

# CAUSES AND ECOSYSTEM CONSEQUENCES OF MULTIPLE PATHWAYS OF PRIMARY SUCCESSION AT GLACIER BAY, ALASKA<sup>1</sup>

CHRISTOPHER L. FASTIE<sup>2</sup>

*Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775 USA*

**Abstract.** The classic account of primary succession inferred from a 220-yr glacial retreat chronosequence at Glacier Bay National Park, Alaska was compared to reconstructions of stand development based on tree-ring records from 850 trees at 10 sites of different age. The three oldest sites (deglaciated prior to 1840) differ from all younger sites in the early recruitment of Sitka spruce (*Picea sitchensis*), the presence of western hemlock (*Tsuga heterophylla*), and the inferred importance of early shrub thickets. The nitrogen-fixing shrub Sitka alder (*Alnus sinuata*) has been an important and long-lived species only at sites deglaciated since 1840. Black cottonwood (*Populus trichocarpa*) has been an overstory dominant only at sites deglaciated since 1900. These single-species additions or replacements distinguish three pathways of vegetation compositional change which are segregated spatially and temporally. The communities of different age at Glacier Bay do not constitute a single chronosequence and should not be used uncritically to infer long-term successional trends.

Among-site differences in texture and lithology of soil parent material cannot account for the multiple pathways. However, distance from each study site to the closest seed source of Sitka spruce at the time of deglaciation explains up to 58% of the among-site variance in early spruce recruitment. Multiple pathways of compositional change at Glacier Bay appear to be a function of landscape context, which, in conjunction with species life history traits (dispersal capability and generation time), affects seed rain to newly deglaciated surfaces and thereby alters the arrival sequence of species. Differences among the pathways probably include long-term differences in ecosystem function resulting from substantial accumulation of nitrogen at sites where nitrogen-fixing shrubs are important.

**Key words:** alder; chronosequence; facilitation; forest history; Glacier Bay; landscape context; multiple pathways; primary succession; seed rain; spruce; tree rings.

## INTRODUCTION

Information about long-term change in plant communities has been collected from resampling of permanent study plots, from vegetation history reconstructed from fossil plant parts or tree rings, and from study sites of different ages (chronosequences). Our understanding of long-term community dynamics is based primarily on inferences from chronosequences because (1) there is a lack of permanent plot records spanning more than a century, (2) paleoecological studies have relatively low temporal and spatial resolution, and (3) dendroecological reconstructions provide limited information about the early dynamics of nontree species and very young trees. A critical assumption in all chronosequence studies is that the communities at the oldest sites have developed through stages similar to the younger communities (Pickett 1989). If sites of different age have followed different pathways of change, the pattern of differences across a series of

progressively older sites may have little relationship to the pattern of actual change at any site. The juxtaposition in one putative chronosequence of pathways that differ in either developmental trajectory or rate can produce a misleading inference.

Suggested causes of multiple successional pathways at similar sites include the state of pre-disturbance vegetation (Christensen and Peet 1984, Abrams et al. 1985, Inouye and Tilman 1988), the type or intensity of disturbance (Cattalino et al. 1979, Collins and Adams 1983, Oliver et al. 1985, Halpern 1988, del Moral and Bliss 1993), seed rain (Abrams et al. 1985, McCune and Allen 1985, van Dorp et al. 1985, McClanahan 1986, Wood and del Moral 1987, Whittaker et al. 1989), micro-environment (Matthews 1979, Whittaker 1989, Vitousek et al. 1992), and resource supply rates (Inouye and Tilman 1988). A causal relationship between the sequence of species arrivals and multiple successional pathways has been demonstrated for marine fouling organisms (Sutherland 1974, Sutherland and Karlson 1977), plankton in microcosms (Robinson and Dickerson 1987, Robinson and Edgemon 1988), and early plant invasion on volcanic substrates (Wood and del Moral 1987), and has been inferred for other terrestrial

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<sup>2</sup> Present address: Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona 85721 USA.

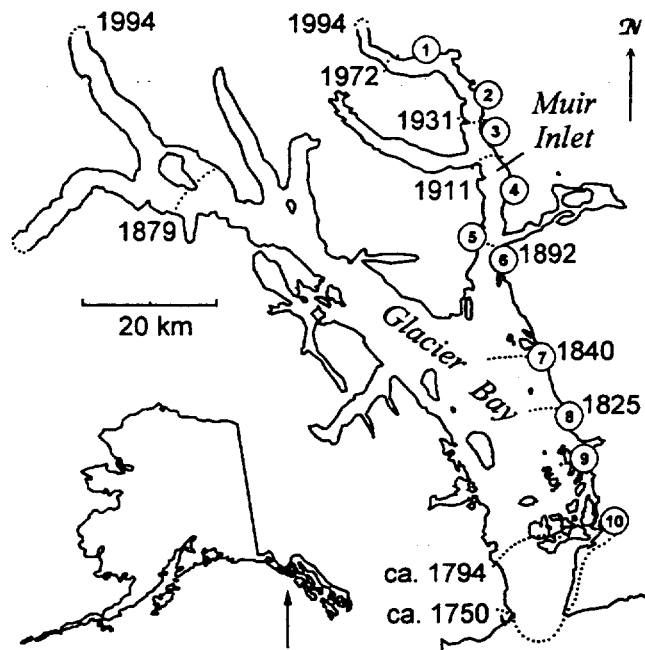


FIG. 1. Location of 10 study sites at Glacier Bay. Positions of glacier termini from historical maps and photographs (1794 and 1879-1994) or from dendrochronology (1750, 1825, 1840) are indicated. Location of Glacier Bay National Park and Preserve in southeastern Alaska is indicated (arrow).

plant communities (McClanahan 1986, Whittaker et al. 1989).

There is universal recognition of the importance of disturbance and patch dynamics for ecosystem function (Pickett and White 1985) and landscape pattern (Forman and Godron 1986). However, the nature and scale of a disturbance-caused landscape mosaic is a function not only of disturbance history but of vegetation response to each past disturbance. The additional landscape variability that can result from multiple responses to similar disturbances may be substantial and has been largely overlooked (but see McCune and Allen 1985). In this study I document the causes and consequences of multiple pathways of primary succession following glacial retreat at Glacier Bay National Park and Preserve in southeastern Alaska. Research at Glacier Bay benefits from a long record of documentation and study, beginning with a crude map made during Vancouver's exploration in 1794 (Vancouver 1798), which showed the general position of the tidewater terminus of the Glacier Bay glacier near its neoglacial terminal moraine. Although no records exist for the subsequent 85 yr, John Muir's visits between 1879 and 1892 began a period of research and documentation (e.g., Reid 1892, Cooper 1923a, Field 1947, Lawrence 1958, Mirskey 1966) which allows surfaces younger than 115 yr to be accurately dated. The only permanent vegetation plots established in Glacier Bay prior to 1980 have a total area of only 9 m<sup>2</sup> (Cooper 1923b), precluding a meaningful comparison of directly measured long-term

changes in vegetation with those inferred from the chronosequence.

The object of this study is to reconstruct the invasion history of woody plants (cf. Oliver and Stephens 1977) at 10 sites of different age at Glacier Bay. I test the hypothesis that the changes in density (in stems per hectare) of Sitka spruce (*Picea sitchensis* [Bong.] Carr.), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and black cottonwood (*Populus trichocarpa* Torr. & Gray) that are inferred from a putative chronosequence of sites are the same as changes reconstructed at each site. In search of a cause for the among-site variability in invasion history, I test for its association with three measures of initial conditions at each site: (1) texture and (2) lithology of soil parent material, and (3) proximity to seed sources of tree species. I assess the implications of multiple pathways for previous inference from the Glacier Bay chronosequence, and for spatial and temporal heterogeneity in ecosystem properties within an environmentally homogeneous landscape unit.

## METHODS

### Study area

Glacier Bay is a fiord in southeastern Alaska (59° N, 136° W). Since ≈1750, the world's most rapid and extensive glacial retreat in modern times has eliminated a lobe of ice ≈2500 km<sup>2</sup> in area that had filled the entire 100-km length of the basin now occupied by Glacier Bay (Fig. 1). Several hundred square kilometres of glacial till and outwash along the shores of Glacier Bay have been progressively exposed to biotic colonization, creating an extensive successional chronosequence near sea level. Recently exposed areas near the head of the fiord were under >1100 m of glacial ice in the middle 18th century (Haselton 1966). All vegetation on the surrounding valley walls was destroyed up to that elevation, which is well above the regional timberline of 750–800 m. The neoglacial high ice trimline grades downward for 100 km toward the mouth of the bay. There it joins the neoglacial terminal moraine near sea level, where it is adjacent to rain forests of old-growth western hemlock and Sitka spruce.

Recently exposed surfaces of unconsolidated glacial deposits on the east side of Glacier Bay are colonized during the first 15–25 yr by several woody species including *Dryas drummondii* (Pursh.), several willows (including *Salix sitchensis* Sanson, *S. barclayi* Anderss., *S. commutata* Bebb., and *S. alaxensis* [Anderss.] Cov.), black cottonwood, and Sitka alder (*Alnus sinuata* [Reg.] Rydb.). Surfaces 35–45 yr old typically have 100% cover of shrubs and young cottonwood trees, and Sitka alder is the dominant species. Sitka spruce is the dominant species on surfaces older than 100 yr. On surfaces older than 160 yr spruce has nearly

100% overstory cover. Western hemlock is common in the understory on surfaces older than 160 yr.

Glacial deposits at Glacier Bay are derived from rocks of at least four terranes (Brew 1988) and include a large variety of igneous, metamorphic, and sedimentary rock types including diorite, granite, volcanic rocks, schist, marble, dolomite, graywacke, argillite, and limestone (Brew et al. 1978). These rock types have been homogenized in deposits of till and outwash, although ice flowing from the western side of the bay deposited material that is lithologically distinct from till along the eastern shore of Glacier Bay (Ovenshine 1968), where all sites for the current study were located. Four studies of soil development in glacial deposits at Glacier Bay have documented dramatic increases in nitrogen concentration and organic matter, and decreases in pH and bulk density along the chronosequence, but have found no age-related trend in the particle-size distribution of mineral soil (Crocker and Major 1955, Ugolini 1966, Bormann and Sidle 1990, Chapin et al. 1994).

