tree layer is less distinct in pine and mixed-species stands, where wax myrtle is less important and generally more shrub-like in habit. The shrub and ground cover layers are also structurally heterogeneous, but all stand types involve a dense, 1.0-2.5 m tall shrub layer that is pervasive across most of the forest (Table 5). A ground cover layer of slough sedge or grass is also important in limited portions of the pine and spruce types. Additionally, bearberry mats and associated

Table 10. General comparison of stand type characteristics.

	Pine type	Spruce type	Mixed-species type
Basal area	low	high	intermediate
Stem density	high	low	intermediate
Important overstory species (in decreasing order)¹	beach pine Sitka spruce	Sitka spruce beach pine	Sitka spruce/beach pine grand fir
Important understory species (in decreasing order)²	evergreen huckleberry salal bearberry wax myrtle	evergreen huckleberry wax myrtle twinberry	evergreen huckleberry salal
Age structure	multiple age classes normally distributed	multiple age classes normally distributed	multiple age classes normally distributed

¹Includes only species that are greater than 5% important.

² Includes only species that are greater than 5% important.

herbaceous plants form a patchily distributed but important component of the ground cover layer in the pine type.

The forest at Lanphere Dunes is characterized by species assemblages that are similar yet distinct from those described in Oregon (Wiedemann 1966, Franklin and Dyrness 1973, Wiedemann 1984). Western red cedar, western hemlock, and Port Orford-cedar do not occur here, and Douglas-fir is much less important than in Oregon. Grand fir is apparently much more important here than in coastal dunes forests farther north.

The spruce and mixed-species types at Lanphere Dunes are distinguished by a dense understory shrub layer in which evergreen huckleberry is the most important species (Table 6). Silk tassel, rare in Oregon dune forests, is moderately important overall in the forest at Lanphere Dunes (Table 6). Alternatively, rhododendron is a common shrub in the understory layer of pine stands in Oregon dune forests but is unimportant in the pine type here.

While I did not formally investigate factors affecting the distribution of stand types at Lanphere Dunes, my data (Tables 3 and 6) in some cases suggest ecological patterns and raise questions regarding the distribution and composition of these types. In particular, the importance of wet-associated wax myrtle (Reed 1988) and moist-associated twinberry (Hickman 1993) in the spruce type corroborate informal observations that spruce stands typically inhabit moist, low-lying, protected areas in the dunes. In the pine type, the greater importance of sclerophyllous shrubs like bearberry, evergreen huckleberry, and salal support observations that the type typically occupies dry, elevated, and exposed sites, although beach pine may also be found on extremely wet sites with seasonal standing water and an understory of slough sedge.

The position of the mixed-species type along the environmental continuum generally observed for pine and spruce remains unclear. That the importance values of beach pine and Sitka spruce (Table 3) in the mixed-species type are intermediate to those of pine and spruce suggests that the type may occur between two environmental extremes. However, the type's importance values for grand fir and common understory species such as evergreen huckleberry, salal, and wax myrtle relative to pine and spruce (Table 6) do not support a hypothesis of intermediacy. It is possible that historical factors are as important as environmental ones in explaining the distribution of the mixed-species type at Lanphere Dunes.

Age structure

Historical descriptions (Irvine 1915, Loud 1918, U.S. Coast Survey 1870) suggest that a mature forest occupied the study area when European explorers arrived around 1850. Beach pine and evergreen huckleberry are both described as being important at that time. Mature Sitka spruce stands are confirmed as early as 1918 (Loud 1918). Thus, sampled pine, spruce, and mixed-species stands derive from a mature forest that has existed at the study site for at least 150 years, and perhaps much longer.

The pine type

The age structure of the pine type is both spatially and temporally complex (Figures 3, 4, 5). Neither the J-shaped age distribution typically attributed to self-replacing stands, nor an even-aged distribution resulting from catastrophic disturbance (Oliver and Larson 1990), applies here. Age data depicting as many as twelve distinct age

classes of trees indicate past pulses of regeneration (Figure 3), which typically result when disturbance events disrupt the overstory canopy (Oliver and Larson 1990). Frequent disturbance therefore appears to be an important explanation for the age structure of the pine type.

That pine plots can be separated into at least three distinct groups based on mean age (Figure 4a, see Results) suggests a spatial stratification of the forest with respect to age. However, a careful survey of the data reveals no clear spatial relationship between like plots such that any one of the three groups could be said to represent a spatially contiguous block of forest.

That age classes are shared among groups (Figure 4b) does not support the notion that the young, intermediate, and old categories represent distinctly aged stands of unique origin. Rather, each group is comprised of numerous, disjunct patches of forest that have responded similarly to an array of widespread disturbance events in the past. As such, the categories may be viewed as statistical abstractions that help to express the dimensions of a local disturbance regime.

Statistical differences between groups imply variation in the severity (or impact) of disturbance events across the forest. Such variation applies to individual events as well as the collective impact of multiple events occurring over time. Meanwhile, that age classes correspond among widely dispersed plots implies that individual disturbance events are typically forest-wide in extent.

