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**Two centuries of primary succession at Glacier Bay, Alaska: A test
of a classic glacial retreat chronosequence**

Fastie, Christopher Lee, Ph.D.

University of Alaska Fairbanks, 1994

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**TWO CENTURIES OF PRIMARY SUCCESSION
AT GLACIER BAY, ALASKA:
A TEST OF A CLASSIC GLACIAL RETREAT CHRONOSEQUENCE**

**A
THESIS**

**Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of**

DOCTOR OF PHILOSOPHY

By

Christopher Lee Fastie, B.A., M.S.

Fairbanks, Alaska

May 1994

TWO CENTURIES OF PRIMARY SUCCESSION
AT GLACIER BAY, ALASKA:
A TEST OF A CLASSIC GLACIAL RETREAT CHRONOSEQUENCE

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ABSTRACT

The classic account of primary succession inferred from a 220-year glacial retreat chronosequence at Glacier Bay, Alaska was tested against site-specific dendroecological reconstructions of successional development and against measured 37-year changes in soil nitrogen pools. Differences between young and old portions of the chronosequence in the invasion and radial trunk growth of Sitka spruce (*Picea sitchensis*) indicate that the nitrogen-fixing shrub Sitka alder (*Alnus sinuata*) has been an important and long-lived species only at sites deglaciated since 1840. Confirming this result, the soil nitrogen pool at sites deglaciated since 1840 has accumulated rapidly (2.3 to 3.6 g N m⁻² yr⁻¹) and is currently larger at some sites than at older sites where alder has not been important. A late-successional decrease in soil nitrogen inferred from the chronosequence did not occur at sites where soil nitrogen was measured in 1952 and again in 1989. Consequently, uncritical use of the entire Glacier Bay chronosequence to infer successional trends in community composition, nutrient dynamics, or soil development is unwarranted.

Although the nitrogen and organic matter added by alder thickets have an apparent facilitative effect on the growth of individual spruce trees, alder thickets are associated with substantially reduced stand density of spruce. Thus, at the level of the population, a long-term, net facilitation of spruce by alder has not been demonstrated at Glacier Bay.

Differences in texture and lithology of soil parent material cannot explain the differences in successional development between young and old portions of the Glacier Bay chronosequence. 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 successional pathways have apparently resulted from changes in seed rain to newly deglaciated surfaces caused by (1) linear ice retreat exposing land surfaces more distant from refugial old growth forests, and (2) shifts in the species composition of the advancing front of successional vegetation and in its seed output.

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INTRODUCTION

The study of plant succession has been a constant and substantial component of ecology from the inception of the discipline at the turn of the twentieth century (McIntosh 1981). Because succession happens slowly relative to human lifespans, ecologists have based their understanding of long-term successional dynamics primarily on chronosequences -- collections of sites of different age that are assumed to represent the progression of a single plant community through time. This approach provides valid information about successional change when all chronosequence sites are well dated, are developing along the same successional trajectory, and are developing at the same rate (Pickett 1989). Chronosequences were instrumental in revealing the existence, basic nature, and significance of succession to early ecologists (Warming 1891, Cowles 1899, Shelford 1911). The early formulation of succession as a deterministic process with a single endpoint, in which succession at similar sites was expected to follow the same pathway (Clements 1916), reinforced the validity of the chronosequence approach. But there was early recognition of the potential for succession to be less than deterministic (Gleason 1927). There was also early recognition that non-deterministic succession would cause problems with the interpretation of chronosequence studies. Gleason (1927) drew early attention to the critical assumption in chronosequence studies and said about the relationship between temporal sequence and spatial chronosequence "Never the twain shall meet." Throughout the twentieth century, our understanding of succession has grown closer to a Gleasonian individualistic concept (McIntosh 1981) as the perceived importance of disturbance (Pickett and White 1985), multiple pathways (Cattalino et al. 1979), and chance and initial conditions (del Moral and Bliss 1993) has increased. As these changes have eroded the theoretical basis of the chronosequence approach, plant ecologists have not lessened their dependence on the method (Pickett 1989).

Although some plant ecologists have drawn attention to the pitfalls of the chronosequence approach (Colinvaux 1973, Zedler and Goff 1973, Miles 1979, Collins and Adams 1983, Pickett 1989), the most important theoretical developments and analyses of the method have been carried out by soil scientists (Stevens and Walker 1970). Hans Jenny formalized the method of selecting sites at which, except for site age (time), all of the factors affecting soil formation (time, climate, parent material, relief, and

organisms) are the same (Jenny 1941, 1958, 1961, 1980). Crocker (1959) clarified the close relationship between plants and the abiotic factors of soil formation. Both Crocker (1952) and Jenny (1958) recognized that, in practice, the different aged sites constituting a chronosequence are rarely identical in all of the other soil forming factors, and they stressed that the rare cases in which the other factors are constant should be deliberately sought out and studied. Stevens and Walker (1970) presented guidelines for the study of chronosequences and repeated the need to eliminate variation in soil-forming factors other than time. They recommended that sites where natural disturbance had occurred should be avoided. Consequently, some researchers studying soil chronosequences have restricted their studies to the most fully developed soils at each chronosequence stage (Mellor 1987, Messer 1988). Although this approach can have the desired effect of reducing among-site variation in soil-forming factors, it can also exclude from study alternate pathways of soil and vegetation development that have been followed at similar sites. This may misrepresent succession as a more predictable process than it is.

Plant ecologists routinely restrict their chronosequence sites to areas of similar topography, aspect, elevation, hydrology, or parent material (e. g., Bard 1952, Bazzaz 1968, Marks 1974, Aber 1979, Vitousek et al. 1983, Chapin et al. in press). This approach limits the extent to which results can be extrapolated to the landscape, but will not systematically exclude sites solely because alternate successional pathways have been followed. This approach does not eliminate the risk of misinterpretation if multiple pathways are present but are not recognized. For example, if all young sites have followed one pathway and all old sites another, then low among-site variance within each successional stage may lead the researcher to conclude erroneously that a single pathway is present. The single successional pathway inferred from the entire chronosequence may have little resemblance to either of the actual pathways being followed. Similarly, if all sites at an old stage are similar, but much among-site variance is measured at young stages, the probable conclusion is that convergence has occurred during succession. An alternate explanation is that multiple, non-convergent successional trajectories are being followed at young sites, and only one pathway has been followed at the old sites that were included in the study. Thus, the chronosequence approach by itself does not have the power to detect the multiple successional pathways that can invalidate the conclusions of these studies.

In 1952, with the prospect of studying one of the rare chronosequences in which sites differ only in age, R. L. Crocker made an expedition to Glacier Bay, in southeastern Alaska. The descriptions and measurements of soils at sites exposed by glaciers that had been rapidly retreating for two centuries (Crocker and Major 1955) have become a classic study of the effects of early vegetation on soils in primary succession. Plant ecologists had previously recognized the value of the relatively well-dated surfaces of glacial deposits at Glacier Bay that formed a continuous chronosequence dating back to the middle eighteenth century. Nine small vegetation sampling plots were permanently marked in Glacier Bay in 1916 by W. S. Cooper (1923b), who also made thorough descriptions of the vegetation at dozens of other sites along the chronosequence (Cooper 1923a, 1931, 1939). D. B. Lawrence focused attention on the role of nitrogen-fixing microorganisms in root nodules of early successional shrubs (Lawrence et al. 1967), and experimentally demonstrated a possible facilitative effect of nitrogen-fixing Sitka alder (*Alnus sinuata* [Reg.] Rydb.) on adjacent cottonwood (*Populus trichocarpa* Torr. & Gray) trees (Lawrence 1953). However, the most widely cited study of primary succession at Glacier Bay is the documentation of the rapid accumulation of soil nitrogen under thickets of Sitka alder (Crocker and Major 1955). Although they made no attempt to demonstrate the consequences of this soil nitrogen for vegetation, this study became a key example of the importance of facilitation by early nitrogen-fixers in primary succession. Alder at Glacier Bay incorporates, in less than a century, more than 2500 kg/ha of atmospheric nitrogen into glacial deposits which are essentially devoid of nitrogen initially (Crocker and Major 1955). Plant ecologists recognized that this soil nitrogen must have profound consequences for later successional plant communities, and the Glacier Bay example has been explicitly cited in the presentations of the most influential recent models of plant succession (Connell and Slatyer 1977, Tilman 1988).

The objective of the studies described in this thesis is to determine whether the Glacier Bay chronosequence is one of the rare cases in which the differences in vegetation and soil at study sites of different age are due primarily to their age or can be attributed to other factors. Two approaches are taken to address this question. In the first chapter, the successional history of individual study sites is read from the record in the annual rings of trees that grew at the sites. These site-specific histories of forest stand development are compared to the successional history inferred from a chronosequence

that is assembled from the current plant communities at the sites. In the second chapter, the soil nitrogen measurements made in 1952 by Crocker and Major (1955) are repeated in order to describe the actual successional changes that have occurred during 37 years. These changes in total soil nitrogen are compared to the changes inferred from the chronosequence by Crocker and Major (1955) and from a modern chronosequence which is assembled from the current study sites.

CHAPTER ONE

A DENDROECOLOGICAL TEST OF THE CHRONOSEQUENCE

INTRODUCTION

Information about long-term successional 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). Due to a lack of detailed permanent plot records spanning more than a century, to the low temporal and spatial resolution of palaeoecological studies, and to the limited information about the early dynamics of non-tree species and very young trees available from dendroecological reconstructions, our understanding of long-term successional dynamics is based primarily on inferences from chronosequences. A critical assumption in all chronosequence studies is that the communities at the oldest sites have developed through stages similar to the younger communities (Fig. 1a). If sites of different age have followed different successional pathways, the pattern of differences across a series of progressively older study sites may have little relationship to the pattern of actual change at any site (Fig. 1b). Thus, the existence of multiple successional pathways within a chronosequence can violate a key assumption of the chronosequence approach (Pickett 1989).

A chronosequence can include multiple pathways because (1) an environmental mosaic causes succession to proceed differently at different places, or (2) a regional environmental change occurring during the course of chronosequence development causes succession at young sites to differ from succession at older sites. In heterogeneous environments multiple successional pathways are commonly associated with an environmental mosaic (Tisdale et al. 1966, Matthews 1979, Birks 1980, Whittaker 1989), or a mosaic of disturbance regime (Collins and Adams 1983, Jackson et al. 1988). If the area comprising the chronosequence study sites is overlain by such a mosaic, all sites will not necessarily have the same successional history, and vegetation differences among sites cannot be attributed solely to differences in successional age. Multiple successional

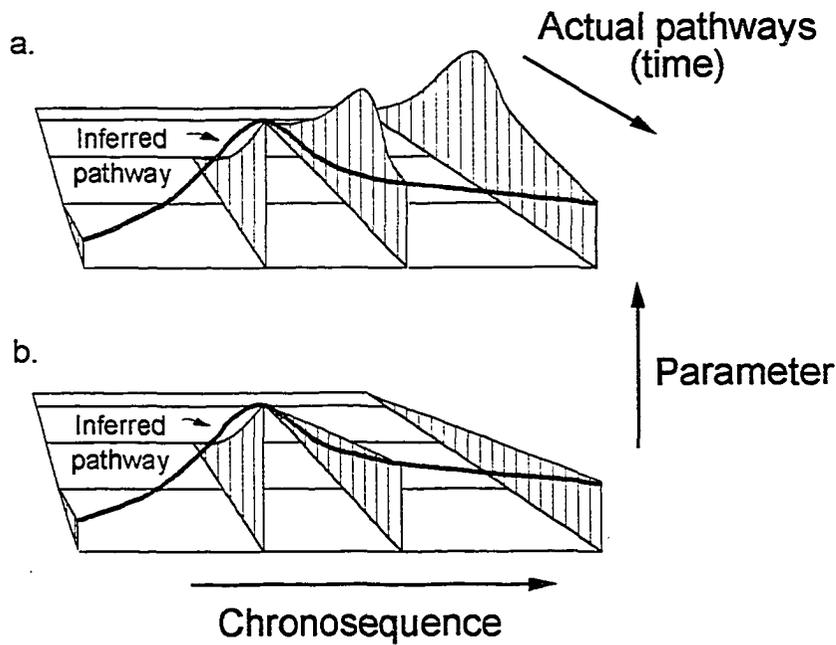


Fig. 1. Relationship between actual change and change inferred from a chronosequence. The pattern of differences among chronosequence sites is a good surrogate for past changes if site ages are known and if the pathway of change at all chronosequence sites has been similar (a). If different pathways have been followed at some chronosequence sites, the pattern of change inferred from the chronosequence may differ from the actual pathways (b). Note that only the rate of change need differ among chronosequence sites to cause a misleading inference.

pathways can also result from changes affecting all sites, but occurring during the course of chronosequence development. For example, if the regional environment (e.g., climate, groundwater, disturbance regime) changed after succession had begun at the oldest sites, the early environment, and therefore the successional pathway, at young and old sites could differ, making inference from the entire chronosequence misleading (Matthews 1992). Erroneous inference from a chronosequence is possible if either of the above causes of heterogeneity results in among-site differences in successional pathway. Differences in successional trajectory can produce the most misleading results, although only the *rate* of successional development need differ among chronosequence sites to produce a misleading inference (Fig. 1b).

Results of the few tests of inferences from chronosequences are mixed but generally suggest that uncritical inference of temporal trends was not justified. Resampling of permanent plots has confirmed short-term (<28 yr) changes in species abundance inferred from two glacial retreat chronosequences (Richard 1973, Whittaker 1991). However, periodic resampling of permanent plots over 33 yr failed to find two out of four of the successional stages inferred from a chronosequence in tallgrass prairie (Collins and Adams 1983). Three paleoecological tests have failed to confirm the general successional sequences inferred from chronosequences. Walker's (1970) reconstruction from pollen and macrofossils of 10000 yr of vegetation change in British wetlands revealed multiple successional pathways far more complex than the patterns of change from open water to forest inferred from different aged sites (Tansley 1939). A 3000 yr record of pollen and macrofossils in dune ponds near Lake Michigan (Jackson et al. 1988) demonstrates that the late successional increase in importance of *Typha* inferred from different aged ponds by Shelford (1911) and Wilcox and Simomin (1987) is an artifact of anthropogenic disturbance affecting only the oldest ponds. Pollen records from two out of three peat cores on moraines of the Klutlan Glacier in the Yukon Territory, Canada, failed to confirm the general successional changes inferred from a chronosequence of moraines (Birks 1980).

The objective of the present study is to test the validity of the classic glacial retreat chronosequence 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 m² (Cooper 1923b), precluding a meaningful comparison of directly measured long-term changes in vegetation with those inferred from the chronosequence.

In the 1960s, Stephens (1991) noted that Sitka spruce (*Picea sitchensis* [Bong.] Carr.) trees growing on the 18th century terminal moraine at Glacier Bay were smaller in diameter than spruce half their age growing on younger terrain. He hypothesized that differences in soil hydrology on the terminal moraine caused a distinct successional pathway there, a situation that could invalidate inference from the chronosequence. However, no measurements were made at Glacier Bay to test this hypothesis. Ugolini (1966, 1968) observed that only surfaces younger than 100 yr at Glacier Bay met Jenny's (1958) criterion that the vegetation at all chronosequence sites be similar so that soil changes can be attributed exclusively to pedological processes. No other authors have questioned the validity of the Glacier Bay chronosequence, and no formal test has been performed on any part of the chronosequence.

This study uses a dendroecological approach (Henry and Swan 1974) to reconstruct the invasion history of woody plants at ten sites of different age at Glacier Bay. I test the hypothesis that the changes in density (stems/ha) of Sitka spruce, western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and black cottonwood that are inferred from a 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 successional tree species.

METHODS

Study area

Glacier Bay is a fiord in southeastern Alaska (59°N, 136°W) near the southern end of a coastal arc of glaciated mountains which encompasses the fourth largest area of glacial ice on Earth. Since ca. 1750, the world's most rapid and extensive glacial retreat in modern times has eliminated a lobe of ice approximately 2500 km² in area that had filled the entire 100 km length of the basin now known as Glacier Bay (Fig. 2). Several hundred km² 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 more than 1100 m of glacial ice in the middle eighteenth 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 to 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 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 to 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. Surfaces 35 to 45 yr old typically have 100 percent cover of shrubs and young cottonwood trees, and Sitka alder is the dominant species. Sitka spruce is the dominant species on surfaces older than 90 yr, and on surfaces older than 160 yr has nearly 100% overstory cover. Western hemlock is common in the understory only on surfaces older than 160 yr.

Glacial deposits at Glacier Bay are derived from rocks of four distinct geological 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 in Muir Inlet and the

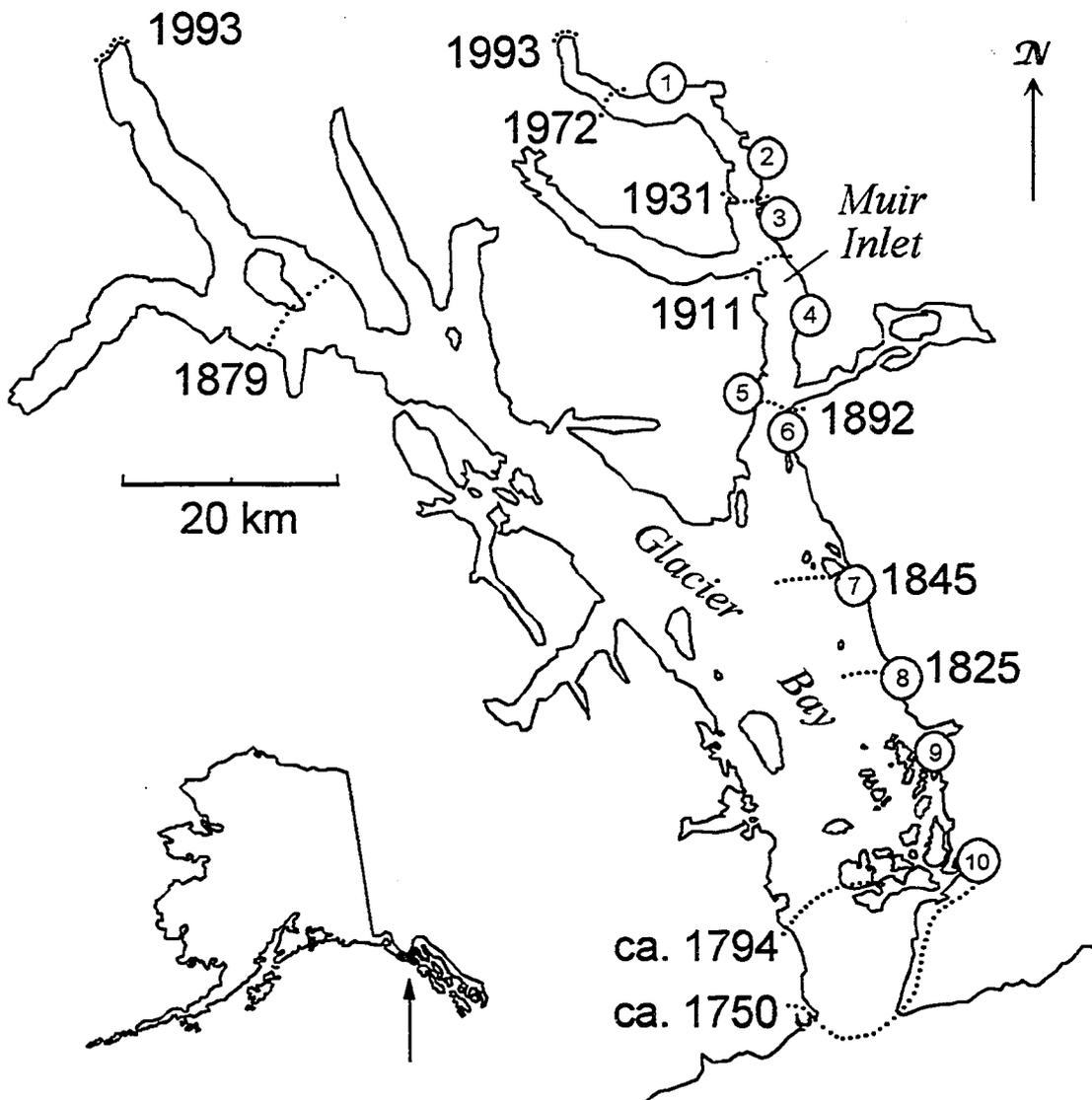


Fig. 2. Location of ten study sites at Glacier Bay. Positions of glacier termini from historical maps and photographs (1794 and 1879-1993) or from dendrochronology (1750, 1825, 1845) are indicated. Location of Glacier Bay National Park and Preserve in southeastern Alaska is indicated (arrow).

eastern shore of lower Glacier Bay (Ovenshine 1968). Four studies of soil development in glacial deposits at Glacier Bay have documented dramatic increases in nitrogen (N) 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. in press).