Glacier Bay has a maritime climate with cool summers and mild, wet winters. Maximum and minimum temperatures at sea level rarely exceed 24° and -23°C, respectively (Loewe 1966). The mean annual temperature at Gustavus, at the neoglacial terminal moraine, is 4.9°C; annual precipitation is 1800 mm; monthly precipitation varies between 80 and 300 mm, with the wettest months between September and January (National Oceanic and Atmospheric Administration 1990).

#### Study sites

Ten areas of at least 10 ha were chosen along the eastern shore of Glacier Bay and in Muir Inlet (Appendix A, Fig. 1). These 10 areas are distributed more or less evenly between the 18th century terminal moraine and the tidewater terminus of Muir Glacier and met the following criteria: Each was within 2 km of tidewater and <110 m above sea level; the soil parent material of each was glacial till with minor areas of fluvial deposits; and each was a level surface (slope angle < 10°) without major areas of exposed bedrock or continuously saturated soil. Most of these study areas are sites of previous research on succession (Appendix A), making results of this study directly comparable to previous results. A 10-ha study site was centered in each study area, and 10 10 × 15 m sampling plots were located throughout each site using random coordinates. Five 15 × 20 m plots were established in a 6-ha site at the youngest area where level terrain is uncommon. Plots were permanently marked with metal corner stakes, and each tree in each plot was marked with a numbered aluminum tag. Plot locations are archived with Glacier Bay National Park and Preserve (Gustavus, Alaska). To improve estimates of tree density and basal area, additional tree data (tree diameter and stand density) were collected in 10 temporary 10 × 15 m plots randomly located in 10-ha areas adjacent

to the five oldest study sites (sites 6–10). To improve the accuracy of the reconstructions of spruce stand history, all spruce trees were cored in these 10 additional plots at sites 6 and 10, and all spruce were also cored in three additional randomly located 10 × 15 m plots at site 5, two additional randomly located 10 × 15 m plots at site 4, and 10 additional randomly located 20 × 30 m plots at site 3. Plots were sampled between 1987 and 1990.

#### Live trees and stand reconstructions

Increment cores were collected from all live Sitka spruce, western hemlock, and black cottonwood trees in each plot. Trees (all stems >4 cm diameter at 1.4 m height [diameter breast high, dbh]) were cored as close to the ground as possible, and 95% were cored <90 cm above the upper surface of mineral soil. No cores were collected from mountain hemlock (*Tsuga mertensiana* [Bong.] Carr), which accounted for <1% of the tree basal area at the site where they were most abundant. No other tree species were encountered at the study sites. Each tree was cored up to six times until the pith or wood within 5 mm of the pith was sampled. Species, dbh, and height of the core above the mineral soil surface (the level where most tree seeds probably germinated at these primary successional sites) were recorded. Each tree was assigned to either the overstory (>75% of crown area exposed to the sky), subcanopy (≤75% of crown area exposed to the sky), or understory (≤75% of crown area exposed to the sky and tree height <50% of canopy height). Seedlings in three height classes (<20 cm, 20–50 cm, and 51–140 cm) and saplings (<4 cm dbh and >1.4 m tall) of each tree species were counted.

Increment cores were sanded and annual rings were counted and measured with a precision of 0.01 mm on a sliding bench micrometer (Swetnam et al. 1985). Basal area increment for each tree was calculated for each year of growth as  $b_t = \pi r_t^2 - \pi r_{t-1}^2$ , where  $b_t$  is basal area increment in year  $t$ ,  $r_t$  is the sum of all ring widths up to and including year  $t$ , and  $r_{t-1}$  is the sum of all ring widths through the previous year. Tree ages reported are ring counts plus an estimate of the number of years required to reach core height. For this estimate, 13 seedlings between 20 and 120 cm tall of each tree species were harvested from young sites and sectioned at the root crown. Seedling ages were determined from ring counts on sanded basal sections. Annual height growth curves were derived for spruce and cottonwood from ages at multiple heights along the stem of each seedling (Table 1). For spruce, each annual node was aged by counting terminal bud scars down from the current leader, and for cottonwood annual rings were counted in sanded sections at two heights above the root crown. These height growth curves were also used to estimate the age of seedlings growing in sampling plots.

To describe height-related changes in spruce growth

TABLE 1. Regression equations used to estimate the time required for trees to grow to core height, and to estimate the age and date of germination of dead spruce trees. The slope of all regressions is significantly different from 0 ( $P < 0.001$ ).  $\ln$  = natural logarithm.  $s_b$  = standard error of the regression coefficient.

Relationship described	Equation	$n$	$s_b$	$r^2$
Seedling height (cm) vs. age (yr) for:				
Sitka spruce	Age = $1.19(\text{height})^{0.57}$	129*	0.04	0.88
Western hemlock	Age = $8.89 \ln(\text{height}) - 17.37$	13	1.99	0.64
Black cottonwood	Age = $5.72 \ln(\text{height}) - 9.28$	34*	1.02	0.50
dbh (cm) vs. age (yr) of dead spruce trees at:				
Site 9	Age = $29.9 \ln(\text{dbh}) + 12.2$	57	2.27	0.50
Site 10	Age = $41.2 \ln(\text{dbh}) + 16.0$	61	4.59	0.58
Appearance class (1 to 12) and time since death (yr) of dead spruce trees at:				
Site 9	Yr dead = $23.7 \ln(\text{class}) - 12.3$	35	3.01	0.70
Site 10	Yr dead = $41.9 \ln(\text{class}) - 19.4$	42	4.25	0.74

\* Regression analysis was performed on measures at multiple heights on each of 13 seedlings of each species.

rate, spruce trunk radial increment was measured at different heights above ground level (Oliver and Stephens 1977) at sites 6 and 10. At site 10, increment cores of four overstory spruce that were felled by the National Park Service in 1988 were taken at 4-m intervals along the trunks. At site 6, four overstory spruce between 17 and 23 m tall were climbed to collect increment cores at every 4 m of height up to 12 m. Cores were also taken from these eight trees at a height of 2 m and at a height of 0.5 or 0.6 m. Annual rings were measured as above.

#### Dead trees and stand reconstructions

Where dead spruce trees were present in sampling plots (sites 8–10), each dead spruce, including fallen trunks, was assigned to 1 of 12 appearance classes (Table 2) and dbh was recorded. Each dead tree was classified as overstory, subcanopy, or understory based on its height or trunk length. Cores were collected from 66 and 48% of the dead spruce in the permanent plots at sites 9 and 10, respectively. Only 12 dead spruce were present in sampling plots at site 8, and no cores were collected from them. Cores were prepared and

annual rings measured as above. Ring-width series for 35 dead spruce at site 9, and 42 dead spruce at site 10 were crossdated against site-specific master dating series from at least 20 live overstory spruce at each site using program Cofecha (Holmes 1983) and visual confirmation (Stokes and Smiley 1968). Site-specific logarithmic regressions of years since death vs. appearance class for these trees were used to estimate the time since death for trees that were not cored or not successfully crossdated (Tables 1 and 2). Crossdating indicated that dead standing spruce at sites 9 and 10 had been dead for as long as 52 and 101 yr, respectively. Of the 137 dead spruce that could not be cross-dated, 14 belonged to appearance classes beyond the range of the regressions for cross-dated trees (Table 2), but the logarithmic regression equations made conservative estimates of time since death for trees in high (older) appearance classes. The ages of dead trees that were not cored were estimated using logarithmic regressions of age vs. dbh for the dead trees that were successfully aged (Table 1). Equations from site 9 were used to estimate age and time since death for dead trees at site 8. Appearance-class equations for spruce at site 10

TABLE 2. Appearance classes of dead Sitka spruce at two study sites. Data are the number of trees in each appearance class for which the date of death was determined by crossdating or estimated using regression equations in Table 1.

Class	Condition of dead tree	Site 9		Site 10	
		Cross-dated	Estimated	Cross-dated	Estimated
1	Dead needles present	0	0	1	0
2	No needles, but many fine twigs present	3	1	7	1
3	No needles, few fine twigs present	11	3	11	1
4	No twigs but many small branches present	6	5	9	5
5	No small branches but all bark in place	4	5	5	1
6	No small branches, fungal brackets present	1	2	2	2
7	Entire length of trunk covered with moss	1	3	2	5
8	<30% of bark detached	6	13	3	15
9	>60% of bark detached	3	19	1	20
10	Trunk broken above 1.5 m	0	1	1	22
11	Entire trunk on the ground	0	0	0	9
12	Stump only, trunk obscured by moss	0	0	0	4
	Totals	35	52	42	85

were used to estimate time since death for five dead western hemlocks in plots at site 10, the only dead hemlocks encountered in plots. The estimated germination dates of all cored live trees and the estimated germination and death dates of all dead trees in permanent plots were used to reconstruct the stand density of each tree species (live plants per hectare) during each 10 yr of forest development at each site.

At both sites 9 and 10, the estimated germination dates for several dead spruce that were not cross-dated predate the earliest germination dates derived more reliably from live or cross-dated dead trees at each site (Fig. 2). These unlikely early dates are assumed to be the result of errors inherent in estimating tree age from dbh and estimating time of death from appearance class. These dates therefore provide an index of the amount of error involved in this technique and suggest that the estimated germination dates for dead spruce that were not cross-dated could be in error by from 1 to 2 decades. This error reduces the resolution of the reconstructed history of spruce density at sites 8 through 10, but these reconstructed densities are very accurate for three important time periods:

1) Stand initiation: The dates of first recruitment derived from live and cross-dated dead spruce are subject primarily to errors in estimating tree age below core height, and based on the height-growth curves for harvested seedlings (Table 1), are expected to be accurate within  $\pm 5$  yr. Thus, the dates of stand initiation (when spruce density was last equal to zero) are known with little error.

2) Period of maximum density: The stand density of spruce during the period of maximum density is known with little error because most of the dead spruce were alive for more than half of the total stand age, and therefore their life-spans must have overlapped with one another. This maximum density (trees per hectare) is probably reconstructed within 5% at sites 8–10. The reconstructed dates of this period of maximum density are the primary source of error in the reconstructions at these sites. Based on the discrepancy between the germination dates reconstructed from cross-dated vs. noncross-dated dead trees (Fig. 2), the dates of maximum density are probably reconstructed within  $\pm 10$  yr at site 8 and  $\pm 20$  yr at sites 9 and 10. This probably results in errors of  $<10\%$  in reconstructions of spruce density during the 10–30 yr preceding and following the reconstructed period of maximum density at sites 8–10, and could not alter the conclusions of this study.