The uneven age distribution of trees on individual 0.04 ha sample plots (Figure 5a) suggests that disturbances have been low to moderate severity events, as opposed to catastrophic, stand-replacing ones. The diversity of ages also implies that the average

disturbance patch size is small (<0.04 ha). The term patch size refers to the spatial dimensions of canopy gaps resulting from individual disturbance or mortality events (Oliver and Larson 1990). At Lanphere Dunes, forest disturbances generally manifest themselves as small canopy gaps resulting from the loss of individual trees or clusters of trees.

The relatively narrow range of ages on each 0.04 ha plot, usually less than 65 years (Figure 5b), suggests that canopy turnover and subsequent regeneration rates can be high at the 0.04 ha scale. That the trees (Figures 3b and 5a) occurring on a given plot became established over such a short period of time implies a corresponding rate of canopy disturbance and degeneration. Forest development at this scale apparently involves long periods in which the canopy remains virtually intact, followed by short periods of intense degradation as successive disturbance events rapidly eliminate the overstory layer.

Although slow-growing beach pine individuals have been known to live up to 300 years in peat bogs of Alaska (Wheeler and Critchfield 1985), the life-expectancy of the subspecies appears to be much shorter in coastal dunes further south. Egler (1934) rarely found trees greater than 100 years old in Oregon, and Wiedemann (1966) suggested few stands ever exceed 150 years in age. The oldest beach pine individual found by this study was 144 years old, supporting the suggested beach pine life expectancy of approximately 150 years on coastal dunes in the Pacific Northwest. Whether the upper age-limit is determined by life-history traits or reflects canopy turnover rates as a result of disturbance remains unclear.

The spruce type

Spruce age distributions (Figure 7) are similar to those of pine, exhibiting neither a J-shaped curve indicative of self-replacing stands nor an even-aged distribution resulting from catastrophic disturbance (Oliver and Larson 1990). Sitka spruce trees characterizing this type, although generally much larger than beach pine individuals, are significantly younger than trees comprising the pine and mixed-species types. Spruce has proportionally more trees in the 70-80 year class, and less in the 95-105 year class, than the other two types (Figures 7, 3, 9).

The relatively young age of spruce stands and the high proportion of trees in the 70-80 year class are both difficult to explain. The former may be partly related to the five year discrepancy observed between beach pine and Sitka spruce trees (see Results). It is also worth noting that age class differences distinguishing spruce from other types are a matter of age class strength rather than of their presence or absence. Also, spruce type age distributions fall well within the range of variation exhibited by plots of the pine type (Figure 4). Age structural differences may therefore reflect the unique response of spruce stands to an array of disturbances that has been similar among types during the last 150 years.

The most striking aspect of Sitka spruce age distributions is the relative youth of stands with respect to the life span of the species, which may exceed 700 years (Harris 1990). At Lanphere Dunes, no sampled trees exceeded 131 years of age. This finding corresponds roughly to the maximum age of 139 years presented by Egler (1934), and supports a life-expectancy of less than 150 years for Sitka spruce on coastal dunes in the Pacific Northwest. Judging by the long life span of the species in other habitats and parts

of its range, it is reasonable to conclude that the 150-year mark reflects canopy turnover rates resulting from disturbances rather than life-history traits.

It is interesting to note that Sitka spruce age classes, both in spruce and mixed-species stands, are consistently about five years younger than their pine counterparts. One explanation for the discrepancy is that seedling establishment of Sitka spruce is slower than that of beach pine following disturbance. That nurse logs are known to play an important role in Sitka spruce regeneration (Agee 1993), especially where water tables and competition from surrounding brush are high (Harris 1990), implies that Sitka spruce seedling establishment may be delayed for several years following disturbance while downed logs decay into suitable substrates.

The mixed-species type

The age distribution of trees in the mixed-species stand type (Figure 9) follows the uneven, normally distributed pattern characterizing pine and spruce. It is worth noting that spruce trees are generally younger than pine trees (13 years on average) in this stand type, and are not represented in the older age classes. Still, Sitka spruce is significantly taller than beach pine in the type (Figure 2b).

Differences in age and height suggest that now spruce trees are emerging from beneath a canopy of pine and beginning to exert dominance. This pattern is consistent with the idea of succession as described by Egler (1934) and Wiedemann (1966) for stands in Oregon, whereby Sitka spruce may eventually replace beach pine in the canopy in the absence of catastrophic disturbance. The mixed-species type provides the clearest

example of this pattern of development at Lanphere Dunes, but constitutes only a limited area.

The two oldest trees I cored both occurred in mixed-species stands. The first was a 144 year-old beach pine. The second was a large diameter (104 cm) grand fir for which I counted 157 rings on a core that did not reach the pith, and for which I estimated an age of 221 years. This age is not particularly unusual for a species of tree that commonly lives for 250 years (Foiles et al. 1990), but is significant because it indicates that some trees can survive in the local dunes for at least two centuries.