Glacier Bay has a maritime climate with cool summers and mild, wet winters. Maximum and minimum temperatures at sea level rarely exceed 24°C and -23°C, respectively, and the mean annual temperature is near 5°C (Loewe 1966). Annual precipitation at Gustavus, at the neoglacial terminal moraine, is 184 cm, and monthly precipitation varies between 8 and 30 cm 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 (Table 1, Fig. 2) to represent different stages of the ca. 250 yr chronosequence studied previously (Crocker and Major 1955, Ugolini 1966, Reiners et al. 1971, Bormann and Sidle 1990, Chapin et al. in press). These ten areas were evenly spaced between the eighteenth 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 outwash; and each was a level surface without major areas of exposed bedrock or continuously saturated soil. Most of these study areas are sites of previous research on succession (Table 1), making results of this study directly comparable to previous results. A 10 ha study site was centered in each study area, and ten 10 X 15 m sampling plots were located throughout each site using random coordinates. Five 15 X 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 their locations were archived with Glacier Bay National Park and Preserve. Plots were sampled between 1987 and 1990.

Table 1. Descriptions of study sites. Site age and date of deglaciation are from historical maps and photographs (sites 1-6), or inference from ages of the oldest spruce trees sampled (sites 7-10), and are average dates for the 6 to 20 ha study sites each of which became ice-free over a 3 to 10 yr period.

BM=U.S.G.S. benchmark.

Site	Location	Age (yr)	Date ice-free	Substrate	Vegetation	Previous studies
1	4 km W of Riggs Glacier terminus	22	1968	till	bare, willows	1.5 km E of "Pioneer" site of Chapin et al. in press
2	3 km N of Nunatak Cove, at BM "Fred"	45	1944	till	continuous alder	none
3	NE of head of Goose Cove	55	1934	till	continuous alder, cottonwood	<0.4 km from cottonwood experiments of Lawrence 1953; <0.5 km from ca. 20 yr old site (and photos 1 and 2) of Crocker and Major 1955; 1 km S of "Alder" site of Chapin et al. in press
4	immediately N of Klotz Hills	78	1910	till	alder, cottonwood, spruce	1.3 km N of profile 6 of Ugolini 1966
5	N side of Morse Creek, 1 km from inlet	93	1895	till	alder, spruce	none
6	S part of Muir Point near BM "Plat"	105	1883	till and outwash	spruce, alder	<1 km from ca. 72 yr old site of Crocker and Major 1955 and profile 37 of Ugolini 1966; <0.2 km E of "Muir Point" site of Bormann and Sidle 1990
7	peninsula N of Spokane Cove	143-153	1837-1847	till	spruce, alder	<1 km from ca. 95 yr old site of Crocker and Major 1955
8	1 km S of mouth of York Creek	159-169	1819-1829	till	spruce, hemlock	approximately 3.5 km from profile 85 of Ugolini 1966
9	S shore of Beartrack Cove, 2 km W of BM "Bear"	148-158	1830-1840	till	spruce, hemlock	<0.5 km from ca. 122 yr old site and photo 4 of Crocker and Major 1955; <3 km from profile 85 of Ugolini 1966; <0.2 km from "Beartrack Cove" site of Bormann and Sidle 1990
10	1 km SW of Bartlett Lake	216-226	1763-1773	till and outwash	spruce, hemlock	4 km NE of oldest site of Crocker and Major 1955 and Ugolini 1966 along the same moraine; 4 km ENE of "Lester Island" site of Bormann and Sidle 1990; 3 km NE of "Spruce" site of Chapin et al. in press

Trees

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 [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) trees 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. One core from each tree was retained. 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 ($\leq 75\%$ of crown area exposed to the sky), or understory ($\leq 75\%$ of crown area exposed to the sky and tree height <50% of total canopy height). Seedlings in three height classes (<20 cm, 20 to 50 cm, and 51 to 140 cm) and saplings (<4 cm dbh and >1.4 m tall) of each tree species were counted. To improve estimates of stand density and basal area, additional tree data (dbh and counts per plot) were collected in ten temporary 10 X 15 m plots randomly located in 10 ha areas adjacent to the five oldest study sites (sites 6 through 10). To improve the accuracy of the reconstructions of spruce stand history, all spruce trees were cored in these ten additional plots at sites 6 and 10, and also in three additional randomly located plots at site 5, two additional randomly located plots at site 4, and ten additional randomly located 20 X 30 m plots at site 3.

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 $bai_t = \pi r_t^2 - \pi r_{t-1}^2$, where bai_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 cm 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. 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 (Table 2). These height growth curves were also used to estimate the age of seedlings growing in sampling plots.

At sites 8, 9, and 10, the only sites where dead spruce trees were present in sampling plots, each dead spruce, including fallen trunks, was assigned to one of 12 appearance classes (see below) and dbh was recorded. Each dead tree was classified as overstory, subcanopy, or understory based on its height. Cores were collected from all sound trunks of dead spruce in the ten permanently marked plots. Cores were prepared and annual rings measured as above. To determine the year of death for dead spruce trees, ring-width series for each cored dead spruce at sites 9 and 10 were crossdated against site-specific master dating series from live overstory spruce using program Cofecha (Holmes 1992) and visual confirmation (Swetnam et al. 1985). Site-specific logarithmic regressions of years since tree death against appearance class for these trees were used to estimate the time since death for trees that were not cored or not successfully crossdated (Table 2). The ages of dead trees that were not cored were estimated using logarithmic regressions of age against dbh for the dead trees that were successfully aged (Table 2). Only 12 dead spruce were present in sampling plots at site 8, and equations from site 9 were used to estimate age and time since death for these trees. Appearance-class equations for spruce at site 10 were used for the five dead western hemlocks in plots at site 10, the only dead hemlocks encountered in plots. The estimated germination dates of all trees and the dates of death of dead trees were used to reconstruct the stand density (live trees/ha) during each decade of each stand's history. Reconstructions of cottonwood stand density do not include the few dead cottonwood trees encountered in sampling plots because they could not be confidently dated. Stand reconstructions at the oldest sites may underestimate the early density of trees because the remains of trees that died young could be buried by the accumulating organic soil horizon.

To describe height-related changes in spruce growth rate, spruce trunk radial increment was measured at different heights above ground level at sites 6 and 10. At site 10, increment cores of four overstory spruce that were felled by the Park Service in 1988 were taken at 4 m intervals along the trunks. At site 6, four overstory spruce between 17

Table 2. Regression equations used in reconstructions. Seedling height equations were used to estimate the time required for trees to grow to core height. The dbh x age and the appearance class equations were used to estimate age and date of germination of dead spruce trees. ln = natural logarithm.

Relationship described	Equation	<i>n</i>	<i>r</i> ²
Seedling height (cm) vs. age (yr)			
for:			
Sitka spruce	Age = 1.19(height) ^{0.57}	129*	0.88
western hemlock	Age = 8.89ln(height)-17.37	13	0.64
black cottonwood	Age = 5.72ln(height)-9.28	34*	0.50
Dbh (cm) vs. age (yr) of dead spruce trees at:			
site 9	Age = 29.9ln(dbh) + 12.2	57	0.50
site 10	Age = 41.2ln(dbh) + 16.0	61	0.58
Appearance class (1 to 12) and time since death (yr) of dead spruce trees at:			
site 9	Yrs dead = 23.7ln(appearance class)-12.3	35	0.70
site 10	Yrs dead = 41.9ln(appearance class)-19.4	42	0.74

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

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.

Shrubs

Counts were made of individual plants of Sitka alder and all willows 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 (m^2/ha).

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 spruce trees growing under a continuous canopy of alder near site 3 were tied back with nylon cord to produce artificial canopy gaps 3 to 4 m in diameter. Spruce trees were 90 to 290 cm tall (mean = 193 ± 18 cm) at the beginning of the experiment and the top of the alder canopy was 5 to 8 m above the ground. Alder branches encroaching on the gap 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 (mean height in 1987 = 212 ± 14 cm) that were between 15 and 50 m 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 ten yr interval is at least twice the mean ring width for the previous ten 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 first yr of the release was defined as the first yr in which ring width exceeded the maximum ring width during the ten previous yr.

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 1:63360 U.S.G.S. topographic maps. To evaluate their potential as sources of spruce seeds for nearby successional terrain, nine of the forest areas closest to the study sites were visited and increment cores taken from several of the largest spruce for age determination. Field work was concentrated near sites 6, 7, and 8 in order to locate the northernmost stands of old growth 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 eighteenth and nineteenth centuries as the study sites were deglaciated.

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 to 90 yr and current vegetation included Sitka spruce with seed cones as well as spruce that had not begun to produce cones. The diameter (dbh) and presence or absence of cones was recorded for every spruce at each area for a total of 433 trees. The resulting relationship between size and the proportion of trees bearing cones was used as a probability function in stand reconstructions to estimate the proportion of trees in each size class that were reproductively mature. The estimated probability that spruce of a particular diameter bore cones 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/ha) of cone-bearing spruce trees at each study site. The calendar year during which each site supported an estimated density of ten 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 ten cone-bearing spruce/ha, or (if closer) the distance to refugial old growth forests with spruce (see above) 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 nine of the ten 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 micro-pipette 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 metasedimentary 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 (mean \pm 1 SD: 274 \pm 68) from each of the 37 samples were identified.

Statistical analyses

Stepwise multiple regression (SAS: "PROC REG... /SELECTION = STEPWISE") was used to select from eight measures of initial site conditions (percent sand, silt, or clay in mineral soil; percent carbonate, metasedimentary, dike rock, or igneous pebble; and the shortest distance to reproductive spruce forest) which were potential predictors of among-site differences in the early rate of spruce recruitment (spruce stand density [trees/ha] 40, 50, or 60 yr after the first spruce arrived). Three separate regressions predicting early spruce density after 40, 50, and 60 yr of recruitment at each site were developed. Reconstructed stand densities at times later than 60 yr after first recruitment were not used to avoid excluding young sites at which a shorter period of recruitment had occurred. Spruce density prior to year 40 was not used because reconstructions of earlier density at the oldest sites are expected to be more sensitive to errors associated with estimating germination dates of dead trees. Because the soil measures are proportions and include inversely correlated pairs (e.g., sand content is high when clay content is low), multiple regressions were repeated with no correlated pairs of independent variables in order to

inspect for evidence of spurious model behavior due to multicollinearity. Model parameters and variance inflation factors (an index of how much the regression coefficients are inflated because variables are linearly related, Neter et al. 1985) were compared between models.

Among-site differences in soil texture and pebble lithology were identified with a modified Ryan's Q test (SAS: "REGWQ") following significant one-way analyses of variance (SAS: "PROC GLM"). Spruce trunk radial growth in trees growing in experimental canopy gaps was compared for each of four treatment years to control trees with year-specific t tests (SAS: "PROC TTEST"). 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 (SAS: "PROC GLM... CONTRAST..."). 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 in the text and tables \pm 1 standard error of the mean (SE) unless the comparison of means is irrelevant, in which case standard deviation (SD) is used and noted. All statistical analyses were performed with SAS version 6.07 for VMS (SAS Institute Inc. 1989).

RESULTS

Stand reconstructions

Sitka spruce.-- Sitka spruce is the most abundant overstory tree at the six oldest study sites (sites 5 through 10) and is present in the overstory at sites 3 and 4 (Tables 3 through 5). Spruce is also the most common tree in the understory and subcanopy at sites 3 through 9 (Tables 3 through 5). At sites 9 and 10, 43 and 69%, respectively, of all spruce trees in sampling plots were dead (Table 3). At site 9, 79% of these dead spruce were in the understory (Table 3), and all but one dead spruce in the plots were still standing

Table 3. Stand density (plants/ha) of Sitka spruce. 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 X 15 m sample plots per site ($n = 10$ for seedlings, ten of the 20 plots at site 3 are 20 X 30 m).

Site	n	Live spruce						Dead spruce		
		Seed ling-	Sap- ling	Under- story	Sub- canopy	Over- story	Total trees	Under- story	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

Table 4. Stand density (plants/ha) of western hemlock and mountain hemlock. No hemlock were encountered in plots at sites 1 or 2. 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	<i>n</i>	Western hemlock					Total live trees	Dead trees	Mountain hemlock
		Seed-ling	Sap-ling	Under-story	Sub-canopy	Over-story			
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
6	20	0	0	0	0	0	0	0	0
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

Table 5. Stand density (plants/ha) of black cottonwood. Data are means \pm 1 SE. Sample sizes as in Table 3 except for site 1 where there were five 15 X 20 m plots.

Site	<i>n</i>	Seed-ling	Sap-ling	Under-story	Sub-canopy	Over-story	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
9	20	0	0	0	0	0	0	0
10	20	0	0	0	0	13 \pm 6	13 \pm 6	37 \pm 17

(Table 6). Sixty-six percent (57 trees) of all dead spruce at site 9 were cored and aged, and the ring-width series from 35 dead trees were successfully crossdated with a master dating series from 23 live spruce at the site (Table 6). At site 10, 74% of dead trees were in the understory (Table 3), and 72% of the dead spruce in the plots were still standing (Table 6). Forty-eight percent (61 trees) of all dead spruce were cored and aged, and the ring-width series from 42 dead trees were crossdated with a master dating series from 20 live spruce at the site (Table 6). Crossdating indicated that dead standing spruce at sites 9 and 10 had been dead for 3 to 52 yr and 4 to 101 yr, respectively. Of the 137 dead spruce that could not be crossdated, 14 belonged to appearance classes beyond the range of the regressions (of appearance class versus time since death) which were based on crossdated dead trees (Table 6). These logarithmic equations made conservative estimates of time since death for trees in high (older) appearance classes, and the greatest time since death assigned to dead spruce that were not crossdated was 41 yr at site 9 and 84 yr at site 10.

At both sites 9 and 10, the distribution of estimated germination dates of crossdated dead spruce is similar to the distribution for live trees (Fig. 3a and 3b). However, the estimated germination dates for several dead trees that were not crossdated predate the earliest germination dates derived more reliably from live or crossdated dead trees (Fig. 3c). 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 provide an index of the amount of error involved in this technique and suggest that estimated germination dates for dead spruce that were not crossdated could be one or two decades in error. In the following reconstructions of past spruce density, the seven unlikely early germination dates from dead trees that were not crossdated at site 9 and the four unlikely dates at site 10 have been reassigned equally to the first two decades during which live and crossdated dead trees recruited. The error associated with poorly dated dead trees reduces the resolution of the reconstructed history of stand density at sites 8 through 10, but these reconstructions are robust for three reasons:

1. The dates of first recruitment derived from live and crossdated trees are subject primarily to errors in estimating tree age below core height, and based on the height-growth curves for harvested seedlings (Table 2) are expected to be accurate within ± 5 yr of actual first recruitment dates for the study plots. Thus the dates of stand initiation are

Table 6. Appearance classes of dead Sitka spruce at two sites. Data are the number of trees in each appearance class for which the date of death was determined by crossdating and the number for which date of death was estimated using regression equations in Table 2.

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, shelf fungus 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	Rotten stump, horizontal trunk obscured by moss	0	0	0	4
Totals		35	52	42	85

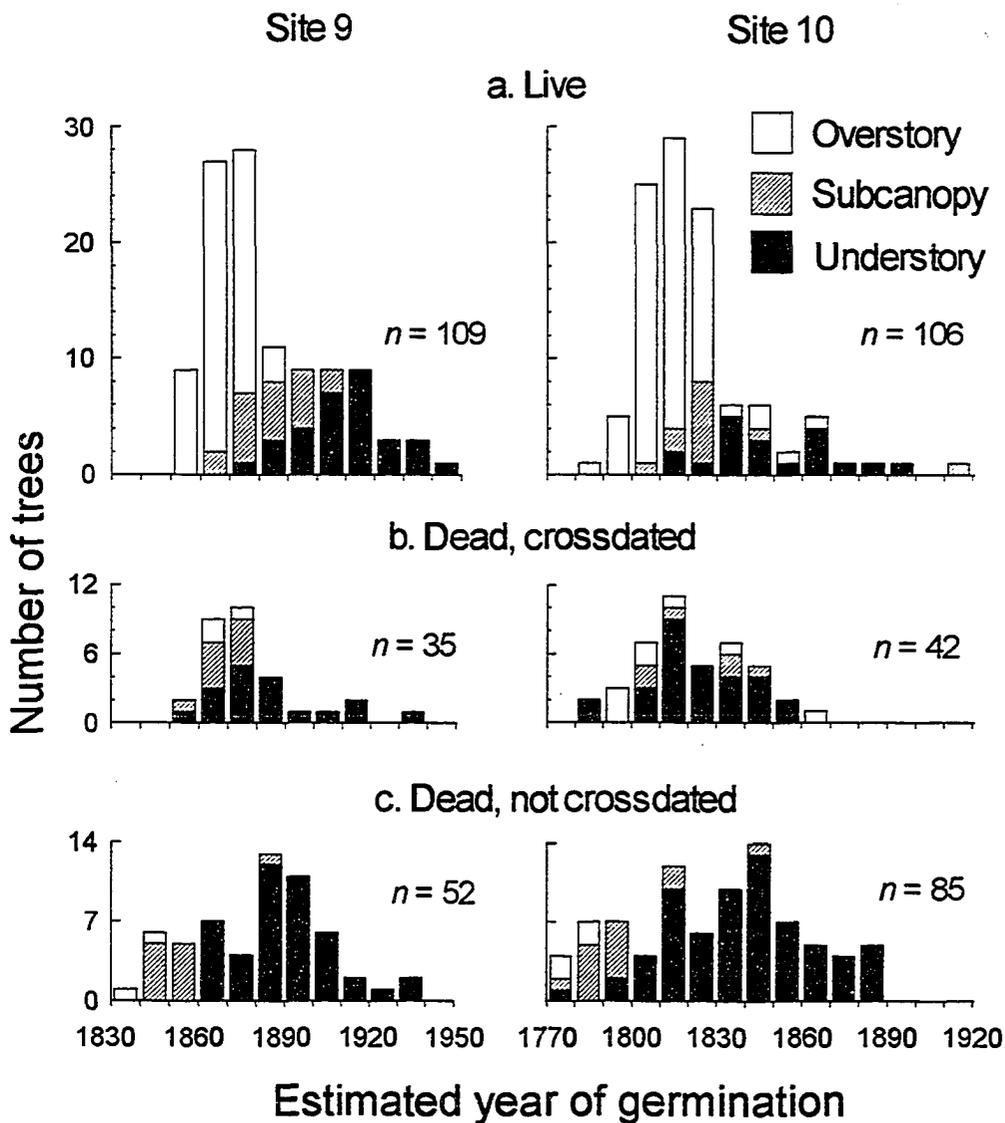


Fig. 3. Distribution of germination dates of Sitka spruce at two sites. Estimated germination dates of all spruce in sampling plots at site 9 (left) and site 10 (right) are included. (a) Live trees. (b) Dead trees that were successfully cored and crossdated. (c) Dead trees that could not be crossdated. Data are from all spruce in ten sampling plots (20 plots for live trees at site 10). The number of trees is indicated (n). The same scale is used for all graphs.

known with little error.

2. The stand density during the most recent decades is known with little error because the date of death of all recently killed trees was determined by crossdating.
3. Although the dates of germination and death of 11, 27 and 37% of the spruce at sites 8, 9, and 10, respectively, are poorly known, this source of error has little effect on the estimation of spruce stand density during the period of maximum density. This is because most of the poorly dated dead trees were alive for more than half of the total stand age, and therefore their lifespans must have overlapped with one another. Consequently, almost all of the living and dead spruce at each site had to be alive at the same time (the period of maximum stand density). This period is between 50 and 100 yr after recruitment began at sites 8 and 9, and between 80 and 140 yr after recruitment began at site 10. Therefore, the error associated with poorly dated dead trees affects the reconstructed stand density primarily for the first several decades after stand initiation, and for the period of rapid stand thinning at sites 9 and 10.