3) Recent decades: The stand density of spruce during the last several decades is known with very little error because the date of death of all recently killed spruce was accurately determined by cross-dating.

There were few dead trees of species other than spruce, and past densities of other species are probably reconstructed within 5% of actual values for the sampling plots. Reconstructions of cottonwood stand density at sites 4–6 do not include dead trees (only one

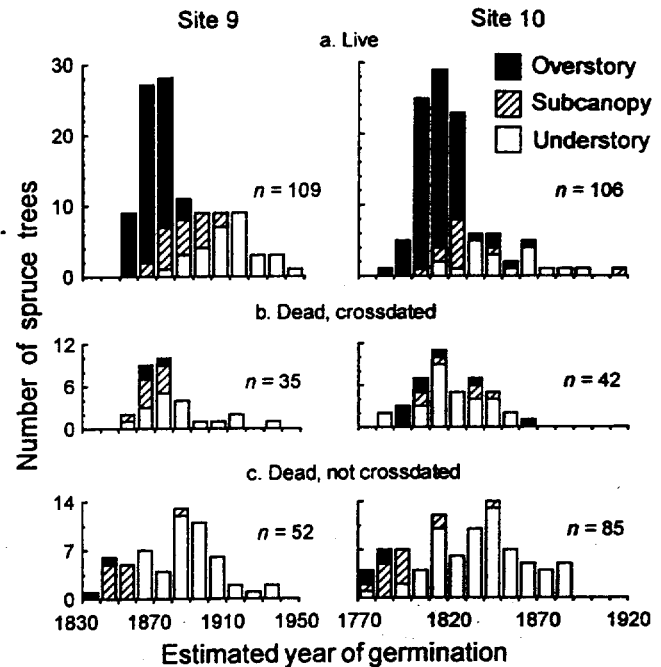


FIG. 2. Distribution of germination dates of Sitka spruce in sampling plots at site 9 (left) and site 10 (right). (a) Live trees. (b) Dead trees that were cored and crossdated. (c) Dead trees that could not be crossdated. Data are from 10  $10 \times 15$  m plots per site (20 plots for live spruce at site 10). The number of trees is indicated ( $n$ ).

dead cottonwood was encountered at each site) because they could not be confidently dated. Few cottonwoods were encountered at older sites (sites 7–10), and no reconstructions of cottonwood stand history were made at these sites.

### Shrubs

Counts were made of individual plants of Sitka alder and each willow species in each permanent plot. Individual genets were distinguished by the orientation of upward-curving stems growing radially from a central root crown. The basal diameter of each stem was measured 10 cm above the ground and was used in computations of shrub basal area (in square metres per hectare).

### Experimental canopy gaps and ring-width releases

To measure the response of young spruce trees to release from competition for light, in May and June of 1987 the branches of alder overtopping 15 widely scattered spruce trees (height:  $193 \pm 18$  cm, mean  $\pm 1$  SE) growing under a continuous canopy of alder near site 3 were tied back with nylon cord to produce 15 artificial canopy gaps 3–4 m in diameter. New alder branches encroaching on gaps were tied back in May or June of 1988 and 1989. In July 1991 increment cores were taken at the base of each spruce and from 15 control spruce of similar size (height in 1987:  $212 \pm 14$  cm, mean  $\pm 1$  SE) that were between 15 and 50 m

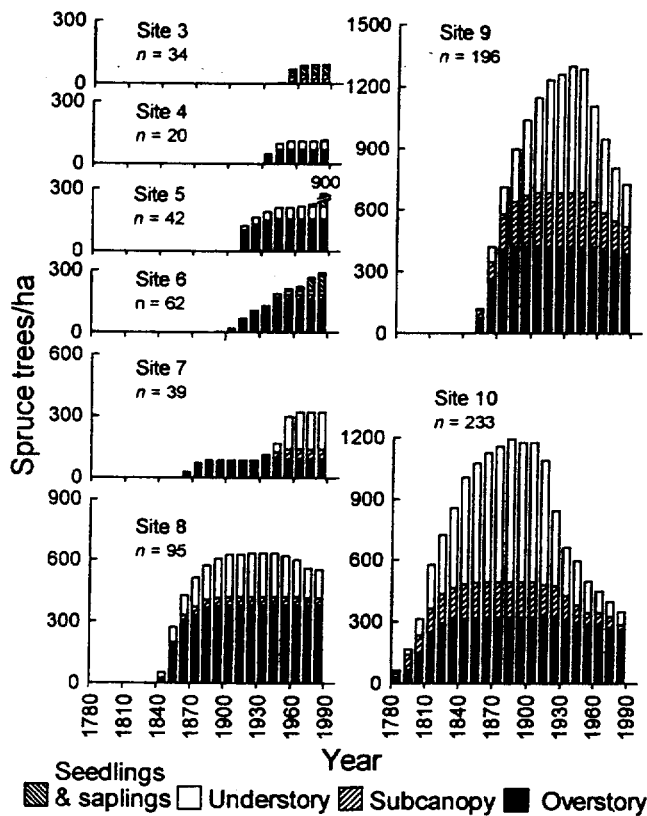


FIG. 3. Stand density of Sitka spruce reconstructed by decade at eight study sites. Strata are the current strata of trees in sampling plots. Data are from all spruce in 10–20 (10 × 15 m) plots at each site. The number of trees used in reconstructions is indicated ( $n$ ). The germination dates of all seedlings and saplings are included in reconstructions only at sites 3–6 where they affect the first 70 yr of recruitment history.

from gap edges. Annual rings were measured as above. To compare the ring-width response produced by this experiment to natural ring-width patterns, ring-width records from all overstory spruce in all sampling plots were searched for releases in which the mean ring width in a 10-yr interval is at least twice the mean ring width for the previous 10 yr. To limit the search to the period when spruce would have been emerging above a shrub canopy, only releases beginning between age 15 and 60 yr (tree age at core height) were included. The 1st yr of the release was defined as the 1st yr in which ring width exceeded the maximum ring width during the 10 previous years.

#### *Proximity to refugial sources of spruce seed*

All refugial old-growth forests within 10 km of the terminal and lateral moraines at Glacier Bay were mapped using color infrared stereo aerial photographs that were taken in August 1979 for the National Park Service and enlarged to match the scale of 1:63 360 U.S. Geological Survey topographic maps. To evaluate their potential as sources of spruce seeds for nearby successional terrain, nine of the mature forest areas closest to the study sites were visited and increment

cores were taken from several of the largest spruce for age determination. This field work was concentrated near sites 6, 7, and 8 in order to locate the northernmost stands of mature Sitka spruce along the eastern shore of the bay. A new map was produced of forest areas with spruce old enough to have supplied seed during the 18th and 19th centuries as nearby study sites were deglaciated. There is no evidence near the study sites that other stands of mature spruce existed 220 yr ago and were subsequently destroyed by wildfire (which is extremely rare in southeastern Alaska) or by other disturbance.

#### *Proximity to successional sources of spruce seed*

At five locations along Muir Inlet near sites 3, 4, and 5, the relationship between first cone production and diameter of Sitka spruce was determined. Each area had been deglaciated for 40–90 yr and current vegetation included scattered Sitka spruce with seed cones as well as spruce that had not begun to produce cones. The diameter and presence or absence of cones (on branches or on the ground) was recorded for every spruce at each area for a total of 433 trees. The resulting relationship between tree diameter and the proportion of trees bearing cones was used to estimate the probability that spruce of a particular diameter bore cones. This was combined with the past diameter distributions (from the tree-ring records of radial growth) at each site to reconstruct the decade-by-decade history of accumulating density (trees per hectare) of cone-bearing spruce trees at each study site. The estimated calendar year during which each site supported a density of 10 cone-bearing spruce/ha was used to map the advance of a front of reproductive spruce. The distance from each study site at the time of deglaciation to the closest successional forest with 10 cone-bearing spruce/ha, or (if closer) the distance to refugial old-growth forests with spruce (see *Proximity to refugial sources of spruce seed*) was used as a site-specific index of potential seed rain of spruce.

#### *Soils*

Samples from the upper 20 cm of mineral soil were collected adjacent to four or five sampling plots at 9 of the 10 study sites (not at site 2). Samples were passed through 1.5-cm mesh in the field and, after oven drying (110°C), pebbles were separated by passing samples through a 2-mm mesh. A micropipette method of particle size analysis (Miller and Miller 1987) was performed on the <2 mm fraction with at least two analytical replicates per sample. All pebbles >0.5 cm from each sample were rinsed and assigned to one of four lithological categories modified from Ugolini (1966). These categories are: (1) igneous (predominately granodiorite and diorite), (2) metasedimentary (predominately fine-grained, black to light gray hard argillite), (3) dike rocks (igneous intrusions into metasedimen-

TABLE 3. Current stand density (plants/ha) of Sitka spruce at eight study sites. No spruce were encountered in plots at sites 1 or 2. Dead canopy spruce includes all standing and fallen, and all subcanopy and overstory trees. Data are means  $\pm$  1 SE. Sample size ( $n$ ) is the number of 10  $\times$  15 m sample plots per site ( $n = 10$  for seedlings, 10 of the 20 plots at site 3 are 20  $\times$  30 m).