Summary

At Lanphere Dunes, similarities in the age structures of pine, spruce, and mixed-species stands are more pronounced than are the differences, implying similar disturbance histories. In terms of age structure, tree populations here are better viewed collectively as an extensive forest stratum than as an assortment of distinctly aged stands.

Three important patterns emerge from age structures for all types in the study area: 1) corresponding age classes among spatially segregated plots and stand types, 2) small disturbance patch sizes, and 3) normal age distributions. These patterns infer much about both the character and source of disturbance in conifer forests at Lanphere Dunes.

Disturbance

It has been argued that the forests of coastal dunes in the Pacific Northwest are subject to a complex array of disturbances that operate at various spatial and temporal scales, including sand movement, fire, human activity, pathogens, and wind (Egler 1934,

Wiedemann 1966, Pacific Watershed Associates 1991). Since disturbance factors in large part determine age structure and underlying stand development patterns, (Oliver and Larson 1990, Agee 1993), forest stands at Lanphere Dunes must be understood within the context of such influences.

Sand movement

Geologic disturbance events have historically affected regional coastlines on a time scale measured in hundreds of years (Rogers 1988, Heaton 1990). Studies indicate that four major incidents have impacted the coastline near Humboldt Bay in the last 1,700 years (Clarke and Carver 1991), resulting in the inundation of low-lying coastal areas by ocean water, sand, and sediment. Those events apparently correspond to four region-wide earthquakes that affected many areas along the Pacific Northwest coastline during the last two millennia. These events have been dated at approximately 300, 1,000, 1,500, and 1,700 years before present (Rogers 1988, Clarke and Carver 1991).

The most recent local subsidence event occurred about 300 years ago (Jacoby et al. 1990), and is hypothesized to have initiated a tsunami that washed over and probably destroyed existing foredunes (Pacific Watershed Associates 1991, Leroy 1998 pers. comm.). By removing the principal barrier to inland sand movement, the tsunami is hypothesized to have initiated the formation of large, active sand dunes that are presently advancing southeastward from the seashore across the landscape. The active dunes are presently overriding an older system of forested "paleodunes" (Cooper 1967, Pacific Watershed Associates 1991) which are presumably derived from one or more past

tectonic events. Conifer forest stands of the paleodunes are being actively buried as a result.

By comparing the current westward extent of mature forest at Lanphere Dunes to that depicted on maps dating to 1870 (U.S. Coast Survey 1870), it is clear that active dunes have entombed large tracts of forest over the last 130 years. Exposed tree corpses and old soil profiles (Varga 1989) observed in the wake of active dunes indicate that the mature forest margin once extended hundreds of meters northwest of its current boundary. Still, at the estimated 1.4-1.7 m per year rate of dune advancement (Pacific Watershed Associates 1991), it would take another 200-300 years before eastern parts of the forest are overtaken. By that time, young stands today establishing themselves in deflation plains to the lee of advancing dunes, along dune ridges, and at other stabilized sites will have had time to develop into mature stands. The destruction of old forest by advancing dunes, and the subsequent initiation of stands upon the new substrate, involves a process that may take hundreds of years at the spatial scale of the study site.

I propose that the modern history of forest development at Lanphere Dunes is framed by two geologic events: 1) an earlier placement of the dune substrate now inhabited by forests, and 2) the later and continuing advance of sand dunes over conifer forests and paleodunes. Based on the rate of sand movement for active dunes initiated 300 years ago, a high-magnitude tectonic event 1,000 years before present (Rogers 1988, Clarke and Carver 1991) would have re-initiated forest development at the study site between 400-700 years ago. That 400-700 year old trees are not found at the study site does not necessarily discount such a theory; it only insinuates that the original trees have since died and been replaced by others.

While geologic disturbance almost certainly played a role in the initiation of the forest at the study site, it does not appear to have had a major influence on the forest's development over the last 150 years. The large-scale, catastrophic disturbance explanation accounts for neither the wide distribution of multiple age classes, nor small disturbance patch sizes encountered in the forest at Lanphere Dunes.

Fire

Egler (1934) assumed an important role for stand-replacing fires in the establishment of pine stands in coastal Oregon, citing both the presence of charcoal and the uniform structure of stands there. Wiedemann (1966) summarized historical accounts of widespread fires in central Oregon's coastal dune forests during the early and mid-1800's. In the open dunes at Humboldt Bay, widely distributed charcoal deposits and charcoal layers in recently exposed soil profiles indicate that the forests entombed here had previously burned (Varga 1989, Leroy 1998, pers. comm., Pickart 1998, pers. comm.).

Reviewing the literature, Agee (1993) concluded that a low frequency/high severity fire regime characterizes coastal forests of the Pacific Northwest. However, any scenario that includes catastrophic fire fails to explain the complex age structure of unburied forest stands here. Additionally, I found no charcoal deposits or fire-scars in sampled areas, or evidence of fire in historical documents (Irvine 1915, McCormick 1918). The presumed occurrence of widespread fire in earlier forests is not evident in living stands.