Because there were no dead spruce at other sites, and few dead hemlock or cottonwood at any site, all reconstructed stand densities at sites 2 through 7, and reconstructed densities of hemlock at all sites, are expected to be within about 5% of actual values for the sampling plots.

Initial recruitment of Sitka spruce at sites 9 and 10 continued for approximately 100 yr (Fig. 4). 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. 4, Table 3). At site 8 the establishment of subcanopy and overstory trees followed a pattern similar to sites 9 and 10, but the subsequent period of understory recruitment was much reduced compared to sites 9 and 10 (Fig. 4). Subsequent thinning by death of these understory trees was proportionally reduced, and the current stand density of spruce at site 8 is intermediate between sites 9 and 10. The small number of saplings (Table 3) and young trees (Fig. 3, data not shown for site 8) indicates that there has been negligible recruitment of spruce trees in the past 50 to 100 yr at sites 8, 9, or 10. Although spruce seedlings are abundant at these sites (Table 3), 72 to 100% are less than 20 cm tall and probably represent continued establishment of seedlings that fail to recruit to sapling size. Live spruce seedlings and saplings (Table 3) are not included in reconstructions at the oldest sites (Fig. 4) because they do not affect early stand density.

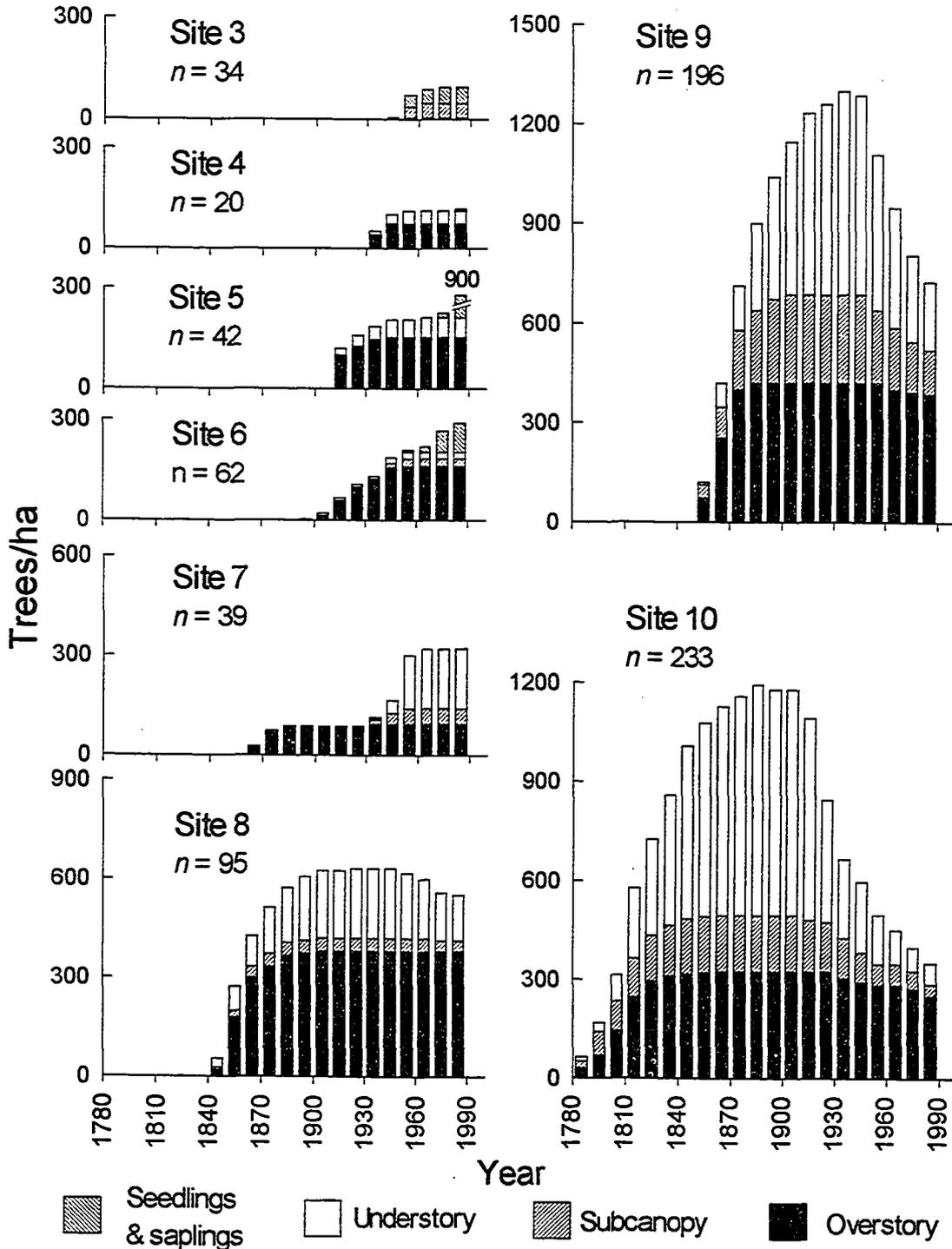


Fig 4. Stand density of Sitka spruce reconstructed by decade. Strata are the current strata of trees in sampling plots. Data are from all spruce in 10 to 20 plots at each of eight sites. The number of tree ages used in each reconstruction is indicated (n). At sites 3 to 6, the estimated germination dates of all seedlings and saplings are included in reconstructions. The same scale is used for all graphs.

At sites 3 through 7 recruitment of spruce has been substantially slower than at the three older sites (Fig. 4). For example, after five decades of spruce recruitment, stand density (including all seedlings and saplings at young sites) is less than 36% of the density attained after five decades at 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. 5), but recruitment has been negligible at all other sites, including sites at which spruce has been establishing for 50 to 100 yr. Other than at the three oldest sites, hemlock seedlings are common only at the next younger site (site 7), although 86% of these seedlings are < 50 cm tall, indicating that substantial recruitment of hemlock did not begin at this 150 yr old site until nearly a century after the start of spruce recruitment. Thus, the early importance of western hemlock at sites 8 through 10 makes tree recruitment at these sites distinct from all younger sites.

Black cottonwood.-- Black cottonwood are abundant only at the four youngest sites where they greatly outnumber spruce (Table 5). At sites 3 and 4, cottonwood recruitment began one or two decades before spruce recruitment (Fig. 6). At site 2, cottonwood recruitment has preceded the start of spruce recruitment by four decades. At site 1, the youngest site, a density of more than 1000 cottonwood seedlings/ha suggests that this species will be at least as important as it is at sites 2 through 4. At sites 5 through 10, however, 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 through 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, respectively, older than site 4, insufficient time for nearly 200 trees per ha to have deteriorated beyond detection at sites 5 and 6.

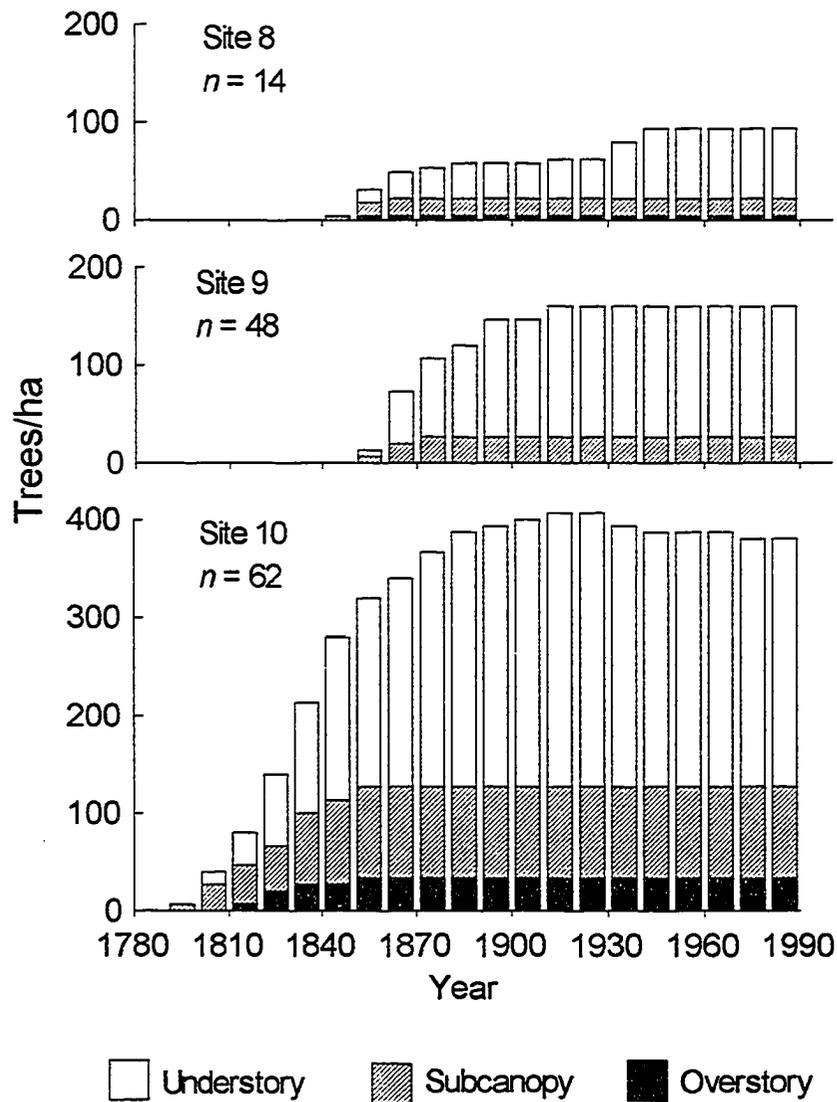


Fig. 5. Stand density of western hemlock reconstructed by decade. Hemlock trees were present in sampling plots only at these three sites. Strata are the current strata of trees in sampling plots. Data are from cored trees in ten sampling plots per site. The number of tree ages used in reconstructions is indicated (n). The same scale is used for all graphs.

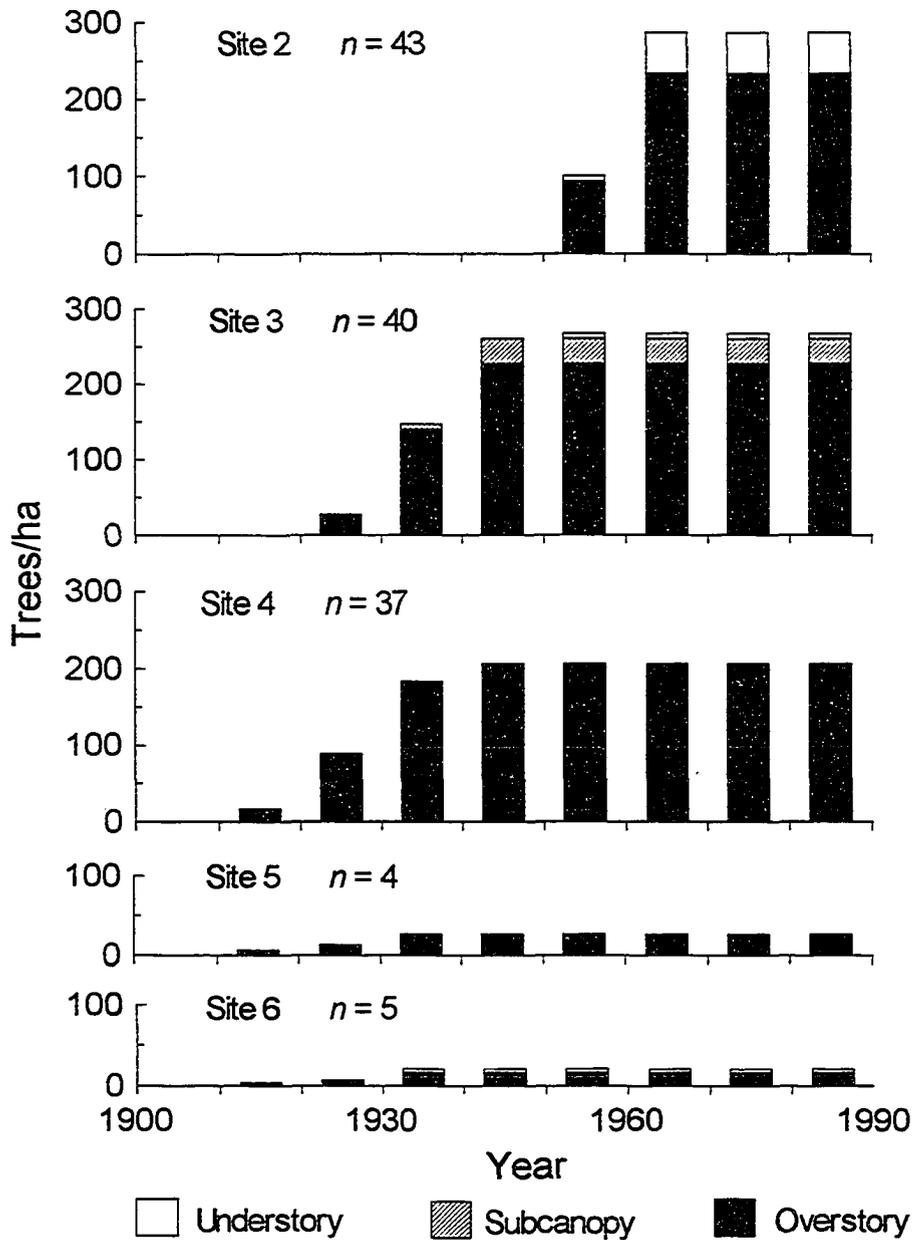


Fig. 6. Stand density of black cottonwood reconstructed by decade. Strata are the current strata of trees in sampling plots. Subcanopy trees have recently begun to emerge above an alder canopy. Data are from living trees in ten sampling plots per site (12 plots at site 4). The number of tree ages used in each reconstruction is indicated (n). At sites 4 and 5, one dead cottonwood per site (6.7 or 3.3 trees/ha, respectively) was also sampled but not included in reconstructions. At site 2, the only site at which cottonwood saplings were present, the density in the final decade would double if saplings were included in reconstructions.

Trunk radial growth and basal area

Experimental canopy gaps and ring-width releases.-- During years 2, 3, and 4 following the creation of experimental gaps in the alder canopy, the mean trunk radial growth of treatment spruce trees was significantly greater than that of control trees (Fig. 7). 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 through 7, where releases were identified in 72 to 100% of the overstory spruce (Table 7). During four years of growth in experimental canopy gaps, mean ring width in treatment trees increased by a factor of 1.9 ± 0.1 ($n = 15$ trees) compared to the five previous years. In spruce recording a natural release at sites 3 through 7, ring width increased by a factor of 2.2 ± 0.1 ($n = 5$ sites) for the same intervals. By comparison, at sites 8 through 10 only 17 to 23% of the overstory spruce record a release (Table 7). The age of release and the relative magnitude of releases at older sites are similar to releases at 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 7). The rarity of releases and the slower growth of released trees at sites 8 through 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 radial growth are recorded in ring widths near the base of four spruce trees at site 6, but not in cores taken from >4 m above the root crown of the same trees (Fig. 8). These trees grew to a height of 4 to 8 m during the decades of slow radial growth after which ring width at all heights along the trunk increased (Fig. 8). The slow radial growth recorded in these trees is associated with the period during which the trees were beneath the 5 to 7 m tall alder canopy, and the growth release is associated with their emergence above that canopy. This pattern is not present in cores of four spruce trees at site 10 in which there is little height-related difference in early ring widths (Fig. 8). This result is consistent with the hypothesis that most spruce trees at young sites are released from competition for light as they emerge above an alder

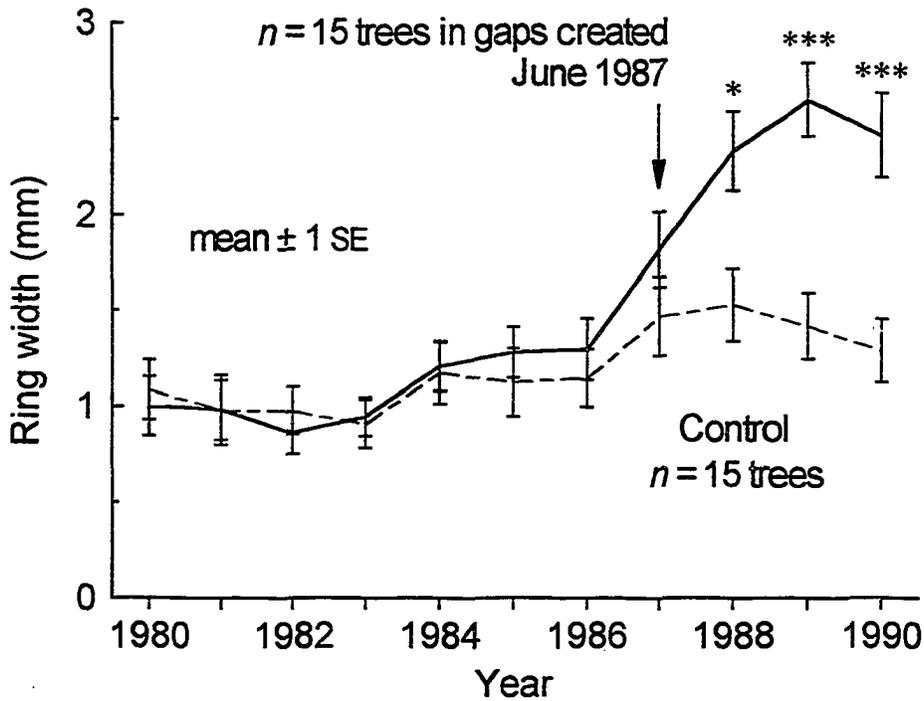


Fig 7. Ring widths of Sitka spruce in artificial gap experiment. Data are mean ring widths for four treatment yr and seven previous yr of 15 trees in experimental canopy gaps and of 15 control trees in the same thicket. Gaps were created in a thicket of Sitka alder near site 3 in June, 1987. Years in which mean ring width of treatment trees was significantly greater (by *t* test) than that of control trees are indicated (* = $P \leq .05$; *** = $P \leq .001$).

Table 7. Ring-width releases in overstory Sitka spruce at eight study sites. Sample size (n) is the number of overstory spruce released between yr 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 between young sites (3 through 7) and old sites (8 through 10) are indicated (***) = $P < .001$, NS = $P > .05$.

Site	n	% of over-story spruce with a release	Tree age at core height at start of release (yr)	Date of release (yr)	Tree diameter at start of release (cm)	Release factor	10 yr mean ring width prior to release yr (mm)	10 yr mean ring width after release yr (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	***	***

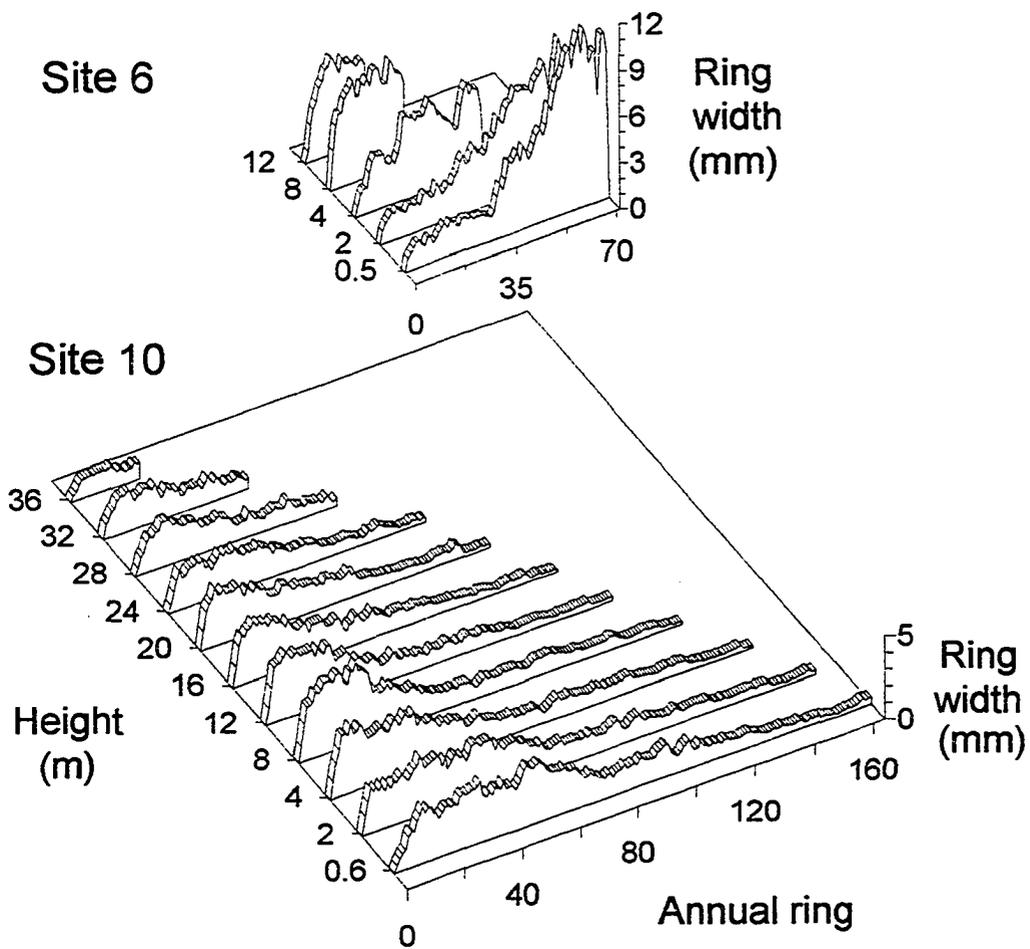


Fig. 8. Stem analysis of Sitka spruce at two sites. Data are mean annual ring width of four trees at multiple heights above the root crown at site 6 (top) and site 10 (bottom). The innermost rings (near the pith) are along the height axis to the left, and the outermost rings (near the bark) are to the right.

thicket, but that the early environment for spruce growth was very different at sites 8 through 10.