Site	$n$	Live spruce					Dead spruce			
		Seedling	Sapling	Understory	Subcanopy	Overstory	Total trees	Understory	Canopy	Total
3	20	11 $\pm$ 4	27 $\pm$ 8	24 $\pm$ 10	0	7 $\pm$ 7	31 $\pm$ 11	0	0	0
4	12	7 $\pm$ 6	0	39 $\pm$ 17	0	72 $\pm$ 17	111 $\pm$ 23	0	0	0
5	13	900 $\pm$ 396	0	51 $\pm$ 19	0	164 $\pm$ 25	215 $\pm$ 35	0	0	0
6	20	93 $\pm$ 49	3 $\pm$ 3	20 $\pm$ 11	33 $\pm$ 19	150 $\pm$ 31	203 $\pm$ 51	0	0	0
7	20	2300 $\pm$ 430	157 $\pm$ 52	87 $\pm$ 27	33 $\pm$ 13	120 $\pm$ 21	240 $\pm$ 31	0	0	0
8	20	2333 $\pm$ 548	33 $\pm$ 16	143 $\pm$ 34	53 $\pm$ 14	330 $\pm$ 28	527 $\pm$ 60	47 $\pm$ 13	17 $\pm$ 6	63 $\pm$ 15
9	20	1907 $\pm$ 417	20 $\pm$ 7	233 $\pm$ 32	103 $\pm$ 21	370 $\pm$ 26	707 $\pm$ 44	423 $\pm$ 58	113 $\pm$ 24	537 $\pm$ 55
10	20	133 $\pm$ 68	0	63 $\pm$ 16	40 $\pm$ 14	250 $\pm$ 21	353 $\pm$ 31	563 $\pm$ 81	170 $\pm$ 28	773 $\pm$ 100

tary beds varying in composition from andesite to basalt), and (4) carbonate (limestone, marble, or dolomite). Visual identification was aided by an acid reaction test on freshly exposed surfaces to verify carbonates. At least 139 pebbles (274  $\pm$  11 pebbles, mean  $\pm$  1 SE) from each of the 37 samples were identified.

#### Statistical analyses

Stepwise multiple regression was used to select from eight measures of initial site conditions that were potential predictors of among-site differences in the early rate of spruce recruitment (spruce stand density [trees per hectare] at 40, 50, or 60 yr after the first spruce arrived). The eight independent variables are: percent sand, silt, or clay in mineral soil; percent carbonate, metasedimentary, dike rock, or igneous pebble; and the shortest distance to reproductive spruce forest. Three separate regressions predicting early spruce density after 40, 50, and 60 yr of recruitment at each site were developed. Because the soil measures are proportions and include inversely correlated pairs, multiple regressions were repeated with no correlated pairs of independent variables in order to inspect for evidence of spurious model behavior due to multicollinearity. The two independent variables selected by the stepping procedure for each model are not intercorrelated, and diagnostics indicate no detrimental effects of multicollinearity (variance inflation factors are  $<1.39$ ).

Among-site differences in soil texture and pebble lithology were identified with a modified Ryan's  $Q$  test following significant one-way analyses of variance. Spruce trunk radial growth in trees growing in experimental canopy gaps was compared to control trees for the four treatment years with repeated measures analysis of variance. The timing and magnitude of ring-width releases in spruce were compared between two groups of study sites (sites with rapidly recruiting spruce [sites 8–10] and all other sites) with single-degree-of-freedom contrasts.

Prior to all analyses, variables were transformed to minimize heteroscedasticity if their means per study site were significantly correlated with their variances. In addition, response variables in multiple regressions

were transformed as necessary to eliminate curvilinear relationships between response and predictor variables. Means are presented  $\pm$  1 standard error of the mean (SE). All statistical analyses were performed with SAS version 6.07 for VMS (SAS Institute 1989).

## RESULTS

### Stand reconstructions

*Sitka spruce.*—Initial recruitment of Sitka spruce at sites 9 and 10 continued for  $\approx$ 100 yr (Fig. 3). After five decades of recruitment, at least 90% of current subcanopy and overstory trees had established. Subsequent germination was restricted primarily to trees that remained in the understory, most of which had died before the sites were sampled (Fig. 3, Table 3). At site 8, early establishment followed a pattern similar to sites 9 and 10, although the recruitment and subsequent thinning of understory spruce was much reduced (Fig. 3). In contrast, at sites 3–7 recruitment of spruce was substantially slower than at the three oldest sites. For example, after 50 yr of spruce recruitment at these five young sites, spruce stand density (including all seedlings and saplings at the youngest sites) is  $<36\%$  of the density attained after 50 yr at any of the three oldest sites. Because reconstructions at old sites are expected to underestimate early density due to the decay or burial of long-dead saplings and small trees, this estimated difference between young and old sites is conservative.

*Western hemlock.*—Saplings and understory trees of western hemlock are common at the three oldest sites but are rare or absent at all younger sites (Table 4). Recruitment of western hemlock at the three oldest sites began within a decade of the first recruitment of spruce (Fig. 4), but recruitment has been negligible at all younger sites including sites at which spruce has been establishing for 50–100 yr. Some hemlock seedlings are present at site 7 (Table 4), but 86% of these seedlings are  $<50$  cm tall, suggesting that substantial recruitment of hemlock at this 150-yr-old site began only a few decades ago. The recruitment of western hemlock therefore distinguishes tree invasion at sites 8–10 from all younger sites.

TABLE 4. Current stand density (plants/ha) of western hemlock and mountain hemlock at seven study sites. No hemlock were encountered in plots at sites 1, 2, or 6. Mountain hemlocks include seedlings, saplings, and trees (no dead mountain hemlocks were encountered). Data are means  $\pm$  1 SE. Sample sizes as in Table 3.

Site	n	Western hemlock					Total live trees	Dead trees	Mountain hemlock
		Seedling	Sapling	Understory	Subcanopy	Overstory			
3	20	0	3 $\pm$ 3	0	0	0	0	0	3 $\pm$ 3
4	12	0	13 $\pm$ 8	0	0	0	0	0	0
5	10	0	0	0	0	0	0	0	5 $\pm$ 5
7	20	147 $\pm$ 113	13 $\pm$ 13	0	0	0	0	0	13 $\pm$ 8
8	20	3013 $\pm$ 921	113 $\pm$ 42	53 $\pm$ 17	0	10 $\pm$ 5	63 $\pm$ 17	0	263 $\pm$ 77
9	20	947 $\pm$ 234	10 $\pm$ 5	83 $\pm$ 27	33 $\pm$ 10	3 $\pm$ 3	120 $\pm$ 30	0	90 $\pm$ 21
10	20	1347 $\pm$ 256	27 $\pm$ 11	237 $\pm$ 39	63 $\pm$ 18	27 $\pm$ 10	327 $\pm$ 49	27 $\pm$ 12	40 $\pm$ 14

*Black cottonwood.*— Black cottonwood are abundant only at the four youngest sites, where they greatly outnumber spruce (Fig. 5). At sites 5–10, there are very few cottonwood (Table 5). Although some cottonwood boles could have decomposed and evaded detection at the oldest sites, the rarity of both live and dead cottonwood trees at sites 5–10 suggests that cottonwood establishment there was substantially lower than at younger sites. For example, sites 5 and 6 are only 15 and 27 yr older, respectively, than site 4, insufficient time for nearly 200 trees/ha (current density at site 4) to have deteriorated beyond detection at sites 5 and 6. Recruitment of cottonwood trees therefore distinguish-

es tree invasion at sites 1–4 from sites 5 and 6 and probably from all older sites. Since the beginning of the twentieth century when site 4 was deglaciated, there is an apparent trend of increasing early recruitment of cottonwood as the species has invaded the four youngest sites (sites 1–4, Table 5, Fig. 5).

#### Trunk radial growth and basal area

*Experimental canopy gaps and ring-width releases.*—During 4 yr in experimental gaps in the alder canopy, the mean trunk radial growth of spruce trees was significantly ( $P < 0.05$ ) greater than that of control trees (Fig. 6). This suggests that spruce growing under this alder canopy are affected by competition for light and that the time of release from this competition is recorded by a sustained increase in annual ring width. This growth release is similar to that recorded in spruce trees naturally emergent above an alder canopy at sites 3–7, where releases were identified in 72–100% of the overstory spruce (Table 6). During 4 yr of growth in experimental canopy gaps, mean ring width in treatment trees was greater by a factor of  $1.9 \pm 0.1$  ( $n = 15$  trees) than during the five previous years. In spruce recording a natural release at sites 3–7, ring width increased by a factor of  $2.2 \pm 0.1$  ( $n = 5$  sites) for the same intervals. By comparison, at sites 8–10 only 17–23% of the overstory spruce record a release (Table 6). The age of release and the relative magnitude of release at older sites are similar to younger sites, although the absolute ring widths before and after the release, and the tree diameter at the time of release, are significantly smaller than at younger sites (Table 6). The rarity of releases and the slower growth of released trees at sites 8–10 suggest that the early environment at those sites was substantially different from the alder-dominated shrub thicket at younger sites.

*Stem analysis.*— Two to three decades of slow initial radial growth are recorded in ring widths near the base of four spruce trees at site 6, but not in spruce at site 10 (Fig. 7). The early growth suppression at site 6 is not evident  $>4$  m above the root crown or in rings produced after the trees were  $\approx 35$  yr old (Fig. 7). These spruce at site 6 grew slowly until they were  $>4$  m tall.

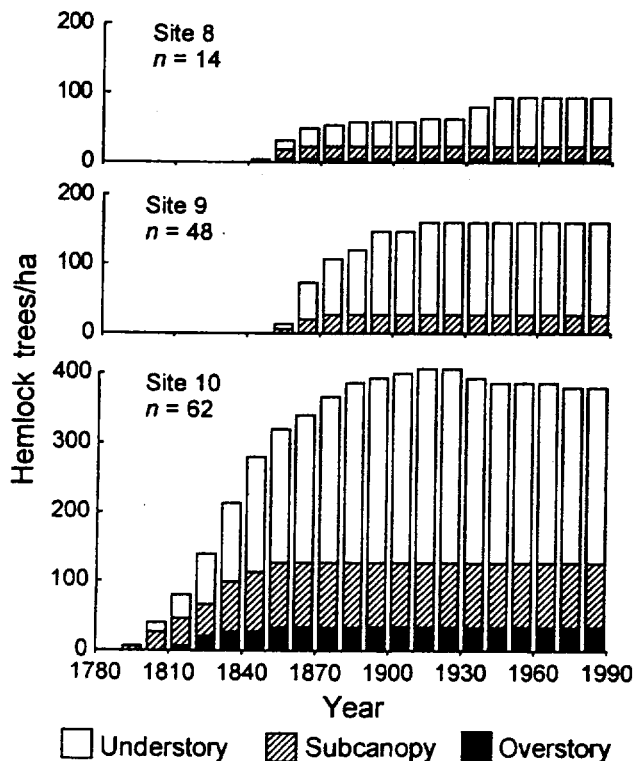


FIG. 4. Stand density of western hemlock reconstructed by decade at three study sites. Hemlock trees were present in sampling plots only at these sites. Strata are the current strata of trees in sampling plots. Data are from 10 10  $\times$  15 m plots at each site. The number of trees used in reconstructions is indicated ( $n$ ).