It is also unlikely that low to moderate intensity fires have influenced age structure and stand development patterns here. Such fires, for which I discovered no record, would have to have occurred roughly every 10-15 years in order to explain the number of age classes implied by my data. Such a high fire frequency corresponds neither to the regional fire regime, nor even to frequencies in drier inland lodgepole pine forests, where fire returns at roughly 60-80 year intervals (Agee 1993). Furthermore, fire-scarred trees and scattered charcoal, generally present in fire-afflicted lodgepole pine forests (Agee 1993), are lacking in the study area.

The presence of charcoal in and among an exposed soil profile that is reportedly contemporary with that of today's forest (Varga 1989) remains a source of mystery. Apparently, past fires affecting western portions of the forest did not spread east into areas now inhabited by mature stands. It is possible that salt water inundation associated with the hypothetical tsunami that struck the coast 300 years ago, or the desiccation that resulted as sand began to entomb the forest, may have killed vegetation and increased flammability in affected areas. Resulting fires are likely to have been extinguished as they spread eastward into living portions of the forest that supported moister conditions and lower dry fuel loads. Any such margin between burned and unburned forest probably lies somewhere beneath active parabolic dunes. Evidence of fire at Lanphere Dunes will remain enigmatic until research is conducted to address the issue more specifically.

Pathogens

Interactions among fire, insects, and fungal pathogens comprise the typical disturbance scenario in inland stands of lodgepole pine, sometimes resulting in uneven-aged stands (Agee 1993). While there is no evidence that sampled stands have ever burned, the importance of pathogenic activity in pine stands is apparent here.

I commonly observed pathogenic fungi damaging or killing beach pines during the course of my fieldwork. Lodgepole pine¹ is considered subject to attack by many fungal pathogens, which are responsible for reduced growth and mortality (Lotan and Critchfield 1990). I most often encountered the fruiting bodies of red ring rot (*Phellinus pini*), a common disease that causes heartwood decay along the trunk of conifers. Perhaps one out of every five or six trees could not be aged because rotten heartwood and sometimes sapwood prevented the extraction of intact cores.

Signs of pathogenic activity were rarely observed in spruce stands, although damaged Sitka spruce are considered highly susceptible to decay when injured (Harris 1990). In several cases, trees inhabiting low-lying areas prone to flooding exhibited symptoms commonly caused by root or butt rots (rounded tops, lacy crowns, and distressed cone crops). It is difficult to say whether those symptoms result from disease or slow drowning caused by excessive inundation during recent wet years. In general, disease does not currently appear to be a major factor causing mortality in spruce stands.

Although the sequoia moth (*Vespamima sequoiae*) is known to damage local beach pine trees (Haggard 1999, pers. comm.), I saw nothing to indicate that insect

¹ Presumably including beach pine, though findings derive from studies primarily involving other subspecies of lodgepole pine.

damage is a major source of mortality in the study area. Similarly, dwarf mistletoe attacks some trees in beach pine stands of Canada (Smith and Wass 1976, Wass 1976), but was not observed at Lanphere Dunes.

While insects and fungal pathogens probably weaken or kill many trees (particularly in pine stands), age distribution patterns throughout the forest suggest that other important factors are involved. Diseases that are far more obvious among beach pine trees fail to explain similarities in the age class distribution of pine and spruce stands. Also, distinct cohorts are an unlikely result of live-rots alone, since those organisms typically weaken and kill individuals over a period of many years (Sinclair et al. 1987). Patterns of mortality indicating disease centers or widespread, epidemic die-offs are not apparent in the age data and were not otherwise observed. A more complete explanation is therefore required for the age structures found in the study area.

Grazing and firewood foraging

Except for grazing in limited areas and the possibility of fire-wood foraging, there is generally little evidence of forest disturbance by human activity during the last 150 years. An old road goes through much of the study site, but no comprehensive network of access roads is apparent. Old tools and cables typically used in logging were not found lying about during the course of this study. Age structure characteristics (i.e. multiple age classes, small patch size) at Lanphere Dunes do not conform to disturbance patterns expected from logging or other intensive human activities. While human development

and activity threaten coastal dune forests elsewhere, they do not appear to have significantly influenced stand structure at the study site.

Wind

So far, I have rejected the likelihood that disease, fire, human activity, and sand movement are primary mechanisms explaining age distribution patterns at Lanphere Dunes. Finally I examine the role of wind, the disturbance factor that best explains age structures found here.

Both Egler (1934) and Wiedemann (1966) considered wind to be the most important disturbance factor affecting Oregon coastal dune forests since they were subjected to widespread fire in the early 1800's. Wind is also considered to be the most important disturbance factor in the coastal Sitka spruce zone of the Pacific Northwest (Agee 1993). It is not entirely surprising then that out of all possible factors, wind disturbance best explains the age structures characterizing local stands. In particular, and unlike other explanations, wind disturbance accounts for the wide distribution of corresponding age classes and the small disturbance patch sizes implied by my age data.