Tree basal area.-- Basal area increment (bai) of overstory spruce at sites 8 through 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 less than 40% of maximum mean bai at sites 5 through 7 (Fig. 9). Overstory spruce at sites 9 and 10 reached a maximum mean bai of $<25 \text{ cm}^2/\text{yr}$ at age 45 yr (age at core height). Bai was at least twice that rate at age 45 at sites 5 through 7 and continued to increase at those sites for at least another decade (Fig. 9). By year 65, the average overstory spruce at sites 5 and 6 had been accumulating basal area at three times the maximum average rate at any of the three oldest sites. The rapid growth in individual tree basal area at young sites is offset by substantially lower tree densities (Table 3), and sites 3 through 6 have $<50\%$ of the spruce stand basal area of the three oldest sites (Table 8). However, at site 7, where spruce density is less than half that of older sites, total basal area of spruce approaches that of the three oldest sites (Table 8). Current rates of spruce bai at sites 3 through 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 trees and contribute only 2 to 17% of the stand basal area at these sites (Table 9).

Basal area of black cottonwood is highest at site 4 (Table 10). 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 through 4 (Table 10). It is unlikely that the age difference between site 4 and sites 5 and 6 is enough time for cottonwoods constituting approximately $7 \text{ m}^2/\text{ha}$ of basal area 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 through 7 (Table 11, compare Tables 3 through 5). Sitka alder is the most common shrub species except at site 1 where young willows are abundant and alder is absent. Although the number of shrubs exceeds that of trees at sites 1 through 7, the basal area of shrubs

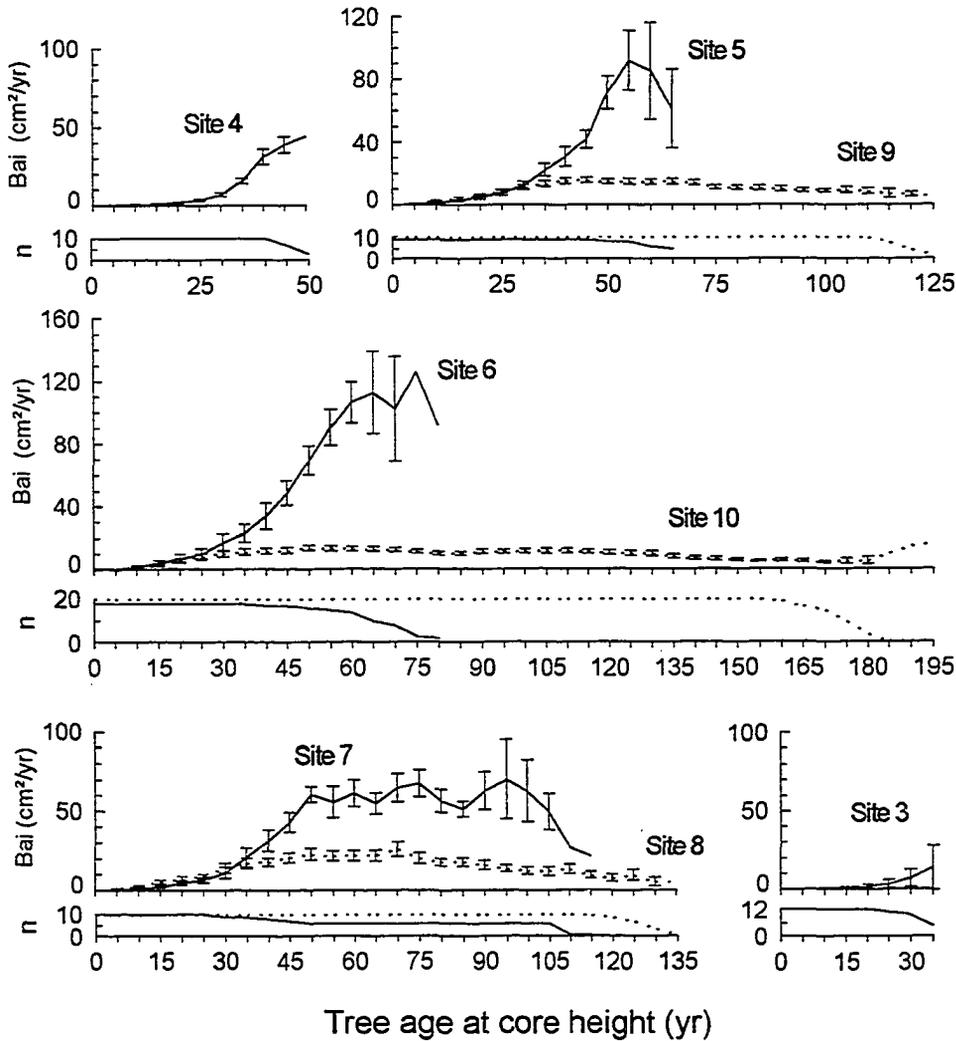


Fig 9. Basal area increment (bai) of Sitka spruce at eight sites. Data are means \pm 1 SE of five-yr plot means of annual bai of all living overstory spruce (understory spruce are included at sites 3 and 4) at each site. Sample depth (n), used for calculation of SE, is the number of sample plots with spruce of that age or older. Error bars are not shown if sample depth is 3 or fewer. Pairings of young and old sites are for graphic convenience. The same scale is used for all graphs.

Table 8. Basal area (m²/ha) of Sitka spruce at eight 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 X 15 m sampling plots per site (ten of the 20 plots at site 3 are 20 X 30 m).

Site	<i>n</i>	Live spruce				Dead spruce		
		Under-story	Sub-canopy	Over-story	Total	Under-story	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

Table 9. Basal area (m²/ha) of two hemlock species at four sites. No hemlock were encountered in plots at sites 1 through 6. Dead trees includes standing and fallen trees. Data are means \pm 1 SE. Sample size (*n*) is the number of 10 X 15 m sampling plots per site.

Site	<i>n</i>	Western hemlock				Dead trees	Mountain hemlock
		Under-story	Sub-canopy	Over-story	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 10. Basal area (m²/ha) of black cottonwood at ten sites. Dead trees includes all standing and fallen trees. Data are means \pm 1 SE. Sample size (n) is the number of 10 X 15 m plots per site (except five 15 X 20 m plots at site 1).

Site	n	Under-story	Sub-canopy	Over-story	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
9	20	0	0	0	0	0
10	20	0	0	1.8 \pm 0.8	1.8 \pm 0.8	2.3 \pm 1.0

Table 11. Stand density (plants/ha), and basal area (m²/ha) of shrubs. Data are means \pm 1 SE of ten 10 X 15 m plots at each study site (five 15 X 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.

exceeds that of trees only at sites 1 through 4 (Table 11, compare Tables 8 through 10). Shrubs reach their peak in importance at sites 2 through 4 where a thicket of alder stems and, in summer, a continuous canopy of alder foliage dominates the community. At sites 5 through 7, alder and willows are abundant and create a nearly continuous canopy between scattered trees, but the combined basal area of shrub stems does not exceed that of trees. At the three oldest sites, small, isolated alders are common in the understory, but contribute only a minor proportion to stand basal area (Table 11).

Advance of cone-bearing spruce

Sites 3 through 6 are the only sites that are young enough that their dates of exposure by deglaciation are known from historical maps or photographs but are old enough to have been invaded by spruce. At these four sites, the time lag between deglaciation and arrival of the first spruce varies from 10 to 20 yr (mean \pm 1 SD: 15.3 ± 4.3 yr, $n = 4$, Table 12). Consequently, the year of deglaciation of all older sites, for which no historical records exist, was estimated by subtracting 15 yr from the estimated date of germination of the oldest Sitka spruce cored at the site (Table 12).

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 seed cones (Fig. 10) 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 to 60 yr (mean \pm 1 SD: 52.8 ± 5.0 yr, $n = 8$) are required to attain a density of ten cone-bearing spruce/ha (Table 12). Because this reconstruction is based on tree diameter and calibrated at young sites, it could be inaccurate at the three oldest sites where early radial growth of spruce was slower than at young sites (Fig. 9). However, because tree size is more important than age in determining time of first reproduction (Harper 1977, Kramer and Kozlowski 1979), growth rate may have a minor effect on the relationship between size and the onset of reproduction. In addition, because more than 300 spruce/ha recruited during the first three decades of invasion at the three oldest sites (and the first few dozen trees probably reached reproductive size during the same decade), the reconstruction of the arrival date

Table 12. Results of reconstruction of advance of Sitka spruce at eight sites. Results include: calendar yr of ice retreat, the dates of first spruce establishment and of arrival of ten cone-bearing spruce/ha and the ice-free time required for these events, and the shortest distance from each site to sources of spruce seed at the time of ice retreat. At sites 8 through 10, there were no successional stands with ten cone-bearing spruce/ha at the time of ice retreat (NA).

Site	Date (yr A.D.) 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

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

† 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.

‡ Estimated from the mean of sites 3 through 6.

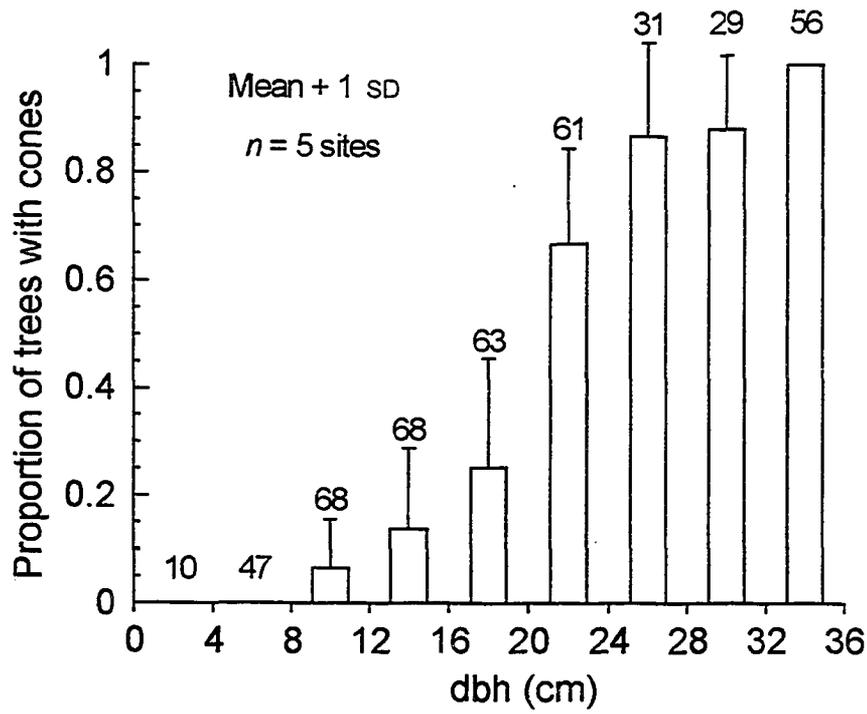


Fig 10. Proportion of Sitka spruce with seed cones. Data are means + 1 SD of five sampling areas in 4 cm dbh classes. The number of trees in each diameter class is indicated.

of only ten cone-bearing spruce/ha is not very sensitive to minor differences in size at first reproduction. Consequently, the patterns revealed by the reconstructions are probably valid.

Interpolation among reconstructed dates of arrival of ten cone-bearing spruce/ha at each site allows the advance of reproductive spruce to be mapped (Fig. 11). At the time of deglaciation of the three oldest sites (1768-1835), successional stands that were mature enough to have included ten cone-bearing spruce/ha were rare or absent on post-neoglacial surfaces. As each younger site was deglaciated, a progressively larger area of the neoglacial surface supported successional stands with cone-bearing spruce. However, stands with ten cone-bearing spruce/ha were always more than 20 km from newly exposed sites (Table 12). 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 to 75 yr. This advancing front of ten reproductive spruce/ha has moved at about the same rate as the retreating ice, 30 to 40 km/century, and remained 20 to 30 km from the ice front. 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 and the Great Lakes Basin (Davis 1981, 1983, Ritchie and MacDonald 1986). However, at Glacier Bay, this rate of advance is the same as, and could therefore have been limited by, the rate of ice retreat.

Old growth refugia

The three oldest study sites (sites 8 through 10) are within 4 km of old growth forest patches that include Sitka spruce trees more than 400 yr old (Table 12, Fig. 12). The old growth spruce stands nearest to sites 8 and 9 are at least 480 m above sea level. These forests are dominated by mountain hemlock with scattered overstory Sitka spruce which grow only below an elevation of 630 m. Ten spruce between 480 m and 630 m above sea level near sites 8 and 9 have 300-650 annual rings at breast height, and these stands include dozens of other spruce of similar size from which cores were not taken. Thus, these stands included many mature spruce that were capable of supplying seeds as sites 8 and 9 were deglaciated in the early nineteenth century. In contrast, north of site 8 the elevation of the trimline exceeds the timberline of Sitka spruce. The northernmost old

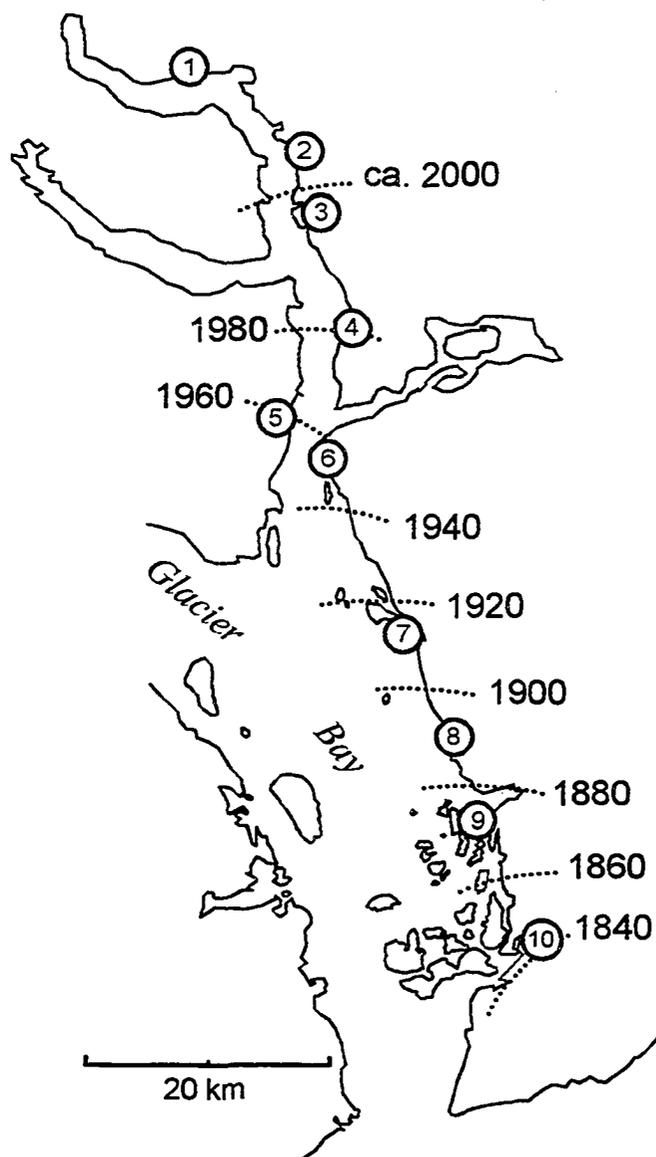


Fig. 11. The advance of reproductive Sitka spruce. Twenty-year isochrones indicate the reconstructed positions of the advancing front of a successional community of Sitka spruce with ten cone-bearing trees/ha. The locations of ten study sites between which isochrones are interpolated are also indicated (circled numbers).

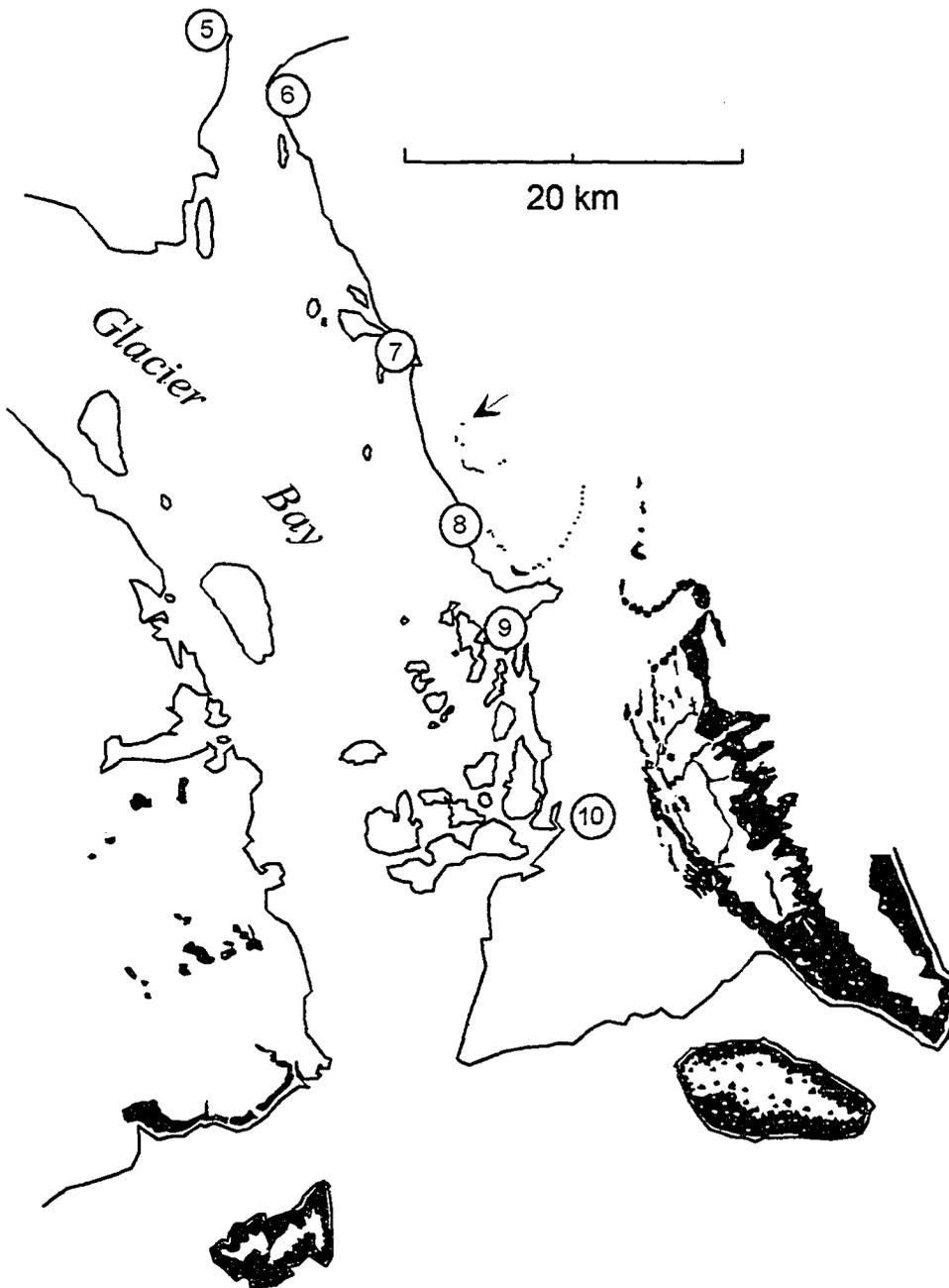


Fig. 12. Old-growth Sitka spruce forests near the mouth of Glacier Bay. Dark areas include mature stands of spruce which could have supplied seed to newly deglaciated surfaces during the eighteenth and nineteenth centuries. On the west side of the bay, only the largest forest patches are shown. The location of the northernmost forest patch visited in which an old-growth Sitka spruce was found is indicated (arrow). Locations of study sites 5 through 10 are also indicated (circles).

growth spruce found, a single tree 7.5 km south of site 7, is the nearest tree found that could have supplied spruce seeds to that site when it was deglaciated in the 1840s (Fig. 12). There are extensive old growth stands of mountain hemlock above the trimline near site 7, but no spruce or western hemlock were found in these stands. 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 old growth western hemlock, Sitka spruce, and mountain hemlock (Fig. 12). Unlike the higher elevation stands with only scattered Sitka spruce and western hemlock near sites 8 and 9, western hemlock and Sitka spruce are the dominant species in many of the stands near site 10.