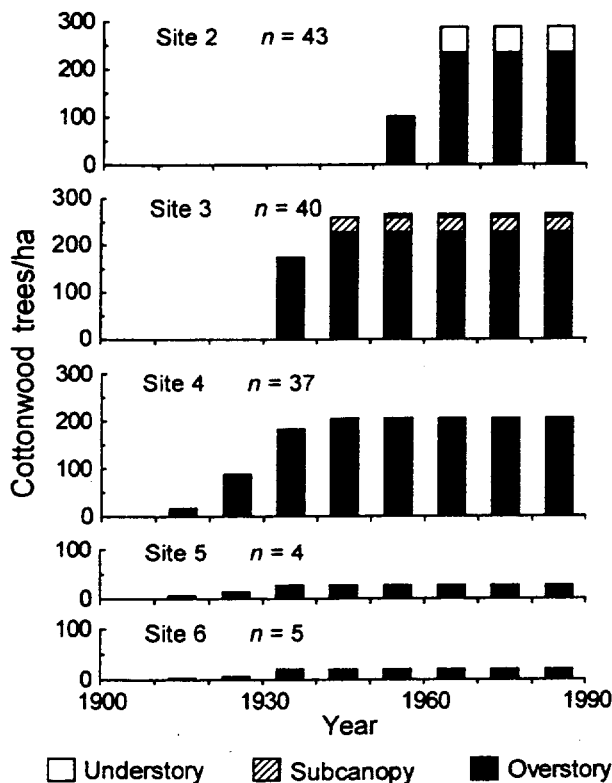


FIG. 5. Stand density of black cottonwood reconstructed by decade at five study sites. Subcanopy trees have recently begun to emerge above an alder canopy. Strata are the current strata of trees in sampling plots. Data are from living trees in 10  $10 \times 15$  m plots per site (12 plots at site 4). At sites 4–6, one dead cottonwood per site was also encountered but is not included in reconstructions. The number of trees used in reconstructions is indicated ( $n$ ). At site 2, the only site where cottonwood saplings were present, the density in the final decade would be doubled if saplings were included in the reconstruction.

This suggests that (1) the slow radial growth is associated with a period during which the young trees grew beneath the alder canopy which is currently 5–7 m tall at this site, and (2) the growth release is associated with their emergence above that canopy. This pattern is not present in four spruce trees at site 10 in which there is little height-related difference in early ring widths (Fig. 7). This result is consistent with the hy-

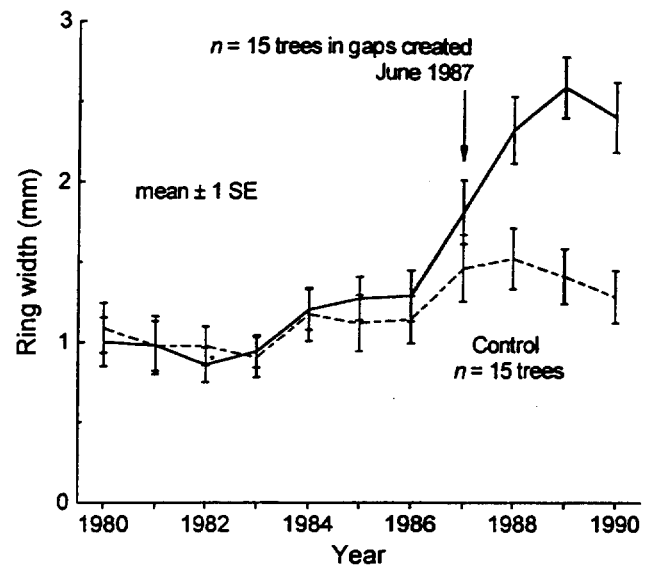


FIG. 6. Ring widths for four treatment years and seven pre-treatment years of 15 Sitka spruce in experimental canopy gaps and of 15 control trees.

pothesis that most spruce trees at young sites are released from competition for light as they emerge above an alder thicket, but that the early environment for spruce growth was very different at sites 8–10.

*Tree basal area.*— Basal area increment (bai) of overstory spruce at sites 8–10 followed a pattern different from that at all younger sites. The maximum mean bai of individual spruce trees at the three oldest sites is <40% of maximum mean bai at sites 5–7 (Fig. 8). The rapid growth in individual tree basal area at young sites is offset by substantially lower tree densities (Table 3), and sites 3–6 have <50% of the current spruce stand basal area of the three oldest sites (Table 7). Current rates of increase of spruce basal area at sites 3–7 suggest that spruce basal area there may exceed current values at the three oldest sites long before the current age of those sites is attained.

Western hemlock trees are common at the three oldest sites and are nearly as abundant as spruce at site 10 (Table 4), but most hemlocks are small understory

TABLE 5. Current stand density (plants/ha) of black cottonwood at nine study sites. No cottonwood were encountered in 20 plots at site 9. Data are means  $\pm$  1 SE. Sample sizes as in Table 3 except for site 1 where there were five  $15 \times 20$  m plots.

Site	$n$	Seedling	Sapling	Understory	Subcanopy	Overstory	Total live trees	Dead trees
1	5	1747 $\pm$ 339	0	0	0	0	0	0
2	10	33 $\pm$ 25	287 $\pm$ 105	53 $\pm$ 25	0	233 $\pm$ 44	287 $\pm$ 50	0
3	20	0	0	3 $\pm$ 3	17 $\pm$ 11	210 $\pm$ 33	230 $\pm$ 39	0
4	12	0	0	0	0	206 $\pm$ 40	206 $\pm$ 40	6 $\pm$ 5
5	10	7 $\pm$ 6	0	0	0	21 $\pm$ 11	21 $\pm$ 11	5 $\pm$ 5
6	20	0	0	0	3 $\pm$ 3	20 $\pm$ 8	23 $\pm$ 11	3 $\pm$ 3
7	20	0	0	0	0	3 $\pm$ 3	3 $\pm$ 3	0
8	20	0	0	0	0	3 $\pm$ 3	3 $\pm$ 3	0
10	20	0	0	0	0	13 $\pm$ 6	13 $\pm$ 6	37 $\pm$ 17

TABLE 6. Ring-width releases in Sitka spruce at eight study sites. Sample size ( $n$ ) is the number of overstory spruce released between year 15 and 60 (tree age at core height) with a release factor (10-yr mean ring width  $\div$  mean ring width for the previous 10 yr) of at least 2.0. Data are means  $\pm$  1 SE. Release measures that differ significantly between young sites (3–7) and old sites (8–10) are indicated.

Site	$n$	% of trees*	Tree age (yr)†	Release date (yr)	dbh (cm)‡	Release factor	Ring width before (mm)§	Ring width after (mm)
3	2	100.0	23 $\pm$ 4	1979 $\pm$ 2	10.2 $\pm$ 1.2	2.2 $\pm$ 0.3	3.8 $\pm$ 1.0	7.9 $\pm$ 1.2
4	11	84.6	27 $\pm$ 2	1972 $\pm$ 2	6.3 $\pm$ 7.0	3.7 $\pm$ 0.5	1.6 $\pm$ 0.2	5.5 $\pm$ 0.6
5	18	78.3	31 $\pm$ 2	1962 $\pm$ 2	11.1 $\pm$ 1.0	2.7 $\pm$ 0.3	2.3 $\pm$ 0.2	6.0 $\pm$ 0.4
6	41	91.1	35 $\pm$ 1	1968 $\pm$ 2	11.6 $\pm$ 0.8	2.5 $\pm$ 0.2	2.2 $\pm$ 0.2	5.8 $\pm$ 0.4
7	13	72.2	25 $\pm$ 3	1924 $\pm$ 5	9.2 $\pm$ 1.9	2.5 $\pm$ 0.2	2.1 $\pm$ 0.2	5.1 $\pm$ 0.5
8	13	22.8	29 $\pm$ 2	1904 $\pm$ 4	8.1 $\pm$ 1.3	2.5 $\pm$ 0.2	1.5 $\pm$ 0.2	3.4 $\pm$ 0.1
9	10	17.2	22 $\pm$ 2	1900 $\pm$ 3	5.1 $\pm$ 0.7	2.6 $\pm$ 0.2	1.4 $\pm$ 0.2	3.4 $\pm$ 0.4
10	17	22.7	28 $\pm$ 2	1848 $\pm$ 4	5.5 $\pm$ 1.0	3.3 $\pm$ 0.4	1.1 $\pm$ 0.1	3.1 $\pm$ 0.2
Sites 3–7 vs. 8–10:			NS	***	***	NS	***	***

\* Percentage of all overstory spruce in plots in which a release was recorded.

\*\*\* =  $P < 0.001$ , NS =  $P > 0.05$ .

† Tree age at core height at start of release.

‡ Tree diameter at start of release.

§ Mean ring width for the 10 yr prior to release year.

|| Mean ring width for the 10 yr following the release.

trees and contribute only 2–17% of the stand basal area at these sites (Table 8).

Basal area of black cottonwood is highest at site 4 (Table 9). The substantial difference in basal area of live and dead cottonwood between this site and the next older sites confirms the indication discussed above that cottonwood establishment was much reduced at older sites compared to sites 1–4 (Table 9). It is unlikely that the age difference between site 4 and sites 5 or 6 is enough time for cottonwoods constituting  $\approx 7$  m<sup>2</sup>/ha of basal area (current basal area at site 4) to have decomposed sufficiently to evade detection at sites 5 and 6.

*Shrubs.*—The stand density of shrubs exceeds that of saplings and trees at sites 1–7 (Table 10, compare Tables 3–5), but the basal area of shrubs exceeds that of trees only at sites 1–4 (Table 10, compare Tables 7–9). Shrubs reach their peak in importance at sites 2–4 where a thicket of alder stems and, in summer, a continuous canopy of alder foliage dominates the community. At the three oldest sites, small, isolated alders are common in the understory, but contribute only a minor proportion to stand basal area (Table 10).