My wind hypothesis also incorporates disease as a secondary component, particularly in explaining pine stands. That fungal pathogens increase the likelihood of blowdown is well-recognized (Sinclair et al. 1987, Allen et al. 1996,) and I observed many pine trees that had been snapped off, seemingly by wind, within several meters of the ground. Alternatively, uprooted trees were seldom observed.

My wind hypothesis must also explain the normal age distributions found for all stand types (Figures 3, 7, 9). That such distributions should result from the irregular

influence of wind is counterintuitive. In order to address this enigma, I obtained wind data from the National Weather Service at Eureka, California (National Weather Service 1998), and plotted the peak wind gusts greater than 82.5 km/hour for the years 1887 to 1948¹. A comparison of wind events to pine and spruce age distributions revealed strong similarities (Figures 10 and 11).

In the pine type, the trend of gradually decreasing regeneration over the last century or so corresponds to a similar decline in the frequency of severe wind gusts during that time (Figure 10). Additionally, both the chronology and strength of age classes established during that period follow a pattern similar to that characterizing the occurrence of intense wind events.

Correspondence between high intensity wind events and seedling establishment in spruce stands is not as clear as in pine stands, but general similarities are apparent (Figure 11). In particular, Sitka spruce establishment in these stands follows the pattern of severe winds for the periods 60-80 years before present, and 90-105 years before present.

Strong wind gusts alone do not explain abundant seedling establishment in pine and spruce stands 80-90 years ago, and other discrepancies between the wind and age distributions are apparent upon close examination (Figure 12). Such discrepancies are to be expected, since I examined only one variable among many that probably influence wind-related disturbance patterns. Other important variables may include biological factors such as canopy height, crown surface area, and decay levels, decreased stand resistance as a result of prior windfall, soil saturation, and wind direction. Additionally,

¹ Wind data are only available for the years 1887-1948 and 1978-present. Most individuals established on sample plots since 1978 were probably inventoried as saplings or seedlings, neither of which I aged.

the wind velocity threshold (>82.5 km/hr) I utilized for comparisons was arbitrarily chosen so that events of slightly lower velocity are not considered. In spite of all this, overall similarities between wind and age distribution patterns suggest a historical relationship between wind storms and seedling establishment at Lanphere Dunes.

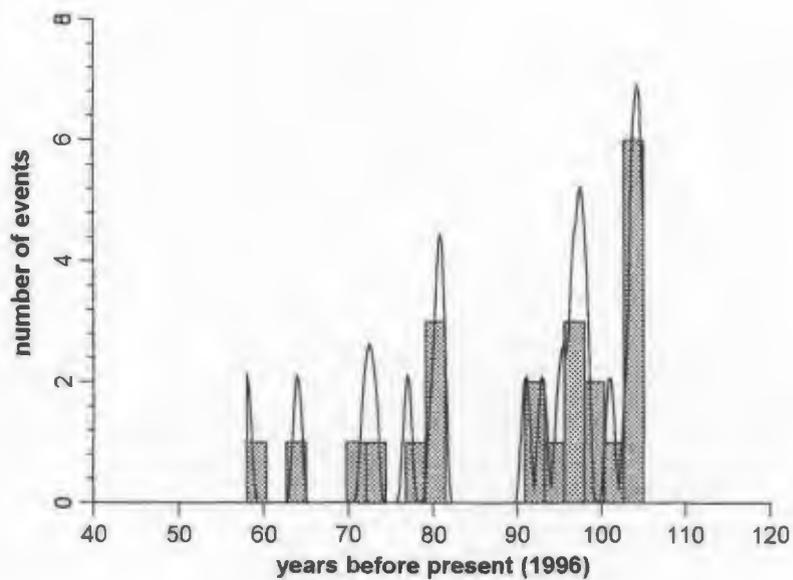
Patterns in my age data imply that windfall events occur frequently and are forest-wide in extent. Impacts vary with location, but are typically of low to moderate severity, blowing down some canopy trees individually or in small clusters (>0.04 ha) while leaving others intact. Might numerous, small-scale wind disturbances occurring over space and time explain the lack of older trees in the study area?

The relative youth of spruce stands in relation to both the life span of the species and the long history of forest development here suggest that canopy turnover rates are high as a result of wind disturbances. Sitka spruce canopy turnover times of less than 120 years have been attributed to small-scale wind events elsewhere in the Pacific Northwest (Agee 1993). A similar turnover rate is supported by spruce age data here, where the oldest cored individual was 131 years old and most trees under 100.

Sitka spruce may be particularly vulnerable to blowdown in the dunes environment. Here it grows in a sand substrate that provides little resistance against heavy winds. Additionally, Sitka spruce tends to grow taller than surrounding beach pine (Figure 2), has a relatively large crown surface area, and tends to develop a shallow root system where the water table is high (Harris 1990), all factors that should theoretically increase the susceptibility of the species to windfall here.