Soils

There were no significant differences among sites in soil texture (except a higher silt content at site 9 than at site 6; Table 13). 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 (Table 14). 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). By contrast, site 5 has the lowest pebble count for carbonates ($6.1 \pm 0.9\%$) and the highest count for igneous pebbles ($52.6 \pm 2.2\%$; Table 14), 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 five-fold difference in carbonate pebble content among sites (Table 14) 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.

Table 13. Particle size distribution of mineral soil at nine sites. Data (% of < 2 mm fraction) are means \pm 1 SE of four or five soil pits at each site. Means within columns with the same letter (or no letter) are not significantly different ($P > .05$) by Ryan's Q which followed one-way ANOVAs (P values are indicated).

Site	n	% Sand	% Silt	% Clay
1	4	59.9 \pm 2.8	30.1 \pm 1.2 ^{ab}	10.0 \pm 2.2
3	4	67.1 \pm 2.2	29.0 \pm 2.3 ^{ab}	4.0 \pm 0.4
4	4	67.8 \pm 3.5	27.9 \pm 2.8 ^{ab}	4.2 \pm 0.9
5	5	69.5 \pm 2.7	25.6 \pm 2.2 ^{ab}	4.9 \pm 1.4
6	4	78.7 \pm 3.4	18.3 \pm 3.0 ^a	3.1 \pm 0.5
7	5	62.3 \pm 3.7	33.3 \pm 2.9 ^{ab}	4.4 \pm 1.0
8	4	68.6 \pm 1.9	28.3 \pm 1.8 ^{ab}	3.1 \pm 0.2
9	4	56.4 \pm 6.8	40.4 \pm 6.2 ^b	3.2 \pm 0.6
10	5	65.7 \pm 4.9	31.3 \pm 4.6 ^{ab}	3.1 \pm 0.7
P		0.082	0.049	0.069

Table 14. Lithological composition of pebbles at nine sites. Data (% of the > 2 mm and < 15 mm fraction) and statistics as in Table 13.

Site	n	% Carbonate	% Meta-sedimentary	% Dike rocks	% Igneous
1	4	30.0 \pm 4.4 ^a	57.8 \pm 5.3 ^a	8.4 \pm 1.7 ^a	3.8 \pm 1.3 ^d
3	4	10.0 \pm 1.4 ^{bc}	64.9 \pm 2.9 ^a	15.4 \pm 1.3 ^{ab}	9.7 \pm 1.5 ^{cd}
4	4	10.4 \pm 2.2 ^{bc}	43.0 \pm 6.3 ^{ab}	17.3 \pm 1.9 ^b	29.4 \pm 2.4 ^b
5	4	6.1 \pm 0.9 ^c	30.4 \pm 1.4 ^b	11.0 \pm 2.8 ^{ab}	52.6 \pm 2.2 ^a
6	4	12.6 \pm 1.9 ^{bc}	59.3 \pm 0.6 ^a	17.1 \pm 1.4 ^{ab}	11.0 \pm 1.6 ^{cd}
7	4	17.9 \pm 1.5 ^{ab}	56.5 \pm 2.3 ^a	15.1 \pm 2.2 ^{ab}	10.6 \pm 3.1 ^{cd}
8	4	14.0 \pm 1.8 ^{abc}	55.1 \pm 5.1 ^a	12.3 \pm 2.6 ^{ab}	18.7 \pm 3.7 ^{cb}
9	4	11.1 \pm 2.9 ^{bc}	58.0 \pm 7.2 ^a	8.7 \pm 2.0 ^{ab}	22.3 \pm 3.9 ^{cb}
10	5	18.1 \pm 2.2 ^{ab}	58.1 \pm 4.0 ^a	9.3 \pm 2.0 ^{ab}	14.6 \pm 2.1 ^{cb}
P		0.0001	0.002	0.043	0.0001

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 to 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 15). Soil texture was not a significant component of the regression models, and pebble lithology (the proportion of igneous pebbles) explains only 9 to 19% of the variance in early spruce density (Table 15). The proportion of metasedimentary pebbles was a significant variable explaining 5% of the variance in spruce density after 50 yr, but did not enter models for density at year 40 or 60. This variable was removed from the final model for year 50 because it is significantly negatively correlated with the proportion of igneous pebbles from the same soil samples ($R = -0.84$; $P = .0001$). The two independent variables remaining in each model are not intercorrelated, and diagnostics indicate no detrimental effects of multicollinearity (variance inflation factors are < 1.39). The significance of igneous pebble content in all three models (Table 15) results from its strong univariate relationship with early spruce density at the five youngest sites where spruce has invaded ($r^2 > 0.64$; $P < .001$). By 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 ($r^2 < 0.03$; $P > .37$). Thus, soil lithology is associated with spruce recruitment at the alder-dominated sites (sites 3 through 7) but cannot account for the differences in spruce recruitment between these sites and the three older sites.

DISCUSSION

The early successional dynamics at sites deglaciated since 1840 (sites 1 through 7) at Glacier Bay are substantially different from dynamics at sites deglaciated between ca. 1750 and 1840 (sites 8 through 10). Western hemlock has been an important species only at sites deglaciated prior to 1840 (Table 5). During the first five decades of recruitment,

Table 15. Results of multiple regressions. Potential predictor variables included the proximity of 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 $B = 0$. Partial R^2 indicates the proportion of variance explained by each variable. Adjusted model R^2 is computed for standardized variables.

Variable	B	P	Partial R^2	Adjusted model R^2
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	

Sitka spruce invaded surfaces older than 1840 at a rate 2.8 to 12.0 times greater than at younger sites (Fig. 4). The high initial density of spruce and hemlock at the three oldest sites indicates that initial site conditions there were different from initial conditions at younger sites.

The three oldest sites are also distinguished by a slow rate of spruce trunk radial growth (Fig. 9). Spruce at all younger sites record a contrasting pattern of accelerating growth after three to four decades of slow growth (Figs. 8 and 9). The two- to three-fold higher stand density at sites 8 through 10 (Tables 3 and 4) probably contributed to the slower radial growth of spruce trees there (Jack 1971). However, the rarity of a distinctive ring-width signature of early suppression and subsequent release at sites 8 through 10 (Fig. 8, Table 7) which is recorded in more than 72% of overstory spruce at each younger site (Table 7) and is associated with emergence of spruce crowns above a shrub canopy (Fig. 7), suggests that the dense, long-lived thickets of N-fixing alder characteristic of all young sites were absent at sites 8 through 10. Alder thickets remain important components of the community at all sites where the majority of overstory spruce record early suppression and release (sites 3 through 7), but current shrub basal area is negligible at all older sites (Table 11). Small alder stems are still common in the understory at the three oldest sites (Table 11), and many appear to grow from very old root crowns. Thus, alder was probably an early successional shrub at these old sites, but never formed a continuous shrub canopy. It is possible that dense young stands of spruce formed a closed canopy above the shorter shrubs many decades earlier than at younger sites. Of these younger sites, closure of the spruce canopy over alder thickets has begun to occur only at sites 6 and 7, which have been ice-free for 105 to 150 yr. Before sites 8 through 10 were 100 yr old, the shade of dense conifer canopies probably would have eliminated most understory alder.

During the first century of succession at young sites where alder has been the dominant plant, soil nitrogen has accumulated at rates between $1.3 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Bormann and Sidle 1990) and $2.9 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Crocker and Major 1955). Symbiotic fixation in alder root nodules is the primary source of this N (Crocker and Major 1955, Tarrant and Trappe 1971) which has been shown experimentally to have a facilitative effect on Sitka spruce seedlings (Chapin et al. in press). Alder may have been an important species at old sites for relatively few years compared to the 100 to 150 yr dominance by alder at younger sites. This difference in the importance and persistence of N-fixing shrubs could result in ecosystem-level divergence in successional processes between the young and old portions

of the Glacier Bay chronosequence. Consequently, uncritical use of the entire chronosequence to infer long-term successional trends in nutrient dynamics, soil development, or plant growth is unwarranted.

Differences in the presence of western hemlock and in the early stand density and radial growth rate of Sitka spruce delineate two distinct groups of sites on the east side of Glacier Bay. The two groups are clearly distinguished both spatially and chronologically; sites 8 through 10 (the only sites with abundant hemlock and dense, slow-growing spruce) are clustered in the southern part of the bay within 4 km of old growth forests (Fig. 12), and are also the three oldest sites (Tables 1 and 12). The differences between these two groups of sites could be a result of either a spatial environmental mosaic or a regional change occurring after succession had begun at the three oldest sites. For example, climatic amelioration during the last few decades of the nineteenth century associated with the end of the Little Ice Age (Calkin 1988, Grove 1988) could have altered initial conditions at all subsequently deglaciated sites and established the bay-length gradient in early successional dynamics. However, gradual warming attributed to the waning of the Little Ice Age was probably inadequate in magnitude, speed, and chronology to account for the dramatic successional differences between sites 7 and 9, which were deglaciated less than 10 yr apart in the 1830s and 1840s (Table 12). Although early succession at these two sites proceeded almost simultaneously, site 7 had the lowest, and site 9 the highest early spruce density of all study sites (Fig. 4). The temporal synchrony of these otherwise disparate sites suggests that the ecological differences between them are a consequence of an environmental mosaic and not a regional change occurring after succession began at site 9.

The significant relationship between rate of early spruce invasion and proximity to stands of reproductively mature spruce (Table 15) is the best available explanation for the distinct successional pathways followed at old versus young sites. Seed dispersal is the likely mechanism behind this relationship. Because conifer seed rain typically decreases exponentially with distance from a seed source (Willson 1993), a negative exponential relationship between spruce recruitment and distance to mature spruce is expected (Fig. 13). The conclusion that sites 8 through 10 are distinct from younger sites because they received substantial seed rain from nearby old growth forests is strongly supported by the fact that these are also the only sites to have been quickly invaded by western hemlock (Table 4), another old-growth forest component. However, among the three oldest sites,

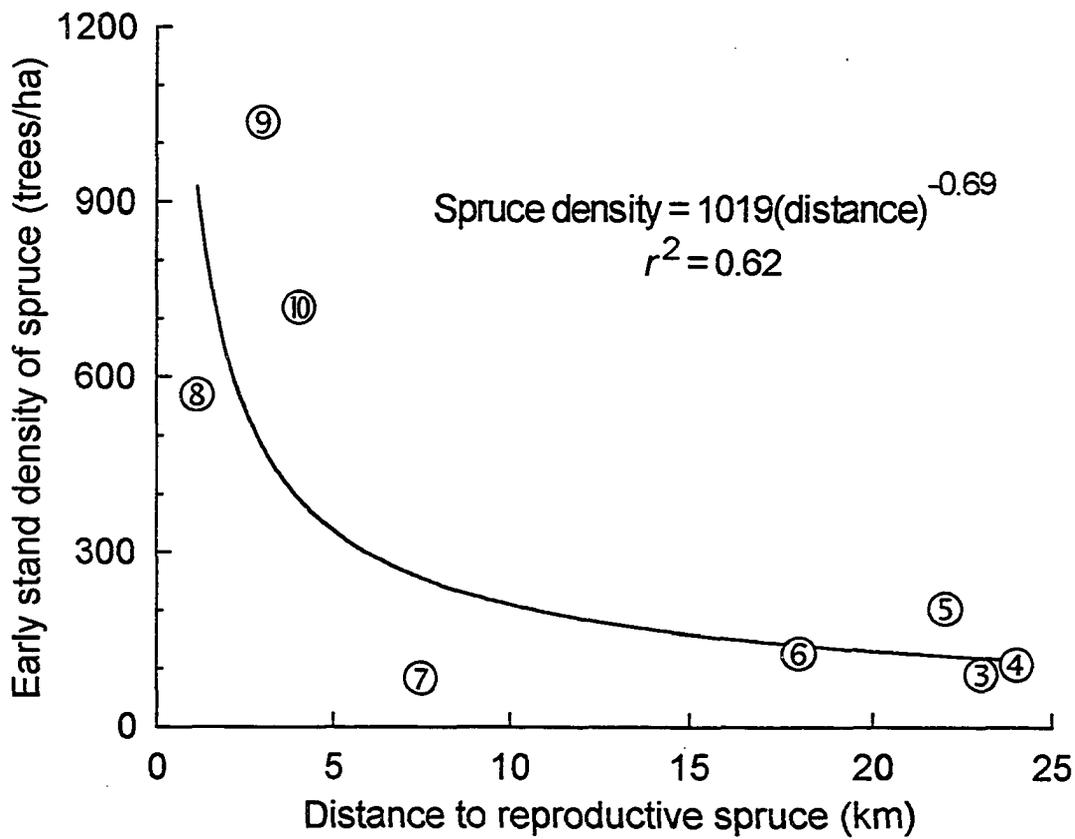


Fig 13. Early spruce density as a function of distance to reproductive spruce. Ordinate is the reconstructed stand density of Sitka spruce after 50 yr of recruitment. Site numbers are in circles. Distance for sites 3 and 4 is to the closest successional forest with ten cone-bearing spruce/ha at the time each site was deglaciated. Distance for sites 5 through 10 is to the closest refugial old growth forest with spruce.

there is much variance in spruce density that is not explained by distance to reproductive spruce (Fig. 13). This suggests that soil characteristics or unmeasured environmental factors have also affected early spruce recruitment. It is also possible that the simple linear distance to seed source used here is not a good predictor of potential seed rain. For example, the old growth forests nearest to sites 8, 9, and 10 vary greatly in elevation, areal extent (Fig. 12) and stand density of spruce, all of which affect their potential to supply seed. In addition, the greatest rate of spruce invasion occurred at sites 9 and 10 which are more than 3 km from the closest possible source of spruce seed (Fig. 13). At the time of deglaciation, these sites were separated from mature spruce forests by 3 to 4 km of either open sea water or neoglacial till and outwash (Fig. 12) that was too young to support stands of seed-producing trees (Fig. 11). Consequently, models of conifer seed dispersal, which are generally calibrated for distances of less than 300 m (Harper 1977, Greene and Johnson 1989, Okubo and Levin 1989), are inadequate to describe the early seed rain arriving at these sites. The very long-distance dispersal of spruce seeds to these sites could have been facilitated by level expanses of treeless glacial deposits or by the surface of the glacier itself, both of which could have been snow-covered during the fall and winter when spruce seeds are released, providing ideal surfaces for wind-aided dispersal (Ryvarden 1975, Glaser 1981, Matlack 1989).

Much of the recruitment of spruce at sites 8 through 10 occurred more than 30 yr after spruce recruitment had begun at each site (Fig. 4). Because Sitka spruce trees begin to produce seeds at age 30 to 50 yr (Chapin et al. in press), most of the spruce establishing 30 to 100 yr after recruitment began at these sites may be the progeny of earlier colonizing trees. However, at young sites in Muir Inlet today, by the time the first spruce trees are producing cones, the landscape is dominated by a dense alder community which strongly inhibits the establishment of spruce (Chapin et al. in press). The long period of recruitment of spruce at sites 9 and 10 (Fig. 4) indicates that the shrub community was not sufficiently developed to inhibit tree recruitment. This is further evidence that shrubs, including Sitka alder, were less important in the early stand history of sites 9 and 10 than at sites 2 through 7. Although Sitka alder was probably an important component of the scattered riparian, wetland, and disturbed habitats on the old-growth landscape surrounding the neoglacial terminal and lateral moraines 200 yr ago, spruce trees were probably much more abundant than alder, as they are today. Consequently, early seed rain to sites 8, 9, and 10 could have been more limiting to the establishment of alder than of

spruce. All younger sites are more than 7 km from old growth spruce forests (Table 12, Fig. 12), but probably received ample seed rain of alder from the successional communities on adjacent older surfaces. Alder begins to produce seeds after only 7 to 10 yr (Chapin et al. in press). This early reproduction, combined with its small seed size and rapid growth in recent glacial deposits (Chapin et al. in press), has allowed an advancing community of alder to keep pace with the rapidly retreating glacier as spruce has lagged behind. For example, in Muir Inlet today, a reproductively mature alder is within 1 km of the retreating Muir Glacier, but the closest known spruce with seed cones is more than 15 km from the ice. Thus, seed rain from old growth forests apparently allowed spruce to invade sites 8 through 10 more densely than alder, but alder's colonizing adaptations allowed new terrain to receive progressively more seeds of alder than of spruce. By the time site 7 was deglaciated, rapid colonization by alder, combined with reduced seed rain from old growth forests, greatly slowed the invasion of spruce.

Changes in seed availability to new surfaces could also explain the recent increase in the importance of black cottonwood at young sites in Muir Inlet. The communities at sites 1 through 4 represent the early stages of a third major successional pathway on the east side of Glacier Bay in which cottonwood is an important early codominant with Sitka alder. As with alder, black cottonwood occupies restricted habitats in old growth landscapes near Glacier Bay. Consequently, its early invasion of sites 8 through 10 could have been limited by seed rain. *Populus* seeds are well dispersed by wind and establish most successfully in exposed mineral soil (Walker et al. 1986), and cottonwood's success at sites 1 through 4 (Tables 5 and 8) indicate that it is capable of successful establishment and growth in early successional environments at Glacier Bay. However, because of its lack of N-fixing symbionts and presumed greater age of first reproduction, cottonwood has been less successful than alder at rapidly advancing across new terrain. It has apparently taken cottonwood longer than alder to position adequately dense, reproductively mature populations within dispersal distance of recently deglaciated surfaces. For example, by the 1840s, an alder community capable of supplying seeds to site 7 apparently had coalesced near that site, but cottonwood populations apparently were not positioned to successfully invade young sites until the early twentieth century when site 4 became ice-free. The broad, lowland surfaces of till and outwash at the mouth of Muir Inlet (surrounding sites 5 and 6) may have allowed cottonwood populations to expand, and for the first time, supply abundant seeds to younger deglaciated terrain. Alternatively, cottonwood seeds could

have reached sites 1 through 4 from sources along Lynn Canal to the east of the Glacier Bay basin.

As ice retreat has created new successional surfaces at Glacier Bay, the seed rain to those surfaces has changed for two reasons; (1) new surfaces have become progressively distant from seed sources in the refugial old growth forests clustered around the mouth of the bay (Table 12, Fig. 12), and (2) as the leading edge of successional vegetation advanced up the bay, it became the primary source of seeds for new surfaces, and gradual shifts in the composition of reproductively mature species in that community altered its seed output. For example, when the first 10 spruce/ha began to produce seeds at site 6 in the 1950s (Table 12, Fig. 11), there were fewer than 30 cottonwood/ha at the site (Table 5), and fewer still that were reproductively mature. However, when 10 spruce/ha begin to produce seeds at site 3 in the 1990s (Table 12, Fig. 11), there will be more than 200 cottonwood/ha in the overstory (Table 5), most of them mature enough to be reproductive. A landscape-scale mosaic of refugial old growth forests is therefore the ultimate cause of the multiple successional pathways at Glacier Bay, and is directly responsible for the early dominance of spruce at sites 8 through 10. A gradual reorganization of the advancing front of successional vegetation has apparently continued to drive changes in the seed rain to young surfaces and has contributed to the early importance of alder at sites 2 through 7, and to the distinct importance of cottonwood at sites 1 through 4.