#### *Advance of cone-bearing spruce*

At five sampling areas in Muir Inlet, the smallest diameter Sitka spruce with seed cones was 8.3 cm dbh. The largest spruce that had not yet produced cones was 29.8 cm dbh. Between these extremes is a sigmoidal relationship between tree diameter and proportion of trees bearing cones (proportion =  $-0.0001$  dbh<sup>3</sup> +  $0.0058$  dbh<sup>2</sup> -  $0.0600$  dbh +  $0.1289$ ,  $r^2 = 0.977$ ,  $P < 0.001$ ,  $n = 32$ ) which is the basis for a probabilistic reconstruction of the arrival and accumulation of cone-bearing spruce at each site. This reconstruction indicates that after the first spruce arrives at a site, 48–60 yr are required to attain a density of 10 cone-bearing

spruce/ha (Table 11). At the time of deglaciation of the three oldest sites (1768–1835), successional stands that were mature enough to have included 10 cone-bearing spruce/ha were rare or absent on post-neoglacial surfaces (Fig. 9). As each younger site was deglaciated, a progressively larger area of the post-neoglacial surface supported successional stands with cone-bearing spruce. However, successional stands with 10 cone-bearing spruce/ha were always  $>20$  km from newly exposed sites (Table 11). This suggests that the leading edge of reproductive spruce was sparse and too distant to supply many seeds to very young surfaces. As ice has retreated along the east side of Glacier Bay and into Muir Inlet, invading stands of spruce of reproductive size have followed with an apparently consistent lag of 60–75 yr. This advancing front of 10 reproductive spruce/ha has moved at about the same rate as the retreating ice, 30–40 km/100 yr. This rate of advance agrees closely with rates of post-Wisconsin northward migration of spruce that have been inferred from pollen records in New England, the Great Lakes Basin, and the west coast of North America (Davis 1981, 1983, Ritchie and MacDonald 1986, Peteet 1991). However, at Glacier Bay, this rate of advance is the same as, and therefore could have been limited by, the rate of ice retreat.

#### *Refugial forests*

The three oldest study sites (sites 8–10) are within 4 km of mature forest patches that include Sitka spruce trees  $>400$  yr old (Table 11, Fig. 9). Site 10, at the neoglacial terminal moraine, is 4 km from a low elevation area that was not covered by ice during the neoglacial period, and which supports extensive stands of mature western hemlock, Sitka spruce, and mountain hemlock (Fig. 9). The mature spruce stands nearest to sites 8 and 9 are 480–630 m above sea level. These

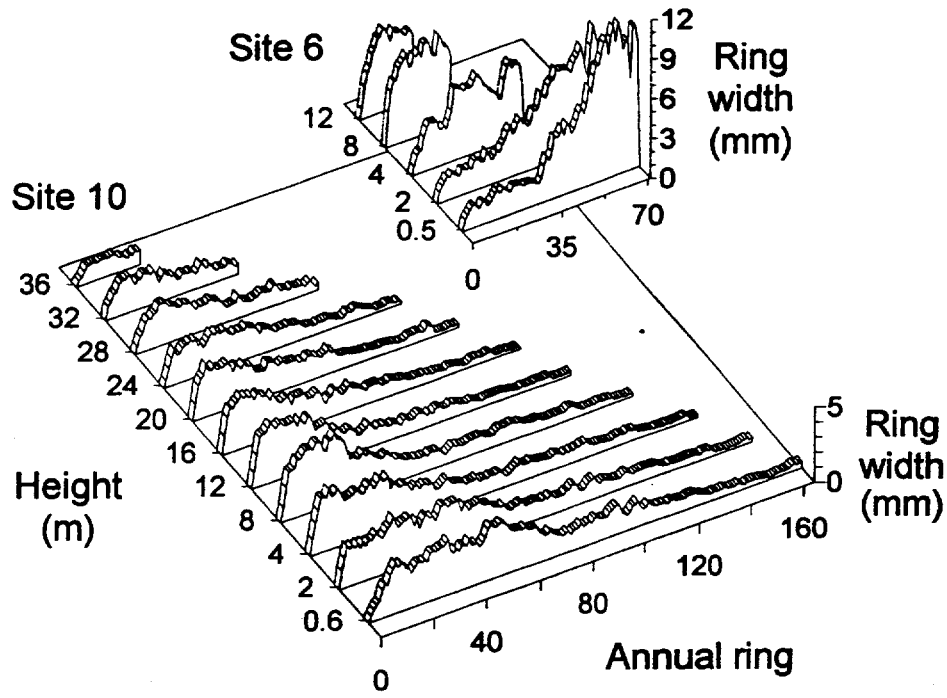


FIG. 7. Mean annual ring widths ( $n = 4$  trees per site) at multiple heights above the root crown of Sitka spruce at two study sites. The innermost rings (near the pith) are along the height axes to the left, and the outermost rings (near the bark) are to the right.

forests are dominated by mountain hemlock with scattered overstory Sitka spruce. Sampled spruce in these stands ( $n = 10$ ) have 300-650 annual rings at breast height. Thus, these stands include spruce trees that were capable of supplying seeds as sites 8-10 were

deglaciated in the early 19th century. In contrast, north of site 8 the elevation of the trimline exceeds the timberline of Sitka spruce. The northernmost mature spruce found is 7.5 km south of site 7 and is the nearest tree found that could have supplied spruce seeds to that

FIG. 8. Basal area increment (bai) of Sitka spruce. Data are means  $\pm 1$  SE of 5-yr plot means of annual bai of all living overstory spruce (understory spruce are included at sites 3 and 4) at eight sites. Sample depth ( $n$ ), used for calculation of SE, is the number of sample plots with spruce of that age or older. Error bars are not shown if  $n$  is fewer than 3. Pairings of sites are for graphic convenience.

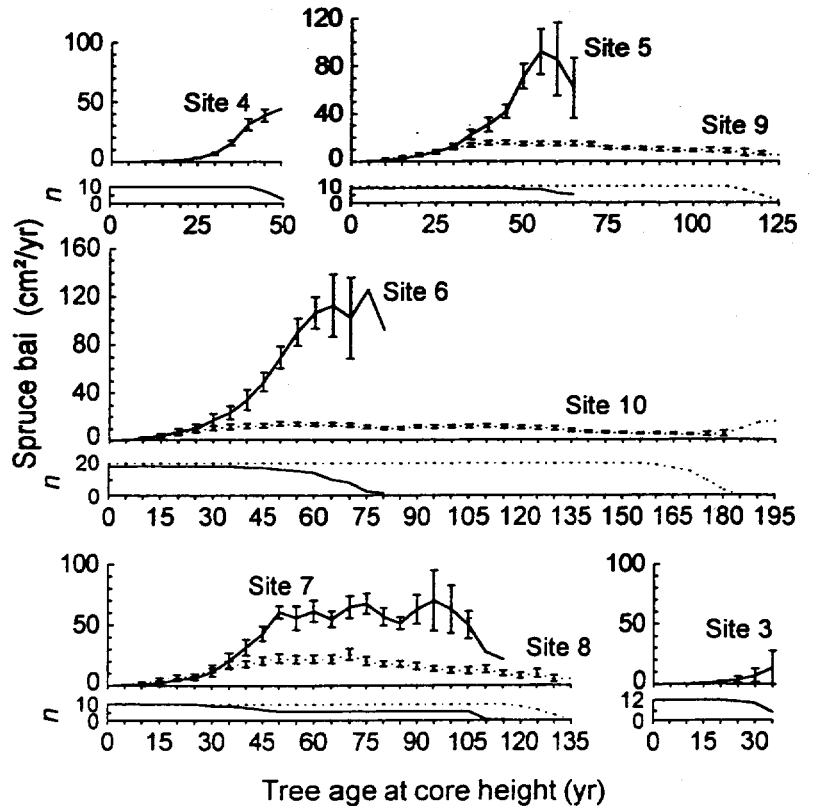


TABLE 7. Basal area (m<sup>2</sup>/ha) of Sitka spruce at eight study sites. No spruce were encountered in plots at sites 1 or 2. Dead spruce includes standing and fallen trees, dead canopy spruce includes subcanopy and overstory trees. Data are means  $\pm$  1 SE. Sample size (*n*) is the number of 10  $\times$  15 m sampling plots per site (10 of the 20 plots at site 3 are 20  $\times$  30 m).

Site	<i>n</i>	Live spruce				Dead spruce		
		Understory	Subcanopy	Overstory	Total	Understory	Canopy	Total
3	20	0.1 $\pm$ 0.0	0	0.3 $\pm$ 0.3	0.4 $\pm$ 0.3	0	0	0
4	12	0.3 $\pm$ 0.2	0	2.9 $\pm$ 0.8	3.3 $\pm$ 0.8	0	0	0
5	10	1.1 $\pm$ 0.6	0	13.4 $\pm$ 3.9	14.5 $\pm$ 4.2	0	0	0
6	20	0.2 $\pm$ 0.1	0.6 $\pm$ 0.3	16.5 $\pm$ 2.3	17.3 $\pm$ 2.3	0	0	0
7	20	0.3 $\pm$ 0.1	0.4 $\pm$ 0.2	40.3 $\pm$ 7.1	41.1 $\pm$ 7.0	0	0	0
8	20	1.9 $\pm$ 0.5	3.9 $\pm$ 1.1	61.9 $\pm$ 4.9	67.8 $\pm$ 5.0	-0.4 $\pm$ 0.1	0.6 $\pm$ 0.3	1.0 $\pm$ 0.3
9	20	1.7 $\pm$ 0.3	4.5 $\pm$ 0.9	39.8 $\pm$ 2.8	45.9 $\pm$ 3.2	2.9 $\pm$ 0.4	8.5 $\pm$ 2.1	11.5 $\pm$ 2.3
10	20	1.5 $\pm$ 0.4	1.7 $\pm$ 0.6	36.6 $\pm$ 3.7	39.8 $\pm$ 3.8	4.8 $\pm$ 0.7	15.5 $\pm$ 3.1	20.3 $\pm$ 3.1

site when it was deglaciated in the 1840s (Fig. 9). There are extensive stands of mature mountain hemlock above the trimline near site 7, but no spruce or western hemlock were found in these stands.