While the wind hypothesis is consistent with the body of available evidence, actual correlation between blowdown events and age structure at Lanphere Dunes is

a)



b)

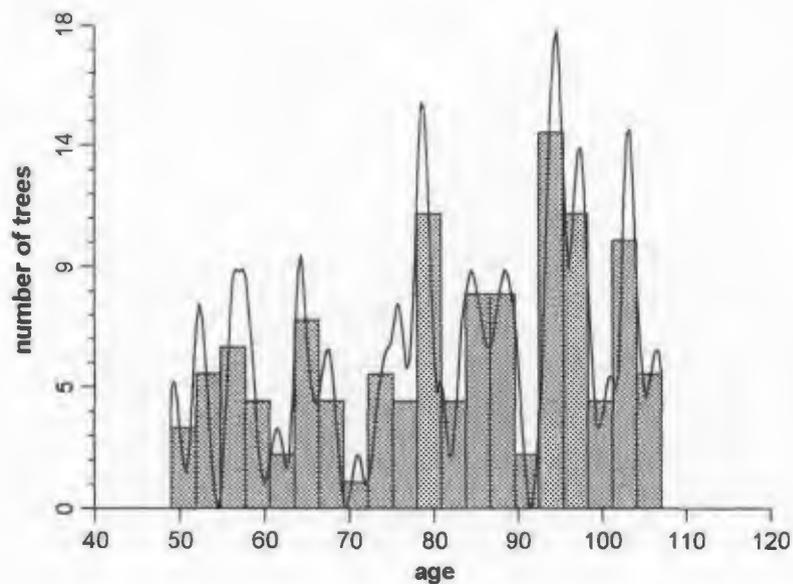
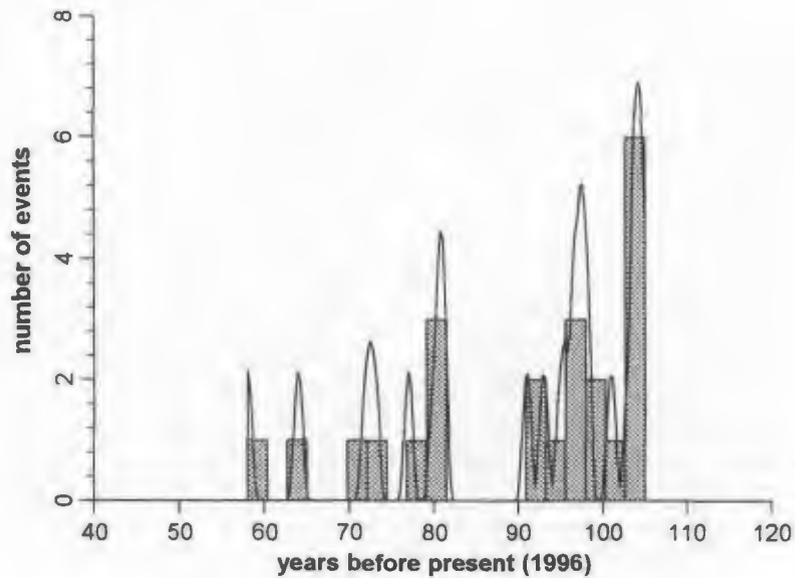


Figure 11. Histograms and density traces comparing: a) the frequency of high intensity wind events (>82.5 km/hr) recorded at Humboldt Bay during the years 1887-1948 and b) the age distribution of trees established in pine stands during the same time interval.

a)



b)

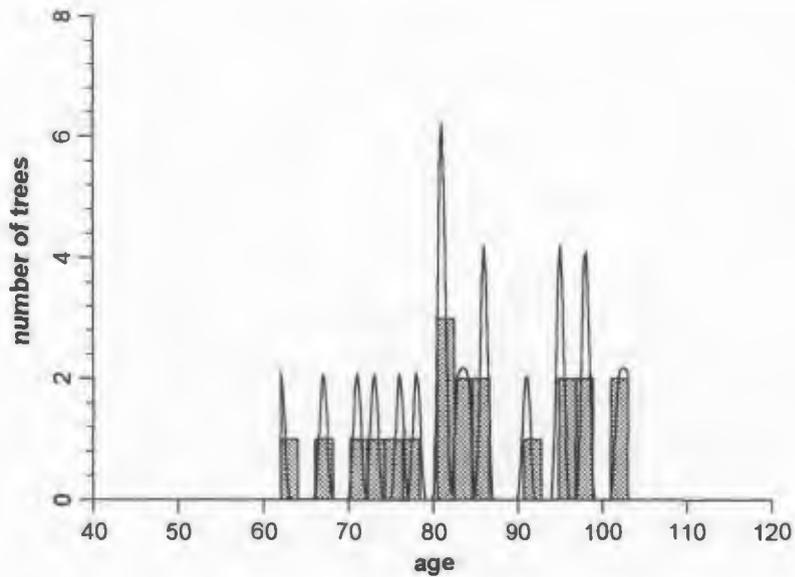


Figure 12. Histograms and density traces comparing: a) the frequency of high intensity wind events (>82.5 km/hr) recorded at Humboldt Bay during the years 1887-1948 and b) the age distribution of trees established in spruce stands during the same time interval. Spruce tree ages have been adjusted by five years (see Results) to make comparisons easier.