CONCLUSIONS

Three successional pathways can be distinguished along the east side of Glacier Bay. Sites 8 through 10 have followed a pathway in which Sitka spruce is an important early species, and in which N-fixing Sitka alder was relatively unimportant compared to younger sites. This pathway may be responsible for nutrient dynamics during succession that are substantially different from nutrient dynamics at younger sites. There is no evidence of differences in the importance of N-fixing shrubs among sites 1 through 7, and general patterns of N accumulation during the first 150 yr of succession can probably be inferred reliably from that part of the chronosequence. However, black cottonwood is an important species only at sites 1 through 4. It is possible that these young cottonwood

stands have altered the within-stand distribution of biomass and nutrients and caused the establishment and success of Sitka spruce to differ from that at sites 5 through 7.

Therefore, inference about vegetation succession, nutrient dynamics, and soil development along the east side of Glacier Bay should be limited to very general temporal trends, or restricted to one of the three shorter chronosequences in which all sites have followed a similar pathway.

CHAPTER TWO

NUTRIENT ACCUMULATION IN SOIL AND BIOMASS

INTRODUCTION

A basic and universal feature of terrestrial primary succession is the accumulation of biomass and organic matter as plant communities develop on sites initially devoid of both. The concomitant accumulation of N in biomass and soil from levels at or near zero is a controlling force on successional changes in plant growth (Tilman 1988), community composition (Connell and Slatyer 1977), and ecosystem function (Gorham et al. 1979, Vitousek and Walker 1987). Our understanding of the long-term accumulation of N during primary succession and its relationship to successional processes has been based exclusively on studies of chronosequences of different aged sites (e.g., Crocker and Major 1955; Crocker and Dickson 1957, Olson 1958, Viereck 1966, Blundon and Dale 1990, Vitousek et al. 1992, Van Cleve et al. 1993, Walker 1993). The classic studies of the accumulation of soil N during primary succession following glacial retreat at Glacier Bay, Alaska (Crocker and Major 1955, Ugolini 1968), provided important early evidence for the presumed facilitation of late successional trees by colonizing plants that have N-fixing bacterial symbionts. These studies documented large pools of soil N at sites dominated by young communities of the N-fixing shrub Sitka alder. Recent experimental studies at Glacier Bay have confirmed a net facilitative effect of the N and organic matter added by Sitka alder on the growth of seedlings of Sitka spruce, a late-successional tree (Chapin et al. in press). However, the long-term (> 100 yr) net effects of early successional communities on late successional trees are less completely understood for Glacier Bay and for all seres because these effects can be investigated only with very long-term studies or by making inferences from chronosequences (Pickett 1989).

Studies at Glacier Bay that rely solely on inferences from the 250 yr glacial retreat chronosequence are subject to errors because succession has proceeded differently at young and old sites (Chapter 1). Dense thickets of N-fixing alder are characteristic of

young surfaces on the eastern side of Glacier Bay and have been described by all who have studied succession there (Cooper 1923a, Crocker and Major 1955, Lawrence 1958, Decker 1966, Reiners et al. 1971, Bormann and Sidle 1990, Chapin et al. in press). However, reconstructions of vegetation history indicate that long-lived shrub thickets were not important in the early history of the oldest stages of the chronosequence near the neoglacial terminal moraine at Glacier Bay (Chapter 1). Consequently, previous inferences about vegetation change, soil development, and accumulation of ecosystem N pools based on the Glacier Bay chronosequence must be reevaluated. For example, Crocker and Major (1955) found the largest pools of soil N at sites deglaciated between 1840 and 1880, and smaller pools at older sites. This pattern was interpreted as a loss of soil N after the first century of succession. However, the inferred decline in soil N could be an artifact of the early importance of N-fixing shrubs at young sites and their lesser importance at older sites. No other measurements of soil N pools have been made at sites deglaciated between 1840 and 1880. Four independent studies of soil development in glacial deposits along the east side of Glacier Bay have documented dramatic early (<70 yr) increases in organic matter and in N content of mineral and organic soil horizons, and decreases in pH and bulk density along the entire chronosequence (Crocker and Major 1955, Ugolini 1966, Bormann and Sidle 1990, Chapin et al. in press).

The objective of this study is to test whether successional changes in soil N pools inferred from the Glacier Bay chronosequence are confirmed by direct observation of changes over a 37 yr period. I repeated soil N measurements at the 1952 sampling sites of Crocker and Major (1955) and compared the actual changes to their inferred changes and to changes inferred from the modern chronosequence. In addition, I test the hypothesis that changes in soil N pools inferred from the chronosequence can be accounted for by the redistribution of N between soil and aggrading plant communities. Specifically, I test whether the late-successional decline in soil N pools inferred by Crocker and Major (1955) can be explained by plant uptake of N in late successional forests. For this test I estimated pools of N in vegetation at each site where soil N was measured.

METHODS

Study sites

The ten study sites used in this study are identical to the study sites in Chapter 1. Five of the ten study sites (sites 3, 6, 7, 9, and 10, Fig. 14) are <4 km from sites where soil was sampled in 1952 by Crocker and Major (1955) and are very similar in age, substrate, topography, and vegetation to those sites. At four of these sites, the ten permanently marked vegetation sampling plots are less than 1 km from the mapped locations of the 1952 soil sampling locations (Crocker and Major 1955). Permanent sampling plots at the oldest site (site 10) on the terminal moraine are less than 4 km from the 1952 soil sampling locations along the same moraine. Soil was collected at each of these five study sites and at the youngest site (site 1) which was still covered by glacial ice in 1952. At these six study sites, single large soil pits were excavated in the summer of 1989 adjacent to four, five, or six of the randomly located vegetation plots. Thus, soil samples were collected from at least four replicate pits located throughout 6 to 10 ha areas at each of the six sites.

Soil nutrient pools

Each of the four to six replicate soil pits at each study site was a square pit approximately 70 X 70 cm with carefully excavated vertical sides. The length of each side was measured at the top and bottom of the pit. One to three organic horizons and four to six mineral horizons were excavated separately from each pit at the five sites previously sampled in 1952. At the youngest site (site 1), only 3 horizons were sampled. Horizons were distinguished by changes in organic matter content and color, and the depth of each horizon was measured. Living moss was sampled and included with organic horizons in calculations of soil nutrient pools following Crocker and Major (1955). Pits were dug 10 to 20 cm below the level of any brown-colored B horizon to ensure sampling of all horizons containing significant N. In addition, soil was collected from immediately below the bottom of at least one pit per site to determine whether the pit extended below all

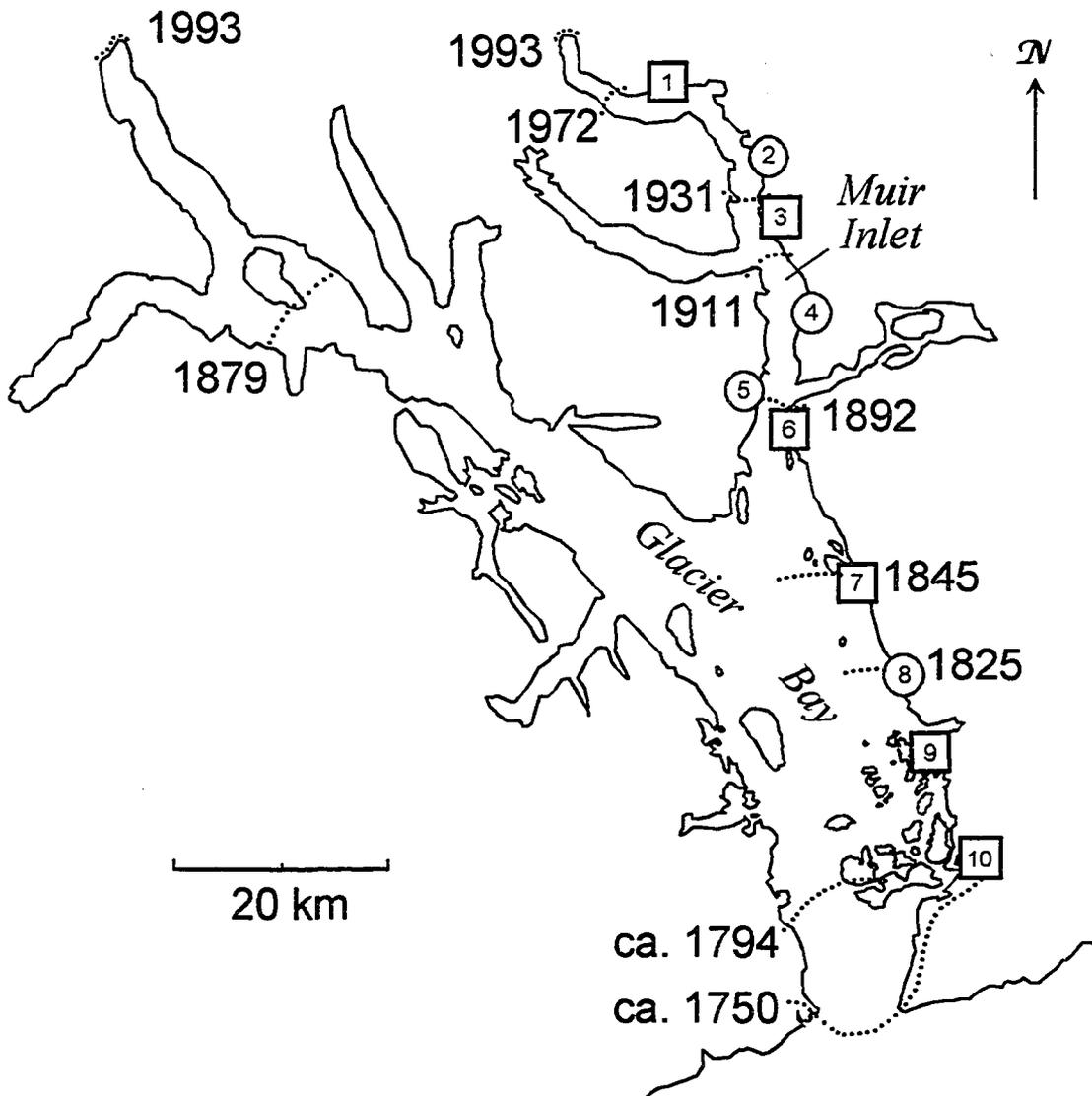


Fig. 14. Location of vegetation- and soil-sampling sites. Numbers in circles and squares are sites where vegetation sampling plots are located. Numbers in squares are sites where soil pits were excavated. Positions of glacier termini from historical maps and photographs (1794 and 1879-1993) or from dendrochronology (1750, 1825, 1845) are indicated (dotted lines).

horizons with significant N. The total depth of the sampling pits below the upper surface of mineral soil was measured at four or more locations in each pit and ranged from 19.0 ± 1.7 (site 1) to 44.4 ± 1.6 cm (site 10). This is similar to the sampling depths of Crocker and Major (1955) who reported results for a 45.7 cm profile in mineral soil, but state that sampling depths at their younger sites were "rarely below 12 in. (30 cm.)." All roots > 1 mm diameter were removed from each horizon, weighed, and a composite sample collected. Although the soil pits were always at least 2 m from large trees and therefore provided a poor sample of root crowns and large woody roots, smaller roots were well sampled, either by the separate root samples or by finer roots included in samples of the upper soil horizons. All soil from each horizon was passed through a 1.5 cm mesh screen in the field, weighed, well mixed, and large samples were collected. The dry mass of collected samples of mineral horizons averaged 914 g ($n = 121$, $SD = 607$), and samples of organic horizons averaged 83 g ($n = 33$, $SD = 61$). Samples were kept cool with icebergs or sea water in the field for up to six days until they could be frozen.

In the laboratory, samples were weighed and oven dried to constant mass (65°C) immediately following thawing, then reweighed and passed through a 2 mm screen. The fines were then weighed for calculations of dry mass of fine soil in pits. Root samples were weighed, dried and reweighed, washed free of soil, dried and reweighed again, and ground in a Wiley mill. At least two replicates from each processed sample were digested in cupric-sulfuric acid (micro-Kjeldahl method) and analyzed colorimetrically for total N (sodium salicylate method) and total P (ammonium molybdate method) using a Lachat autoanalyzer. Autoanalyzer results for total P in some mineral soil horizons were erratic, so no results for P in mineral soil are reported. Pool results are presented as means ($n = 4, 5, \text{ or } 6$ soil pits) for the O (all horizons with no obvious mineral soil content), A (dark, organic-rich mineral soil), B (brown mineral soil), C (gray, unweathered mineral soil) horizons, and roots.

Aboveground biomass

Diameter measurements of all tree and shrub stems in sampling plots described in Chapter 1 were used to estimate aboveground biomass. In addition to these diameter

measurements, the radial width of sapwood in spruce trees was measured in the field in two or three short increment cores taken at breast height from different sides of each tree. Sapwood is easily distinguished in fresh cores of Sitka spruce by its wet, translucent appearance (Bormann 1990). Heights of all cottonwood trees in the plots were measured using a clinometer. Counts were made of live canes of salmonberry (*Rubus spectabilis* Pursh) in the sampling plots. At site 1, the diameter of each mat of *Dryas drummondii* in the plots was measured.

New allometric equations relating basal diameter to aboveground biomass of Sitka willow and Sitka alder were developed from dry mass data from stems of each species harvested in July in Gustavus, Alaska, adjacent to Glacier Bay National Park (Table 16). Harvested stems were divided into leaves, stems ≤ 2 cm diameter, and stems >2 cm diameter, and all tissue was weighed in the field. Subsamples of each tissue component were weighed in the field and then oven dried to constant mass (65° C), and reweighed. No equations were available for other willow species (*S. barclayi*, *S. commutata*, and *S. alaxensis*) which together accounted for less than 5.4% of shrub basal area at each site (Chapter 1), and equations for Sitka willow were substituted. To estimate aboveground biomass from disc diameters of *Dryas*, equations were developed based on five plants that were measured and harvested at site 1, separated into leaves, stems, and flowers, and weighed after oven drying (Table 16). To estimate aboveground biomass from stem counts of salmonberry in sampling plots, the mean dry mass of leaves and stems per cane was calculated from the oven dry mass of randomly selected canes at two sites (Table 16).

Aboveground biomass of trees was estimated using equations from the literature (Table 17). The equations used for Sitka spruce, the most important tree species at the six oldest study sites (Chapter 1), were developed at sites in the northern half of southeastern Alaska, including three sites on neoglacial ice retreat surfaces similar to Glacier Bay, and a site at which spruce trees have emerged above an alder canopy (Bormann 1990). The accuracy of these equations is improved by using sapwood radial thickness as well as dbh to estimate biomass components. Bole bark mass as a percent of bole mass was estimated from an equation ($\log_e(\text{percent bark}) = 2.49 - 0.007\text{dbh}$;) that was developed from allometry of Sitka spruce in Washington, USA (Means et al. 1993). Equations used for black cottonwood, the most important tree species at the four

Table 16. Shrub biomass equations. Parameters are shown for regression equations developed to estimate dry mass of aboveground components of three shrub species. The mean dry mass of harvested salmonberry canes at two sites is also shown. Equations are of the form: $\log_e(\text{grams dry mass}) = a + b \log_e(\text{diameter in cm})$. The number (n) and disc diameter of harvested *Dryas*, and basal diameter range of harvested stems of willow or alder are indicated.

Species	Tissue	a	b	r^2	n	Range
						(cm)
<i>Dryas</i>	leaf	-4.90	2.22	0.96	5	32 - 85
	stem	-6.75	2.57	0.99		
	flower	-5.29	1.86	0.99		
Sitka willow	leaf	1.77	1.76	0.99	8	1 - 19
	stems ≤ 2 cm	3.41	1.69	0.98		
	stems > 2 cm	3.41	2.51	0.99		
Sitka alder	leaf	2.47	1.71	0.97	9	1 - 18
	stems ≤ 2 cm	4.46	1.37	0.94		
	stems > 2 cm	3.60	2.50	0.99		
salmonberry	leaf	Site		Mean dry mass		n
				(g \pm SE)		
	stem	6	10.22 \pm 1.51		10	
		7	9.00 \pm 1.51		8	
	6	35.66 \pm 8.71		10		
	7	25.95 \pm 5.37		8		

Table 17. Sources of equations used to estimate tree biomass. The region where equations were developed, biomass components estimated, and size range of trees harvested in each study are shown. The number of trees in this study (and percent of trees) exceeding the size range for each species is also indicated.

Species	Reference	Location	Biomass components estimated	dbh range (cm)	Trees exceeding dbh range and (%)
black cottonwood	Standish et al. 1985	British Columbia, Canada	bole wood, bole bark, branches >0.5 cm, branches ≤0.5cm, leaves	5.6-31.5	18 (10.8)
Sitka spruce	Bormann 1990	southeastern Alaska, USA	bole, branches, 2nd yr twigs, current yr twigs, previous yr needles, 2nd yr needles, current yr needles	3.0-77.7	4 (0.3)
western hemlock					
≤14 cm dbh	Fujimori 1971	Oregon, USA	bole, branches, needles	2.3-13.4	0
>14 cm dbh	Gholz et al. 1979	Oregon, USA	bole wood, bole bark, branch, needles, current yr needles	15.3-78.0	0

youngest study sites, were developed in British Columbia, Canada, and require measurements of tree height as well as dbh (Standish et al. 1985). The dbh of eighteen cottonwood trees in the sampling plots (10.8% of sampled cottonwoods) exceeded the range for which the biomass equations were developed (Table 17). However, most of these trees were at the four oldest study sites where cottonwood contributes less than 4% of the tree basal area, so the potential errors in estimating cottonwood biomass could have little effect on the conclusions of this study. Equations used for western hemlock were developed in eastern Oregon (Fujimori 1971, Gholz et al. 1979). Current yr twig and needle mass is not estimated for all dbh classes by these hemlock equations (Table 17), so the relationship between branch mass and the mass of current yr twigs, and the relationship between total needle mass and the mass of current yr needles was developed using data from western hemlocks harvested in southeastern Alaska (B. Bormann, unpublished data). Equations for western hemlock were used for estimating biomass of mountain hemlock which accounted for less than 1% of basal area at each site (Chapter 1).

The condition of each dead tree in sampling plots was recorded using 12 appearance classes developed for Sitka spruce at Glacier Bay (Chapter 1). This information was used to subtract components (leaves, twigs, branches, bark, or part of the trunk) from the estimated mass of each dead tree. Dead shrub stems in the sampling plots were not recorded, and no estimate was made of their mass.

Biomass nutrient pools

Tissue for nutrient analysis was collected at the study sites from four shrub species (*Dryas*, Sitka willow, Sitka alder, and salmonberry) and three tree species (black cottonwood, Sitka spruce, and western hemlock). Tissue from each species was collected at most of the study sites where that species was present. Tissue from deciduous species was collected in July and early August, and evergreen species were collected in late August and early September. Tissue types were selected to match the components estimated by the biomass equations (Tables 16 and 17). The equations for Sitka spruce estimate mass of second yr needles and twigs which were not collected for nutrient analysis, so nutrient concentrations in samples of older needles (all needles except

current yr) and of older needle-bearing twigs (all needle-bearing twigs except current yr) were substituted. Tree tissue was collected by climbing about half way into the crown of three to six widely spaced trees and removing at least two branches per tree. Each replicate sample of tree foliage, twigs, and branches is from a single tree. Each bark sample was collected from the trunk of one tree at the height of the sampled branches, and includes all living and dead tissue exterior to the xylem. Wood was sampled with an increment borer, and cores from several trees were combined in each sample. Shrub foliage was collected from five to ten plants and combined in each replicate sample. Shrub stem samples are composites of two or three branches from two or three plants.