#### Soils

There were no significant differences among sites in soil texture (except a higher silt content at site 9 than at site 6; Appendix B). The ranges for sand, silt, and clay content are similar to, and fall entirely within, the total ranges for soils at Glacier Bay reported by Ugolini (1966). Although there are large and significant differences among study sites in the lithology of pebbles from the upper mineral soil, there is no clear bay-length gradient in lithology (Appendix B). Soil from site 1 contains the highest proportion of carbonate pebbles (30.0  $\pm$  4.4%), reflecting the proximity (<5 km) of one of the largest outcrops of Paleozoic sedimentary rocks near Muir Inlet (Brew et al. 1978). In contrast, site 5 has the lowest pebble count for carbonates (6.1  $\pm$  0.9%) and the highest count for igneous pebbles (52.6  $\pm$  2.2%), reflecting this site's location at the mouth of a valley carved primarily from a massive outcrop of Cretaceous igneous rocks (Brew et al. 1978). The fivefold difference in carbonate pebble content among sites suggests that the carbonate content of the fine fraction of freshly deposited parent material could also differ substantially among sites and is a potential cause of early differences in plant success.

#### Effect of initial site conditions on early spruce invasion

Results of multiple regression indicate that distance from refugial or successional forests with reproductive

Sitka spruce explains 48–58% of the variance in early spruce invasion as described by the reconstructed density of spruce after 40, 50, or 60 yr of recruitment (Table 12). Soil texture was not a significant component of the regression models, and pebble lithology (the proportion of igneous pebbles) explains only 9–19% of the variance in early spruce density (Table 12). The significance of igneous pebble content in all three models (Table 12) results from its strong univariate relationship with early spruce density at the five youngest sites where spruce has invaded ( $r^2 = 0.64$ ,  $P < 0.001$ ). In contrast, when the three oldest sites are included in this regression, there is no significant relationship between igneous pebble content and early spruce density across eight sites ( $r^2 = 0.03$ ,  $P > 0.37$ ). Soil lithology is therefore associated with spruce recruitment at the alder-dominated sites (sites 3–7) but cannot account for the differences in spruce recruitment between these sites and the three older sites.

#### DISCUSSION

##### Multiple pathways and their causes

At the three sites deglaciated before 1840 (sites 8–10), the rapid recruitment of spruce and hemlock (Figs. 3 and 4) indicates that initial conditions there were dramatically different from initial conditions at all younger sites. The three oldest sites are also distinguished by the rarity of spruce trees with a distinctive ring-width signature of suppression and release, which is present in >72% of overstory spruce at each younger site (Table 6) and is associated with emergence of spruce above a shrub canopy (Fig. 6). This suggests that the dense, persistent thickets of alder that are char-

TABLE 8. Basal area (m<sup>2</sup>/ha) of two hemlock species at four study sites. No hemlock trees were encountered in plots at sites 1–6. Dead trees includes standing and fallen trees. Data are means  $\pm$  1 SE. Sample size (*n*) is the number of 10  $\times$  15 m sampling plots per site.

Site	<i>n</i>	Western hemlock				Dead trees	Mountain hemlock
		Understory	Subcanopy	Overstory	Total live		
7	20	0	0	0	0	0	0.2 $\pm$ 0.2
8	20	0.9 $\pm$ 0.5	0	0.8 $\pm$ 0.5	1.6 $\pm$ 0.6	0	0.5 $\pm$ 0.2
9	20	0.8 $\pm$ 0.3	0.9 $\pm$ 0.3	0.1 $\pm$ 0.1	1.8 $\pm$ 0.4	0	<0.05
10	20	3.0 $\pm$ 0.7	2.9 $\pm$ 0.8	2.7 $\pm$ 0.9	8.6 $\pm$ 1.6	0.3 $\pm$ 0.1	<0.05

TABLE 9. Basal area (m<sup>2</sup>/ha) of black cottonwood at nine study sites. No cottonwood were encountered in 20 plots at site 9. Dead trees includes all standing and fallen trees. Data are means  $\pm$  1 SE. Sample size (*n*) is the number of 10  $\times$  15 m plots per site (except five 15  $\times$  20 m plots at site 1).

Site	<i>n</i>	Understory	Subcanopy	Overstory	Total live	Dead trees
1	5	0	0	<0.05	<0.05	0
2	10	0.1 $\pm$ 0.1	0	1.0 $\pm$ 0.2	1.1 $\pm$ 0.2	0
3	10	<0.05	0.2 $\pm$ 0.2	7.0 $\pm$ 1.7	7.2 $\pm$ 1.7	0
4	12	0	0	11.1 $\pm$ 1.7	11.1 $\pm$ 1.7	0.2 $\pm$ 0.2
5	10	0	0	3.8 $\pm$ 2.2	3.8 $\pm$ 2.2	0.2 $\pm$ 0.2
6	20	0	0.4 $\pm$ 0.3	3.7 $\pm$ 1.7	4.1 $\pm$ 1.9	0.1 $\pm$ 0.1
7	20	0	0	0.8 $\pm$ 0.8	0.8 $\pm$ 0.8	0
8	20	0	0	0.3 $\pm$ 0.3	0.3 $\pm$ 0.3	0
10	20	0	0	1.8 $\pm$ 0.8	1.8 $\pm$ 0.8	2.3 $\pm$ 1.0

acteristic of young sites (sites 2–7, Table 10) were absent at sites 8–10. In addition, cottonwood has been an important codominant only at sites deglaciated since 1900 (sites 1–4, Table 5). Plant compositional change on the eastern side of Glacier Bay therefore has followed three distinct pathways. Since ice retreat began, the duration and number of early- and mid-successional stages has increased as plants have invaded new surfaces farther from the terminal moraine where pioneer vegetation was replaced quickly by spruce. At sites 5–7, a prolonged alder stage separates the pioneer and spruce communities, and the youngest sites are expected to succeed through at least four stages: pioneer, alder, cottonwood, and spruce.

A chronosequence can be associated with multiple successional pathways because of either spatial or temporal variability in site environmental characteristics (Matthews 1992). At Glacier Bay, prolonged linear ice retreat has resulted in a strong correlation between site location and date of deglaciation (Fig. 1), confounding the possible association of these factors with environmental effects on the pattern of plant invasion. However, the significant relationship between the rate of early spruce invasion and proximity to stands of reproductively mature spruce (Table 12) suggests that the proximity of new surfaces to mature vs. colonizing vegetation is responsible for the difference between

sites 8–10 and all younger sites. The conclusion that sites 8–10 are distinct from younger sites because they received substantial early seed rain from nearby refugial forests is strongly supported by the fact that these are the only sites to have been quickly invaded by western hemlock (Table 4), an important component of refugial forests near Glacier Bay. Younger sites received a greater proportion of their seed rain from new communities colonizing nearby surfaces. Although sites 8–10 apparently supported only scattered alder plants, alder seeds could have dispersed from these sites earlier than spruce seeds because alder begins to produce seed at age 7–10 yr, 20–40 yr earlier than spruce (Chapin et al. 1994). Consequently, alder seeds could have arrived earlier and in greater numbers than spruce seeds at subsequently deglaciated sites. Thus, the reduced success of spruce and hemlock at sites 1–7 is probably due both to the preemption of establishment sites by young alder thickets, and to a more sparse early seed rain of the conifer species.

The substantial difference in cottonwood recruitment between sites 1–4 and older sites (Fig. 5, Table 5) suggests an environmental difference between these young sites and older sites to the south. Sites 1–4 are farther from marine climatic influences than all older sites, and closer (<20 km) to potential sources of cottonwood seeds in the more inland watershed to the east of Muir

TABLE 10. Stand density (plants/ha), and basal area (m<sup>2</sup>/ha) of shrubs at 10 study sites. Data are means  $\pm$  1 SE of 10 10  $\times$  15 m plots at each study site (five 15  $\times$  20 m plots at site 1).

Site	Sitka willow*		Barclay willow†		Salix spp.‡		Sitka alder	
	Density	Basal area	Density	Basal area	Density	Basal area	Density	Basal area
1	2427 $\pm$ 171	<0.005	300 $\pm$ 58	<0.005	1553 $\pm$ 231	<0.005	0	0
2	853 $\pm$ 249	1.48 $\pm$ 0.61	1180 $\pm$ 147	1.17 $\pm$ 0.33	960 $\pm$ 375	0.65 $\pm$ 0.11	5713 $\pm$ 855	36.62 $\pm$ 4.37
3	113 $\pm$ 43	0.49 $\pm$ 0.26	87 $\pm$ 19	0.12 $\pm$ 0.08	87 $\pm$ 30	1.72 $\pm$ 0.57	1860 $\pm$ 81	31.99 $\pm$ 1.72
4	93 $\pm$ 38	1.26 $\pm$ 0.61	60 $\pm$ 37	0.19 $\pm$ 0.18	20 $\pm$ 10	0.28 $\pm$ 0.01	2053 $\pm$ 250	20.78 $\pm$ 2.44
5	193 $\pm$ 55	4.31 $\pm$ 1.38	7 $\pm$ 6	<0.005	27 $\pm$ 10	0.63 $\pm$ 0.37	960 $\pm$ 134	9.10 $\pm$ 3.20
6	307 $\pm$ 79	2.81 $\pm$ 0.63	27 $\pm$ 17	0.18 $\pm$ 0.12	0	0	687 $\pm$ 102	7.44 $\pm$ 1.28
7	40 $\pm$ 19	0.11 $\pm$ 0.08	13 $\pm$ 8	<0.005	7 $\pm$ 6	<0.005	486 $\pm$ 58	4.64 $\pm$ 1.38
8	0	0	0	0	0	0	87 $\pm$ 27	0.13 $\pm$ 0.07
9	7 $\pm$ 6	<0.005	0	0	0	0	127 $\pm$ 26	0.51 $\pm$ 0.17
10	0	0	0	0	0	0	100 $\pm$ 37	0.40 $\pm$ 0.22

\* *Salix sitchensis*.

† *S. barclayi*.

‡ Includes *S. commutata* and *S. alaxensis*, and at site 1 also includes three other species of willow.