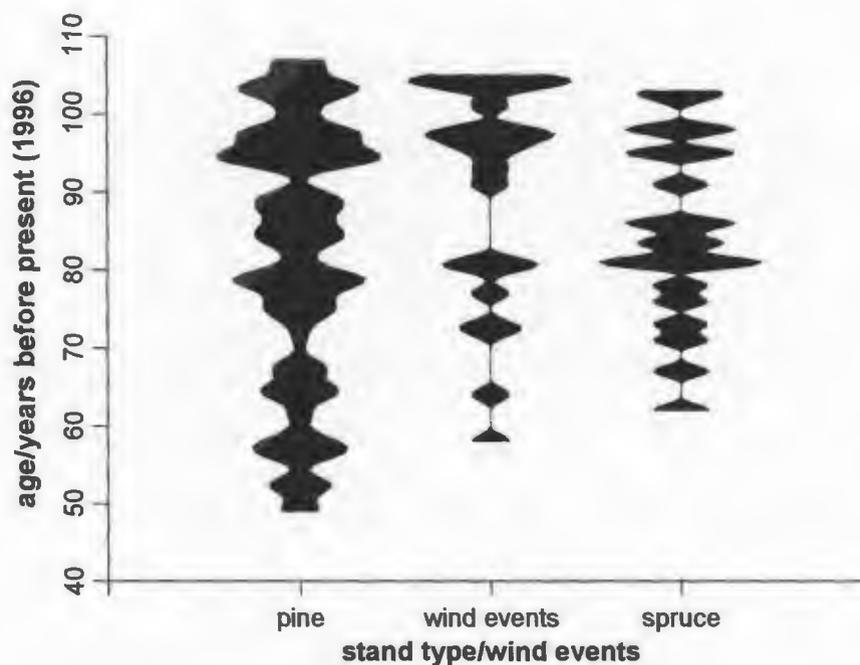


Figure 13. Violin plots comparing the age distribution of trees established in the pine and spruce types between 1887 and 1948 to the temporal distribution of high intensity (>82.5 km/hr) wind events during the same period. Violin plots consist of two identical density traces (for symmetry), one extending right and the other left of an invisible vertical axis (Hintze 1995). Here, violin plots highlight peaks and valleys in the age distribution of each stand type and in the frequency distribution of high intensity wind events, allowing for easy chronological comparison. Spruce ages have been adjusted by five years (see Results) to make comparisons easier.

largely anecdotal. My implication of wind as the most important disturbance mechanism shaping stand development here depends as much on the rejecting of alternative possibilities as on the correlation between high velocity wind events and cohorts of trees.

Size/age relationships

I informally observed that growth rates appear to be highest among trees inhabiting mesic sites and those growing in open sunlight. However, the growth ring patterns I observed for many if not most trees reflect intermittent periods of slow and rapid growth, indicating that the conditions affecting tree growth at a particular site vary considerably over time. That periods of suppression and release do not seem to consistently correspond among trees of a given plot, as would be expected from environmental changes such as rainfall, suggests that fine-scale competition among neighboring individuals is an important dynamic in these stands.

An informal survey of tree ring patterns suggests that the growth rates of beach pine and Sitka spruce trees have generally declined during the last 50 years or so. This observed trend supports the hypothesis that canopy crowding has become progressively more important in these stands since regeneration levels peaked 70-110 years ago. The influence of dynamic processes such as competition, disturbance, and tree growth upon long-term stand development patterns will not be understood until a more rigorous analysis of tree rings is conducted.

Regeneration

Stand types comprising the Lanphere Dunes forest have been characterized by low regeneration during recent decades (Table 8). In the spruce and mixed-species types, the ratio of seedlings and saplings to snags (Tables 8, 4) is too low to support single tree replacement as an important mode of development in those stands. While the ratio is much higher for the pine type, the uneven spatial distribution of seedling and saplings contrasts that of snags, which are evenly distributed across the type. In recent decades, patchy regeneration patterns in the pine type appear to have been more closely related to the distribution of bearberry (see Results) than to mortality patterns.

Bearberry forms a low-lying mat that typically occurs in small patches among scattered shrubs in pine stands. Unlike most areas where taller species such as evergreen huckleberry, salal, and wax myrtle form a dense understory layer, bearberry mats enable light to penetrate to the forest floor. I observed that the litter layer beneath bearberry mats is also typically thinner than in other areas.