Plant tissue was kept cool in the field and oven-dried (65° C) at the Glacier Bay National Park headquarters. Tissue was ground in a Wiley mill (20-mesh screen), digested in cupric-sulfuric acid (micro-Kjedahl method) and analyzed colorimetrically for total N (sodium salicylate method) and total P (ammonium molybdate method) using a Lachat autoanalyzer.

Aboveground biomass estimates from sampling plots were combined with tissue nutrient concentrations from each site to calculate total pools of N and P in aboveground biomass. If nutrient concentrations of a particular tissue were not measured at a site, concentrations from the closest site were substituted. Nutrient concentrations of western hemlock were used to calculate pools in mountain hemlock trees.

Statistical analyses

Among-site differences in plant tissue and soil nutrient concentrations, and in biomass and nutrient pools were identified with one-way analysis of variance followed by a modified Ryan's *Q* test to identify significant differences among sites ($P < .05$). Prior to analyses, variables were natural log transformed to minimize heteroscedasticity if their means per study site were significantly correlated with their variances. Means are presented in the text and tables \pm 1 standard error (SE), unless comparison among means is irrelevant, in which case standard deviation (SD) is used and noted. All statistical analyses were performed with SAS version 6.07 for VMS (SAS Institute Inc. 1989).

RESULTS

Soil nutrient pools

Soils collected beneath the soil pits contained very little N ($0.007 \pm 0.001\%$ N, $n = 6$ sites) and showed no consistent pattern of change with surface age. N concentration was $\leq 0.016 \pm 0.002\%$ in C horizon soil at all sites and also showed no consistent pattern with surface age (Table 18), suggesting that the soil pits were deep enough to include most soil N that accumulated during soil development. N concentration in the O horizon was highest at sites 3, 6, and 7, all of the sites at which alder is an important species (Table 18). N pools in organic horizons were also highest at these three sites and accounted for $> 50\%$ of the soil N at these sites (Fig. 15). At the four oldest sites, a thin A horizon was present (Table 18) and contained about half of the pool of N in the mineral horizons (Fig. 15). The total soil N pool was highest at site 7, the oldest site at which alder was an important early successional species (Chapter 1) and was significantly higher there than at any other site (Fig. 15).

Plant nutrient pools

The concentration of both N and P in roots was highest at site 3 where small alder roots were abundant, but the largest pools of N and P in roots were at older sites (Table 19). The continuous carpet of living moss at sites 9 and 10, and at three pits at site 7, did not contain as much N or P per unit area as the deciduous leaf litter at younger sites, most of which was alder litter (Table 19).

N concentrations in leaves and twigs of willow, cottonwood, and spruce were generally highest at site 3, a 55 yr old surface where a dense alder thicket dominates the community (Tables 20, 21, and 22). Site 3 also had the highest bark N concentrations in spruce and cottonwood trees of any site. There was less among-site variability in tissue P concentration than in N concentration (Tables 20, 21, 22, and 23), although P concentrations of most spruce and cottonwood tissues and of roots and moss were lower at site 7 than at any other site (Tables 19, 20, and 21).

At site 1, *Salix* biomass is underestimated relative to *Dryas* because only *Salix*

Table 18. Thickness and N concentration of soil horizons at six sites. Depth of the A, B, and C horizons is from the top of the mineral soil surface to the bottom of each horizon. Data are means \pm 1 SE. The number of soil pits at each site is indicated (*n*). Within horizons, N concentrations with the same letter do not differ significantly among sites ($P > .05$).

Site	<i>n</i>	Horizon	Depth (cm)	N (%)
1	4	B	12.8 \pm 1.3	0.013 \pm 0.001 ^b
		C	19.0 \pm 1.7	0.009 \pm 0.0004 ^{ab}
3	4	O	5.3 \pm 1.5	1.986 \pm 0.199 ^a
		B	17.8 \pm 2.8	0.058 \pm 0.010 ^a
		C	41.0 \pm 3.9	0.003 \pm 0.0004 ^b
6	4	O	5.0 \pm 1.2	2.127 \pm 0.056 ^a
		A	2.6 \pm 0.2	0.418 \pm 0.075 ^{ab}
		B	32.8 \pm 3.8	0.041 \pm 0.005 ^a
		C	44.6 \pm 4.1	0.012 \pm 0.002 ^a
7	6	O	16.3 \pm 2.0	1.657 \pm 0.109 ^a
		A	2.5 \pm 0.2	0.570 \pm 0.106 ^a
		B	16.7 \pm 2.0	0.052 \pm 0.003 ^a
		C	37.7 \pm 4.3	0.016 \pm 0.002 ^a
9	4	O	13.8 \pm 0.9	1.165 \pm 0.053 ^b
		A	3.0 \pm 0.6	0.641 \pm 0.107 ^a
		B	14.8 \pm 2.1	0.058 \pm 0.008 ^a
		C	42.0 \pm 3.3	0.011 \pm 0.001 ^a
10	5	O	14.5 \pm 3.0	0.819 \pm 0.073 ^c
		A	3.9 \pm 1.5	0.205 \pm 0.028 ^b
		B	28.2 \pm 2.1	0.052 \pm 0.010 ^a
		C	44.4 \pm 1.6	0.009 \pm 0.002 ^{ab}

Table 19. Nutrient concentrations and pools in moss, litter, and roots. Moss and leaf litter were collected separately from underlying organic horizons only at three of the six soil pits at site 7. Data are means \pm 1 SE, and n is the number of soil pits at each site. Nutrient concentrations or pools in roots with the same letter do not differ significantly ($P > .05$) among sites.

Site	n	Tissue	%		Pool (kg/ha)	
			N	P	N	P
3	4	litter	2.50 \pm 0.27	0.111 \pm 0.011	439 \pm 78	20 \pm 4
	4	roots	1.04 \pm 0.03 ^a	0.072 \pm 0.007 ^a	32 \pm 8 ^a	2 \pm 1 ^b
6	4	litter/moss	2.14 \pm 0.17	0.114 \pm 0.006	503 \pm 79	26 \pm 3
	4	roots	0.50 \pm 0.02 ^b	0.045 \pm 0.004 ^b	39 \pm 6 ^a	3 \pm 0.2 ^b
7	3	moss	0.75 \pm 0.04	0.070 \pm 0.003	83 \pm 3	8 \pm 1
	6	roots	0.49 \pm 0.05 ^b	0.036 \pm 0.002 ^b	83 \pm 12 ^a	6 \pm 0.4 ^{ab}
9	4	moss	0.82 \pm 0.04	0.096 \pm 0.004	86 \pm 12	10 \pm 2
	4	roots	0.25 \pm 0.02 ^c	0.050 \pm 0.002 ^b	66 \pm 12 ^a	14 \pm 4 ^a
10	5	moss	0.74 \pm 0.05	0.108 \pm 0.007	53 \pm 10	7 \pm 1
	5	roots	0.22 \pm 0.03 ^c	0.043 \pm 0.007 ^b	46 \pm 10 ^a	8 \pm 1 ^{ab}

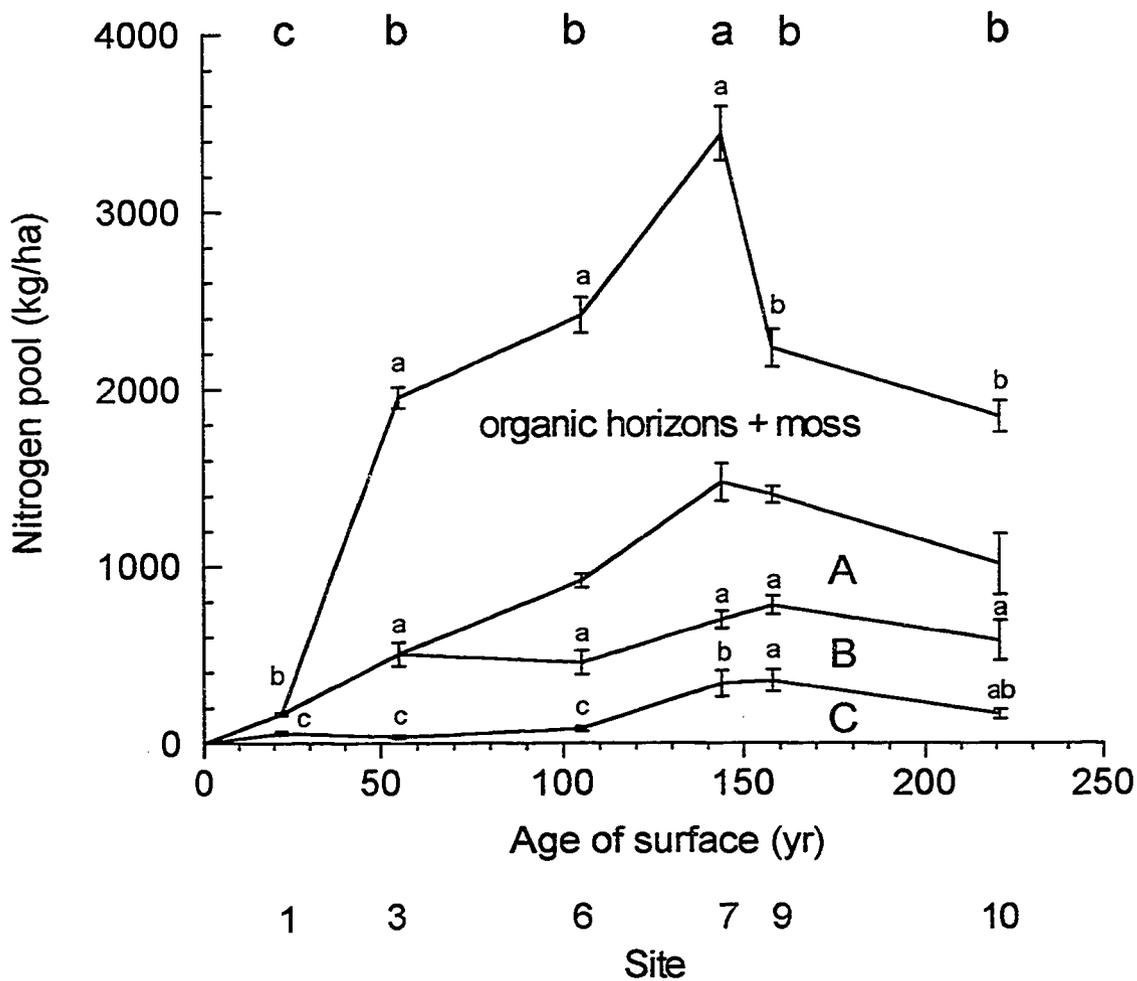


Fig 15. Total soil N pools at six sites. Pools in three mineral horizons (A, B, C) and all overlying organic horizons (including live moss) are shown. N pools in each horizon have been added to the cumulative underlying pool. Error bars are ± 1 SE of individual horizon pools ($n = 4$ to 6 soil pits/site). Within horizons, N pools topped with the same lower case letter do not differ significantly ($P > .05$) among sites (There are no among-site differences in A horizon N pools.). Total soil N pools with the same lower case letter at the top of the figure do not differ significantly ($P > .05$) among sites. This spatial pattern along the chronosequence does not represent successional change.

Table 20. Tissue N and P concentration of four shrub species. Data are means \pm 1 SE. The number of spatially separated replicate samples is indicated (n). Within tissue types, mean N or P concentrations with the same letter (or no letter) are not significantly different ($P > .05$).

Species	Tissue	Site	% nitrogen	% phosphorus	n
<i>Dryas</i>	leaf	1	1.50 \pm 0.12	0.10 \pm 0.01	3
	flower	1	1.77	0.21	1
	stem	1	0.83 \pm 0.11	0.10 \pm 0.01	3
Sitka willow	leaf	1	1.89 \pm 0.02 ^d	0.13 \pm 0.01 ^d	3
		2	3.39 \pm 0.07 ^{ab}	0.25 \pm 0.02 ^{bc}	3
		3	4.04 ^a	0.40 ^a	1
		4	3.03 \pm 0.24 ^b	0.22 \pm 0.02 ^c	2
		6	2.92 \pm 0.15 ^{bc}	0.30 \pm 0.01 ^b	4
		7	2.36 \pm 0.09 ^{cd}	0.18 \pm 0.02 ^{cb}	2
		7	2.36 \pm 0.09 ^{cd}	0.18 \pm 0.02 ^{cb}	2
	stems \leq 2 cm	1	0.38 \pm 0.04	0.07 \pm 0.02	3
		2	0.52 \pm 0.06	0.10 \pm 0.04	3
		3	0.56	0.08	1
		4	0.40 \pm 0.04	0.07 \pm 0.01	2
		6	0.43 \pm 0.07	0.06 \pm 0.01	3
		7	0.35 \pm 0.08	0.05 \pm 0.002	2
		7	0.35 \pm 0.08	0.05 \pm 0.002	2
stems $>$ 2 cm	2	0.14 \pm 0.01	0.04 \pm 0.01 ^a	2	
	6	0.14 \pm 0.01	0.01 \pm 0.002 ^b	3	
	7	0.18	0.02 ^{ab}	1	
Sitka alder	leaf	2	2.57 \pm 0.17	0.21 \pm 0.02 ^b	3
		3	2.88 \pm 0.12	0.34 \pm 0.03 ^a	3
		4	2.66 \pm 0.19	0.22 \pm 0.02 ^b	3
		6	2.56 \pm 0.10	0.21 \pm 0.02 ^b	4
		7	2.69 \pm 0.21	0.21 \pm 0.02 ^b	3
		8	2.77 \pm 0.13	0.21 \pm 0.02 ^b	3
		9	2.78 \pm 0.18	0.26 \pm 0.04 ^{ab}	3
		9	2.78 \pm 0.18	0.26 \pm 0.04 ^{ab}	3
		9	2.78 \pm 0.18	0.26 \pm 0.04 ^{ab}	3
	stems \leq 2 cm	2	0.63 \pm 0.04 ^{ab}	0.08 \pm 0.01	3
		3	0.65 \pm 0.06 ^{ab}	0.08 \pm 0.02	3
		4	0.75 \pm 0.04 ^a	0.10 \pm 0.02	3
		6	0.60 \pm 0.02 ^{ab}	0.08 \pm 0.01	4
		7	0.55 \pm 0.03 ^b	0.05 \pm 0.02	3
		8	0.62 \pm 0.03 ^{ab}	0.08 \pm 0.01	3
		9	0.55 \pm 0.03 ^b	0.05 \pm 0.00	3
		9	0.55 \pm 0.03 ^b	0.05 \pm 0.00	3
9		0.55 \pm 0.03 ^b	0.05 \pm 0.00	3	
stems $>$ 2 cm	2	0.37 \pm 0.01	0.05 \pm 0.01 ^{ab}	3	
	3	0.26 \pm 0.02	0.08 \pm 0.02 ^a	3	
	4	0.37 \pm 0.06	0.05 \pm 0.02 ^{ab}	3	
	6	0.30 \pm 0.02	0.03 \pm 0.01 ^b	4	
	9	0.27 \pm 0.01	0.03 \pm 0.00 ^{ab}	3	
salmonberry	leaf	6	1.93 \pm 0.19	0.17 \pm 0.02	3
		7	2.36 \pm 0.12	0.13 \pm 0.01	3
	stem	6	0.48 \pm 0.01 ^a	0.06 \pm 0.01	3
		7	0.72 \pm 0.07 ^b	0.04 \pm 0.00	3

Table 21. Tissue N and P concentration of black cottonwood. Data are means \pm 1 SE. The number of spatially separated replicate samples is indicated (*n*). Within tissue types, mean N or P concentrations with the same letter (or no letter) are not significantly different ($P > .05$).

Tissue	Site	% nitrogen	% phosphorus	<i>n</i>
leaf	1	1.47 \pm 0.03 ^b	0.14 \pm 0.03 ^b	3
	2	2.57 \pm 0.19 ^a	0.21 \pm 0.01 ^{ab}	3
	3	2.97 \pm 0.12 ^a	0.27 \pm 0.01 ^a	3
	4	2.27 \pm 0.16 ^a	0.24 \pm 0.02 ^a	3
	6	2.13 \pm 0.10 ^a	0.23 \pm 0.02 ^{ab}	3
	7	2.39 \pm 0.39 ^a	0.18 \pm 0.03 ^{ab}	3
	current yr twig	2	1.79 \pm 0.06 ^{ab}	0.22 \pm 0.01 ^{ab}
3		2.01 ^a	0.29 ^a	1
4		1.73 \pm 0.11 ^{ab}	0.22 \pm 0.02 ^{ab}	3
6		1.59 \pm 0.15 ^{ab}	0.20 \pm 0.02 ^{ab}	3
7		1.20 \pm 0.17 ^b	0.16 \pm 0.04 ^b	3
branches \leq 2 cm	1	0.33 \pm 0.02	0.07 \pm 0.02 ^{ab}	3
	2	0.37 \pm 0.017	0.07 \pm 0.002 ^{ab}	3
	3	0.57 \pm 0.06	0.08 \pm 0.01 ^{ab}	3
	4	0.48 \pm 0.05	0.07 \pm 0.01 ^{ab}	3
	6	0.51 \pm 0.08	0.10 \pm 0.02 ^a	3
	7	0.31 \pm 0.09	0.03 \pm 0.01 ^b	2
	branches >2 cm	3	0.20 \pm 0.02	0.04 \pm 0.01
6		0.14 \pm 0.03	0.07 \pm 0.01	2
7		0.21	0.02	1
bole wood	2	0.06 \pm 0.01	0.02 \pm 0.002	3
	3	0.07 \pm 0.01	0.01 \pm 0.001	3
	4	0.06 \pm 0.01	0.01 \pm 0.01	3
	6	0.05	0.02	1
	7	0.05 \pm 0.01	0.004 \pm 0.001	2
bole bark	2	0.49 \pm 0.15 ^{ab}	0.11 \pm 0.03	3
	3	0.69 \pm 0.07 ^a	0.12 \pm 0.02	3
	4	0.38 \pm 0.02 ^{ab}	0.08 \pm 0.02	3
	6	0.37 \pm 0.09 ^{ab}	0.09 \pm 0.02	2
	7	0.24 \pm 0.03 ^b	0.06 \pm 0.002	2

Table 22. Tissue N and P concentration of Sitka spruce. Data are means \pm 1 SE. The number of spatially separated replicate samples is indicated (*n*). Within tissue types, mean N or P concentrations with the same letter (or no letter) are not significantly different ($P > .05$).

Tissue	Site	% nitrogen	% phosphorus	<i>n</i>
current yr needles	3	1.49 \pm 0.23 ^a	0.19 \pm 0.02 ^{ab}	3
	4	1.36 \pm 0.07 ^{ab}	0.17 \pm 0.01 ^{ab}	3
	6	1.25 \pm 0.03 ^{ab}	0.19 \pm 0.02 ^{ab}	4
	7	1.04 \pm 0.05 ^c	0.11 \pm 0.004 ^c	6
	9	0.84 \pm 0.02 ^c	0.15 \pm 0.01 ^b	6
	10	1.05 \pm 0.06 ^b	0.20 \pm 0.01 ^a	4
older needles	3	1.10 \pm 0.08 ^{ab}	0.10 \pm 0.002 ^{bc}	3
	4	1.13 \pm 0.05 ^a	0.10 \pm 0.02 ^{bc}	3
	6	1.07 \pm 0.06 ^{ab}	0.11 \pm 0.01 ^{bc}	4
	7	0.89 \pm 0.05 ^{bc}	0.07 \pm 0.01 ^c	6
	9	0.77 \pm 0.02 ^c	0.16 \pm 0.02 ^{ab}	6
	10	0.97 \pm 0.06 ^{abc}	0.17 \pm 0.02 ^a	4
current yr twigs	3	1.10 \pm 0.14 ^a	0.22 \pm 0.02 ^a	3
	4	1.02 \pm 0.03 ^{ab}	0.21 \pm 0.02 ^a	3
	6	1.03 \pm 0.04 ^{ab}	0.16 \pm 0.01 ^{ab}	4
	7	0.82 \pm 0.03 ^{bc}	0.12 \pm 0.01 ^b	6
	9	0.70 \pm 0.03 ^c	0.15 \pm 0.02 ^{ab}	6
	10	0.85 \pm 0.07 ^{abc}	0.22 \pm 0.03 ^a	4
older needle-bearing twigs	3	0.47 \pm 0.03 ^{ab}	0.11 \pm 0.02	3
	4	0.44 \pm 0.08 ^{ab}	0.10 \pm 0.02	3
	6	0.57 \pm 0.04 ^a	0.13 \pm 0.02	4
	7	0.48 \pm 0.04 ^{ab}	0.10 \pm 0.02	5
	9	0.36 \pm 0.02 ^b	0.12 \pm 0.02	6
	10	0.46 \pm 0.04 ^{ab}	0.12 \pm 0.01	4
branch	3	0.19 \pm 0.03	0.03 \pm 0.01	3
	4	0.19 \pm 0.004	0.02 \pm 0.002	2
	6	0.13 \pm 0.003	0.02 \pm 0.002	4
	7	0.11 \pm 0.01	0.01 \pm 0.002	3
	9	0.13 \pm 0.02	0.02 \pm 0.004	3
	10	0.20 \pm 0.06	0.03 \pm 0.01	4
bole wood	6	0.07 \pm 0.01	0.01 \pm 0.002	4
	7	0.02 \pm 0.003	0.01 \pm 0.003	3
	8	0.05	0.01	1
	9	0.02 \pm 0.002	0.01 \pm 0.001	2
bole bark	3	0.52 \pm 0.04 ^a	0.11 \pm 0.01 ^{ab}	3
	4	0.43 \pm 0.01 ^a	0.13 \pm 0.01 ^a	3
	6	0.32 \pm 0.01 ^b	0.09 \pm 0.02 ^{ab}	3
	7	0.30 \pm 0.01 ^b	0.05 \pm 0.01 ^b	2
	8	0.15 ^c	0.07 ^{ab}	1
	9	0.25 \pm 0.18 ^b	0.06 \pm 0.01 ^b	3

Table 23. Tissue N and P concentration of western hemlock. Data are means \pm 1 SE. The number of spatially separated replicate samples is indicated (*n*). Within tissue types, mean N or P concentrations with the same letter (or no letter) are not significantly different ($P > .05$).