TABLE 11. Results of the reconstruction of the advance of Sitka spruce at eight study sites. At sites 8–10, there were no successional stands with 10 cone-bearing spruce/ha at the time of ice retreat (NA).

Site	Date (yr AD) of:			Time (yr) between ice retreat and:		Distance (km) at time of ice retreat from each site to:	
	Ice retreat	First spruce establishment	10 cone-bearing spruce/ha	First spruce establishment	10 cone-bearing spruce/ha	Successional stand with 10 cone-bearing spruce/ha	Old growth refugium with spruce
3	1934	1944	1995*	10	61	23	34.0
4	1910	1930	1981	20	71	24	26.0
5	1895	1912	1957	17	62	25	22.0
6	1883	1897	1957	14	74	27	18.0
7	1842†	1857	1915	15‡	73	25	7.5
8	1824†	1839	1890	15‡	66	NA	1.2
9	1835†	1850	1898	15‡	63	NA	3.0
10	1768†	1783	1841	15‡	73	NA	4.0

\* Predicted density of cone-bearing spruce at site 3 assumes that the future radial growth of spruce at this site will be similar to growth at sites 4 through 7.

† Date of ice retreat at these sites was estimated by subtracting 15 yr from the dates of first spruce establishment.

‡ Estimated from the mean of sites 3–6.

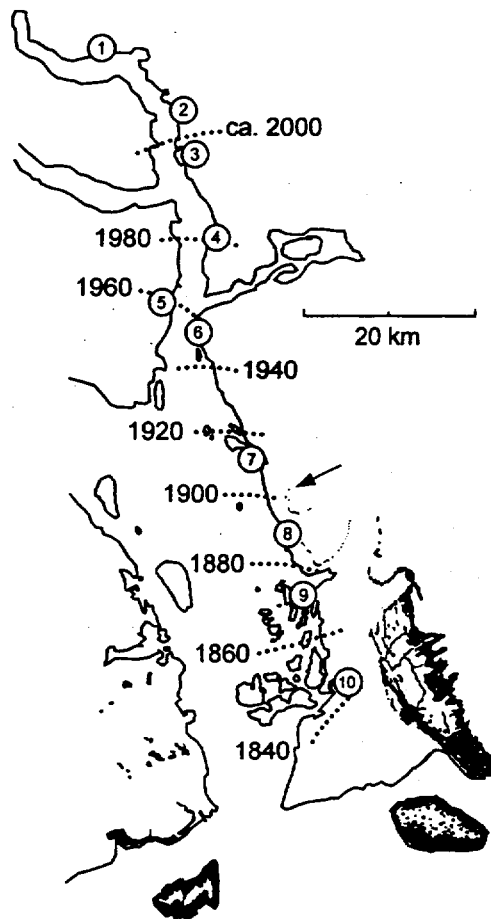


FIG. 9. Refugial Sitka spruce forests near Glacier Bay (dark areas), and 20-yr isochrones (dotted lines) of the reconstructed advance of a successional community of Sitka Spruce with 10 cone-bearing trees/ha. Only the largest patches of mature forest are shown on the western side of the bay. The location of the northernmost forest patch that includes mature Sitka spruce is indicated (arrow). Circled numbers are study sites.

Inlet. Although the reasons for cottonwood's success during this century are unknown, the extensive stands of cottonwood now developing in Muir Inlet have been a new source of seeds for freshly deglaciated surfaces. The positive feedback between this recent recruitment and the subsequent seed dispersal from those stands to newly deglaciated surfaces probably explains cottonwood's continued increase in importance during this century (Fig. 5, Table 5). I predict that during the next century at sites currently being deglaciated in Muir Inlet, cottonwood will be more important, and spruce less important, than at older sites in Muir Inlet. This prediction is based on the abundance of cottonwood and the absence of spruce at young sites (e.g., sites 1 and 2), which will be the primary source of tree seeds for newly deglaciated surfaces.

#### *Mechanisms of plant community change*

The succession from alder to spruce at Glacier Bay has long been used as an example of facilitation. Recent evidence indicates that alder thickets in Muir Inlet strongly inhibit the germination and establishment of spruce, suggesting that alder has a negative effect on spruce population growth (Chapin et al. 1994). Fertile soils under the same alder thickets have a net facilitative effect on the growth of established spruce seedlings (Chapin et al. 1994). These conclusions about spruce–alder interactions and previous inferences about alder's early effects on the development of soil (Crockner and Major 1955) and vegetation (Lawrence 1979) are generally valid for sites in Muir Inlet and the eastern shore of Glacier Bay as far south as site 7, but should not be applied to older sites where long-lived alder stages were never present. At those sites (sites 8–10), dense stands of spruce developed quickly in the ab-

sence of persistent shrub thickets. This is consistent with experimental evidence from young sites in Muir Inlet that facilitation by alder is not a prerequisite for germination, establishment, or growth of spruce (Chapin et al. 1994).

The existence of qualitatively distinct pathways at similar sites at Glacier Bay demonstrates that no single sequence of species replacements and no single mechanistic model of plant community change is mandatory (cf. del Moral and Wood 1993, McCook 1994). The potential for early divergence of successional pathways at Glacier Bay is created by the presence of at least three woody species (Sitka spruce, Sitka alder, and black cottonwood) that can establish at very young sites and quickly attain dominance. The presence of multiple potential colonists suggests that the pathway followed at any site could be determined by the timing and sequence of arrival of these species (cf. Sutherland 1974, Drake 1991). The number of theoretically possible pathways increases with the number of colonizing species available. However, three factors constrain the universe of possible pathways at each site. First, species life history traits (Connell and Slatyer 1977, Noble and Slatyer 1980, Chapin 1993) can exclude certain species sequences. For example, not all species can germinate and establish in the harsh, unmodified environment of newly deglaciated sites. Second, interspecific interactions (competition and facilitation; Connell and Slatyer 1977, Tilman 1985, Walker and Chapin 1987) can exclude certain pathways. For example, the competitive superiority of spruce trees may prevent alder shrubs from invading and succeeding established stands of spruce. However, at Glacier Bay, neither absolute competitive inhibition (species A is not invasible by species B), nor obligate facilitation (establishment requires site modification) has been demonstrated for any successional dominants. Therefore, species interactions are assumed to influence only the rate of community change, not the sequence of dominance (Chapin et al. 1994). For example, inhibition by alder thickets decreases the rate at which spruce invades alder communities, and facilitation by alder increases the rate at which emergent spruce trees achieve dominance (Chapin et al. 1994). Finally, the landscape position of a young site, which determines its proximity to seed sources, can result in the exclusion or delayed arrival of certain species and thereby reduce the number of possible pathways at a site. Landscape position has no direct effect on plant community change, but establishes a site-specific context in which species life history traits related to mobility determine the timing and sequence of species arrivals. This is a critical factor in the northernmost two-thirds of Glacier Bay where the early-arriving species are those that have sustained the most rapid, multi-generational migration from refugial plant communities, a process requiring both long-distance seed dispersal and short generation time. During two centuries of ice retreat, the landscape position of

TABLE 12. Results of multiple regressions. Potential predictor variables included the distance from each study site to sources of spruce seeds, and seven measures of soil texture or lithology at each site. The dependent variable was the stand density of spruce after 40, 50, or 60 yr of recruitment at each site. Distance from spruce forest is the shortest distance from each newly exposed site to refugial or successional forests with reproductive spruce. *B* = standardized partial regression coefficients. *P* = probability that *B* = 0. Adjusted model *R*<sup>2</sup> is based on standardized variables.

Variable	<i>B</i>	<i>P</i>	Partial <i>R</i> <sup>2</sup>	Adjusted model <i>R</i> <sup>2</sup>
Spruce density after 40 yr:				0.76
Distance from spruce forest	-0.91	0.0001	0.58	
% igneous pebbles	0.46	0.0001	0.19	
Spruce density after 50 yr:				0.66
Distance from spruce forest	-0.87	0.0001	0.57	
% igneous pebbles	0.35	0.0035	0.11	
Spruce density after 60 yr:				0.54
Distance from spruce forest	-0.88	0.0001	0.48	
% igneous pebbles	0.36	0.026	0.09	

young sites has selected for species with both of these traits, and the resulting increase in importance of alder and cottonwood has been the ultimate cause of multiple pathways. Within each pathway, interspecific interactions have had a substantial proximate effect on the rate of community change.

#### *Ecosystem effects of alternate pathways*

Although the three successional pathways identified at Glacier Bay are distinguished primarily by single species replacements or additions, the resulting communities have the potential to differ substantially in ecosystem properties (Vitousek 1986, 1990). Long-term dominance by nitrogen-fixing alder shrubs is responsible for the accumulation of substantial soil-nitrogen pools (Crocker and Major 1955) and high rates of community productivity and nutrient cycling (Bormann and Sidle 1990). Black cottonwood may also alter ecosystem properties. Where cottonwood trees currently share dominance with alder shrubs, competition for light or soil resources may accelerate the demise of alder and thereby slow the long-term accumulation of nitrogen. Cottonwood could also affect the succession to conifers by changing litter and soil chemistry (Sugai and Schimel 1993, Van Cleve et al. 1993). Divergence of ecosystem properties may slow or end if all three pathways lead eventually to dominance by conifers.

Spruce and hemlock stands at the terminal moraine (near site 10) are currently being disturbed by the spruce bark beetle (*Dendroctonus rufipennis* Kirby), which has killed all canopy spruce in some stands (Eglitis 1988). This outbreak followed 30–40 yr of re-

duced spruce vigor, which is recorded at site 10 as smaller basal area increments in overstory trees (Fig. 8). The stand-wide senescence (cf. Mueller-Dombois 1986) which facilitated the insect outbreak has been attributed to decreased nutrient availability as nitrogen and phosphorus are sequestered in biomass and recalcitrant organic soil horizons (Bormann and Sidle 1990, McClellan et al. 1990). At younger sites where alder has been important for several decades, the legacy of accumulated nutrient and organic matter pools and of sparse conifer recruitment will prevent rapid convergence toward the spruce and hemlock communities of older successional stages and could delay or prevent the cohort senescence of spruce and subsequent lethal insect outbreak. The single species differences early in succession at otherwise similar sites at Glacier Bay therefore could have substantial consequences for successional pathway and ecosystem function for many centuries.

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