The correlation between conifer regeneration and bearberry mats makes sense considering the germination and seedling survival requirements of resident conifer species. Lodgepole pine germinates best in full sunlight and on bare mineral soil or disturbed duff, but also does well on most organic seedbeds that are free of competing vegetation. Shading and competition inhibit both germination and survival (Lotan and Critchfield 1990). Douglas-fir germinates best on moist mineral soil, but tolerates a light litter layer. Seedling survival is low on heavy accumulations of organic litter, and in the fog belt is often limited by the shade of surrounding plants (Hermann and Lavender 1990). Sitka spruce germinates best in a mineral or mixed mineral/organic soil seedbed,

but organic seedbeds are suitable in the shade and in the open where moisture fluctuations are not too severe (Harris 1990). Therefore, conifer regeneration may currently be limited to bearberry mats precisely because those areas are free of the severe competition, shade, and thick litter layer that generally characterizes the understory in other portions of the forest.

Early historical descriptions of the forest (U.S. Coast Survey 1870, Loud 1918) include reference to a thick understory brush layer that included evergreen huckleberry (Loud 1918, Summerly 1967). Such descriptions imply that bearberry has been relatively limited in extent since at least 1870. That the vast majority of trees in existing stands are younger than 125 years old suggests that regeneration has occurred primarily in the absence of bearberry. The apparent difference between past and present regeneration patterns suggests that bearberry mats are less necessary for conifer reproduction than the complex of conditions they support.

Outside of sampled stands, I occasionally observed conifer regeneration occurring amidst a dense understory shrub layer. In those cases, I noted large gaps in the forest canopy and a perceptible dying-back or thinning of understory foliage where shrubs were exposed to direct sunlight. This observation suggests that large canopy gaps may be required for the successful recruitment of seedlings into a stand. It implies that understory shrubs, particularly evergreen huckleberry, typically inhibit conifer regeneration by preventing sunlight from reaching the forest floor. However, such shrubs may be relatively sun-intolerant and undergo die-back when exposed to high levels of direct sunlight. Successful seedling establishment may therefore require canopy gaps that are sufficiently large to facilitate die-back of understory shrubs. By this argument, the

canopy gaps created by disturbances in recent decades may simply be too small to support widespread beach pine regeneration, particularly where a dense understory shrub layer exists.

In the pine type, Sitka spruce and Douglas-fir individuals comprised less than 2% of all overstory trees (Table 3), but nearly 22% of the seedlings and saplings (Table 9). This finding suggests that Sitka spruce and Douglas-fir may become more important components of the overstory in limited areas of the pine type as time passes. That the two species are uncommon in the overstory suggests that their recruitment into pine stands has occurred only in recent decades.

Sitka spruce regeneration may be under-represented in data for the spruce type. Most regeneration appears to be occurring on the perimeter of those stands, areas I avoided to ensure that each plot fell entirely within the stratum. This observation suggests that spruce stands may be slowly expanding outward, especially into areas where beach pine is currently the most important species.

Forest and stand development

Tree-ring data, early historical descriptions (Irvine 1915, U.S. Coast Survey 1870, Loud 1918), and the existence of recently exposed woody debris among active dunes near the study area (Varga 1989, Leroy 1998, pers. comm., Pickart 1998, pers. comm.) collectively suggest that mature pine stands have persisted at Lanphere Dunes for at least 150 years, and probably much longer. If wind is the primary disturbance agent responsible for age structure and underlying stand development patterns at Humboldt Bay, then Egler's (1934) hypothesis that wind perpetuates Sitka spruce as the "aeolean

subclimax" species in Pacific Northwest coastal dune forests apparently does not apply here. That such a small area of forest is in the mixed-species type at Lanphere Dunes, and that Sitka spruce and Douglas-fir regeneration is occurring only in very limited portions of the pine type, does not support the argument that beach pine is eventually replaced by stands of shade tolerant species. In addition to small-scale wind disturbances, catastrophic events such as sand movement and fire, returning roughly every few hundred years, ensure a lasting place for pine stands among dunes of the Pacific Northwest.

CONCLUSIONS

The five major findings regarding the conifer forest on coastal dunes at Humboldt Bay are: 1) the forest is comprised of at least three distinct stand types: beach pine, Sitka spruce, and mixed-species, 2) species composition varies among types, and differs from coastal dune forests of Oregon, 3) all types are uneven-aged at both large (forest-wide) and small (<0.04 ha) spatial scales, sharing similar age classes that are normally distributed and that correspond among spatially disjunct patches of forest, 4) stand age structures and other evidence suggest that frequent, small-scale wind disturbances, probably exacerbated by pathogenic decay, have been the most important factor driving forest development during the last 150 years, and 5) although regeneration rates have been low in recent decades, beach pine stands have historically been self-replacing.

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PERSONAL COMMUNICATIONS

Haggard, Peter. 1999. Inspector, Humboldt County Agricultural Department. Eureka, CA.

Leroy, Tom. 1998. Geologist, Humboldt State University, Arcata, CA.

Pickart, Andrea. 1998. Ecologist, Lanphere Dunes Unit of the Humboldt Bay National Wildlife Refuge. Arcata, CA.

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