Tissue	Site	% nitrogen	% phosphorus	<i>n</i>
current yr needles	8	0.96 \pm 0.03	0.16 \pm 0.01	2
	9	1.01 \pm 0.07	0.21 \pm 0.03	4
	10	0.96 \pm 0.09	0.23 \pm 0.02	3
older needles	8	0.87 \pm 0.14	0.13 \pm 0.02	2
	9	1.04 \pm 0.07	0.17 \pm 0.02	4
	10	0.98 \pm 0.12	0.20 \pm 0.01	3
current yr twigs	8	0.97 \pm 0.01	0.16 \pm 0.002 ^b	2
	9	0.88 \pm 0.05	0.22 \pm 0.02 ^{ab}	4
	10	1.17 \pm 0.10	0.27 \pm 0.02 ^a	3
older needle-bearing twigs	8	0.50 \pm 0.04	0.09 \pm 0.01 ^b	3
	9	0.48 \pm 0.04	0.11 \pm 0.01 ^{ab}	3
	10	0.46 \pm 0.01	0.12 \pm 0.01 ^a	3
branch	8	0.08 \pm 0.003 ^a	0.01 \pm 0.000 ^b	2
	9	0.09 \pm 0.01 ^b	0.02 \pm 0.003 ^{ab}	3
	10	0.15 \pm 0.01 ^a	0.03 \pm 0.01 ^a	3
bole wood	8	0.05 \pm 0.01	0.01 \pm 0.001	2
	9	0.05 \pm 0.01	0.01 \pm 0.002	4
bole bark	8	0.22 \pm 0.03	0.07 \pm 0.01	2
	9	0.24 \pm 0.01	0.08 \pm 0.01	3

stems with basal diameter ≥ 1 cm were included. This does not alter the clear result that dominance by both *Dryas* and willow is short-lived (Table 24). At site 2, on a surface only 25 yr older than site 1, *Dryas* is absent and the biomass of alder is at least ten times that of willow (Table 24). Biomass of black cottonwood exceeds that of any other tree at sites 1 through 4 (Table 25), but at all older sites, Sitka spruce has the largest biomass of any tree or shrub. Western hemlock and mountain hemlock are minor components of stand biomass at the four oldest sites (Table 25). Belowground biomass estimated from roots collected in the soil pits was 6 to 12% of total stand biomass. Belowground biomass is 17 to 23% of total biomass in several temperate forest types (Ulrich et al. 1981, Vitousek et al. 1988) suggesting that 26 to 70% of root biomass was sampled in this study. This estimate does not include fine roots sampled as part of soil horizons. Because root sampling in this study was biased toward medium to fine roots which have a higher N concentration than large roots, estimates of total ecosystem N pools probably include >50% of the actual pools in belowground biomass.

Because among-site variability in tissue nutrient concentration was small compared to among-site differences in aboveground biomass, total aboveground nutrient pools followed the same general trends across the chronosequence as did biomass. Most biomass N is in alder tissue at sites 2 through 4, and in spruce at all older sites (Fig. 16). Cottonwood is a substantial component of biomass N only at sites 3 and 4 where it accounts for 20 to 25% of aboveground N. The combined N pool in willows, salmonberry, western hemlock, and mountain hemlocks never accounts for more than 15% of the aboveground biomass N at any site other than site 1 (Fig. 16). Aboveground P is also contained primarily in alder and spruce at sites 2 through 10 (Fig. 17).

Among-site differences in estimates of total ecosystem N (soil N + root N + aboveground plant N) paralleled differences in total soil N (Fig. 18). Plant N pools were consistently between 15 and 20% of total ecosystem N pools, providing no evidence for major late-successional redistributions of N pools between soil and biomass.

Table 24. Aboveground biomass of four shrub genera at ten study sites. The mass of fruiting stalks of *Dryas* is included in the total mass. The number of plots sampled at each site is indicated (*n*). Data are means \pm 1 SE. Within species and tissue types, biomass means with the same letter are not significantly different ($P > .05$).

Species	Site	<i>n</i>	Aboveground biomass (kg/ha)		
			Leaf	Stem	Total
<i>Dryas</i>	1	5	56 \pm 15	39 \pm 11	105 \pm 25
<i>Salix</i> spp.	1	5	2 \pm 0 ^{bc}	9 \pm 1 ^{bc}	11 \pm 1 ^{bc}
	2	10	178 \pm 49 ^a	3570 \pm 1045 ^a	3747 \pm 1093 ^a
	3	10	95 \pm 25 ^a	3795 \pm 1038 ^a	3891 \pm 1062 ^a
	4	10	75 \pm 30 ^{ab}	2923 \pm 1200 ^{ab}	2997 \pm 1229 ^{ab}
	5	10	201 \pm 57 ^a	8133 \pm 2264 ^a	8334 \pm 2320 ^a
	6	10	135 \pm 30 ^a	4097 \pm 873 ^a	4232 \pm 903 ^a
	7	10	6 \pm 4 ^{bc}	126 \pm 95 ^{bc}	132 \pm 99 ^{bc}
	9	10	0 \pm 0 ^c	2 \pm 2 ^c	2 \pm 2 ^c
	Sitka alder	2	10	3330 \pm 378 ^a	54981 \pm 6792 ^a
3		10	2664 \pm 135 ^a	51433 \pm 2911 ^a	54097 \pm 3045 ^a
4		10	1691 \pm 195 ^{ab}	34356 \pm 4124 ^{ab}	36047 \pm 4318 ^{ab}
5		10	741 \pm 251 ^{bc}	15169 \pm 5470 ^{ab}	15910 \pm 5721 ^{ab}
6		10	629 \pm 109 ^{bc}	12035 \pm 2058 ^{ab}	12664 \pm 2167 ^{ab}
7		10	408 \pm 115 ^c	7163 \pm 2222 ^b	7571 \pm 2337 ^b
8		10	13 \pm 7 ^c	176 \pm 92 ^d	189 \pm 99 ^d
9		10	47 \pm 15 ^d	762 \pm 253 ^c	809 \pm 267 ^c
10		10	38 \pm 20 ^{de}	597 \pm 329 ^d	634 \pm 349 ^d
salmonberry		5	10	217 \pm 89 ^a	758 \pm 311 ^a
	6	10	298 \pm 99 ^a	1039 \pm 345 ^a	1337 \pm 444 ^a
	7	10	23 \pm 9 ^b	66 \pm 24 ^b	89 \pm 33 ^b
	8	10	3 \pm 1 ^c	9 \pm 3 ^c	12 \pm 4 ^c

Table 25. Aboveground biomass of four tree species at ten study sites. The number of plots sampled at each site is indicated (*n*). Data are means \pm 1 SE. Within species and tissue types, biomass means with the same letter are not significantly different ($P > .05$).

Species	Site	<i>n</i>	Aboveground biomass (kg/ha)			
			Leaf	Branches	Bole	Total
black cottonwood	1	5	2 \pm 1 ^c	--	13 \pm 4 ^d	15 \pm 5 ^d
	2	10	513 \pm 91 ^a	1260 \pm 217 ^{ab}	1990 \pm 334 ^{ab}	3763 \pm 638 ^{ab}
	3	20	1290 \pm 201 ^a	5853 \pm 934 ^a	15652 \pm 2539 ^a	22795 \pm 3670 ^a
	4	12	1864 \pm 298 ^a	9810 \pm 1562 ^a	27878 \pm 4433 ^a	39552 \pm 6292 ^a
	5	10	555 \pm 307 ^b	3167 \pm 1704 ^{cd}	9219 \pm 4976 ^{bc}	12941 \pm 6987 ^c
	6	20	660 \pm 326 ^b	3628 \pm 1754 ^{cd}	10465 \pm 5050 ^c	14752 \pm 7129 ^c
	8	10	85 \pm 85 ^b	461 \pm 461 ^d	1330 \pm 1330 ^c	1876 \pm 1876 ^c
	10	20	181 \pm 83 ^b	1874 \pm 566 ^{bc}	5172 \pm 1591 ^{bc}	7226 \pm 2223 ^{bc}
Sitka spruce	3	20	385 \pm 301 ^c	313 \pm 271 ^c	1000 \pm 881 ^d	1698 \pm 1453 ^c
	4	12	3700 \pm 994 ^b	3197 \pm 858 ^b	9750 \pm 2871 ^c	16647 \pm 4705 ^b
	5	10	21703 \pm 5441 ^a	17377 \pm 4241 ^a	73386 \pm 18934 ^b	112465 \pm 28582 ^{ab}
	6	20	20089 \pm 2733 ^a	16244 \pm 2250 ^a	71608 \pm 10337 ^{ab}	107941 \pm 15197 ^{ab}
	7	10	43514 \pm 8736 ^a	34090 \pm 7408 ^a	207092 \pm 46540 ^{ab}	284696 \pm 62428 ^a
	8	20	48130 \pm 4361 ^a	33227 \pm 2794 ^a	295991 \pm 23207 ^a	377348 \pm 30066 ^a
	9	20	25508 \pm 2244 ^a	20776 \pm 1550 ^a	198735 \pm 12616 ^{ab}	245019 \pm 15590 ^a
	10	20	19057 \pm 2594 ^a	14736 \pm 1424 ^a	233852 \pm 18626 ^{ab}	267645 \pm 21577 ^a
western hemlock	7	10	2 \pm 2 ^c	1 \pm 1 ^c	19 \pm 19 ^c	22 \pm 22 ^c
	8	20	527 \pm 194 ^b	1493 \pm 660 ^b	6116 \pm 2359 ^b	8136 \pm 3204 ^b
	9	20	593 \pm 141 ^b	1083 \pm 254 ^b	6220 \pm 1457 ^b	7896 \pm 1845 ^b
	10	20	2729 \pm 498 ^a	7199 \pm 1550 ^a	32151 \pm 6090 ^a	42079 \pm 8110 ^a
mountain hemlock	7	10	101 \pm 101 ^b	296 \pm 296 ^b	1206 \pm 1206 ^b	1604 \pm 1604 ^b
	8	20	152 \pm 50 ^a	198 \pm 88 ^a	1484 \pm 516 ^a	1834 \pm 652 ^a
	9	20	8 \pm 8 ^b	16 \pm 16 ^b	175 \pm 175 ^b	198 \pm 198 ^b
	10	20	12 \pm 8 ^b	10 \pm 8 ^b	107 \pm 77 ^b	129 \pm 93 ^b

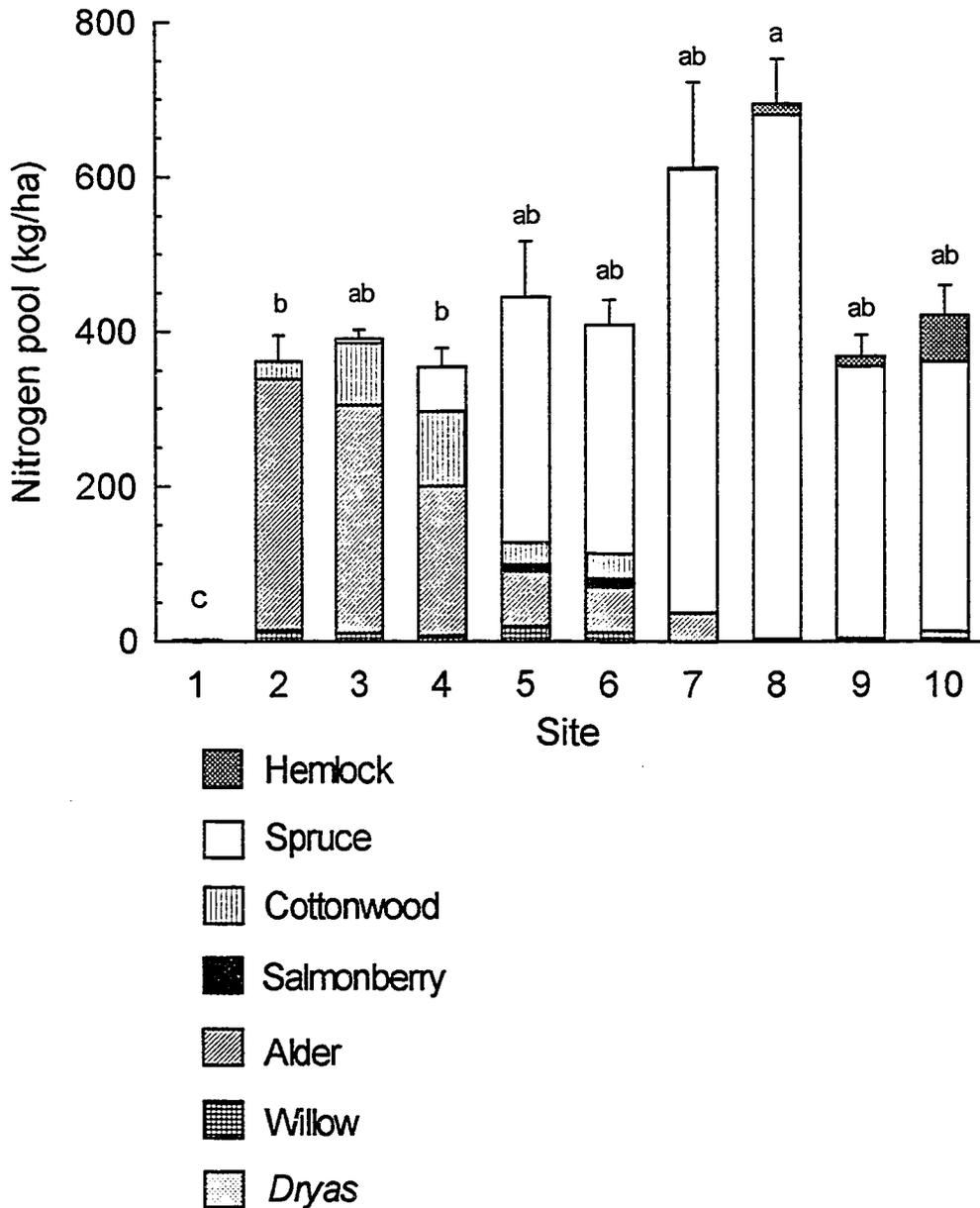


Fig 16. N pools in aboveground biomass of trees and shrubs at ten study sites. *Dryas* is present only at site 1. Hemlock includes western hemlock and mountain hemlock. Error bars are 1 SE of the total aboveground N pool. Site means of total N pool with the same letter do not differ significantly ($P > .05$). This spatial pattern across sites does not represent successional change.

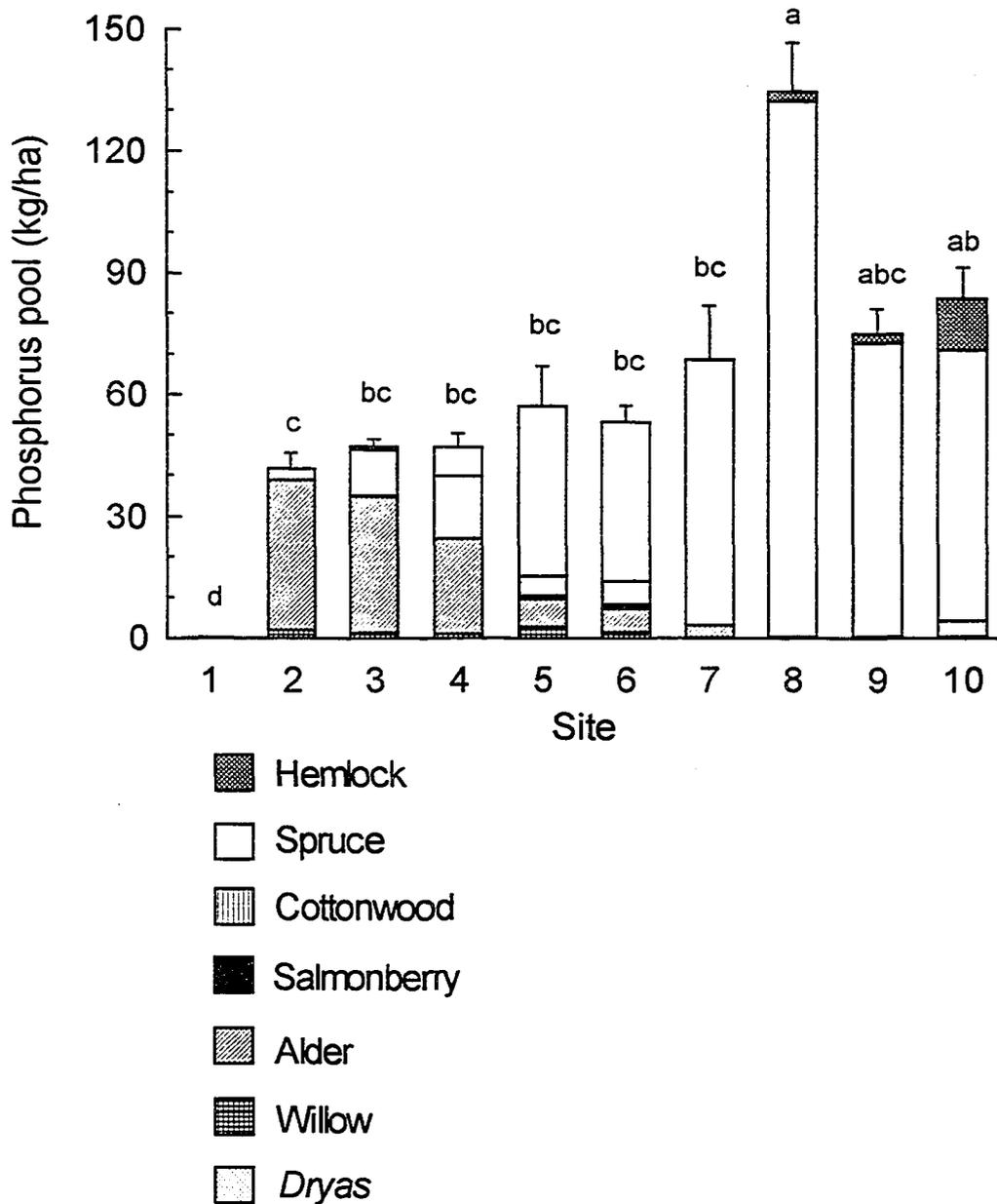


Fig 17. P pools in aboveground biomass of trees and shrubs at ten study sites. *Dryas* is present only at site 1. Hemlock includes western hemlock and mountain hemlock. Error bars are 1 SE of the total aboveground P pool. Site means of total P pool with the same letter do not differ significantly ($P > .05$). This spatial pattern across sites does not represent successional change.

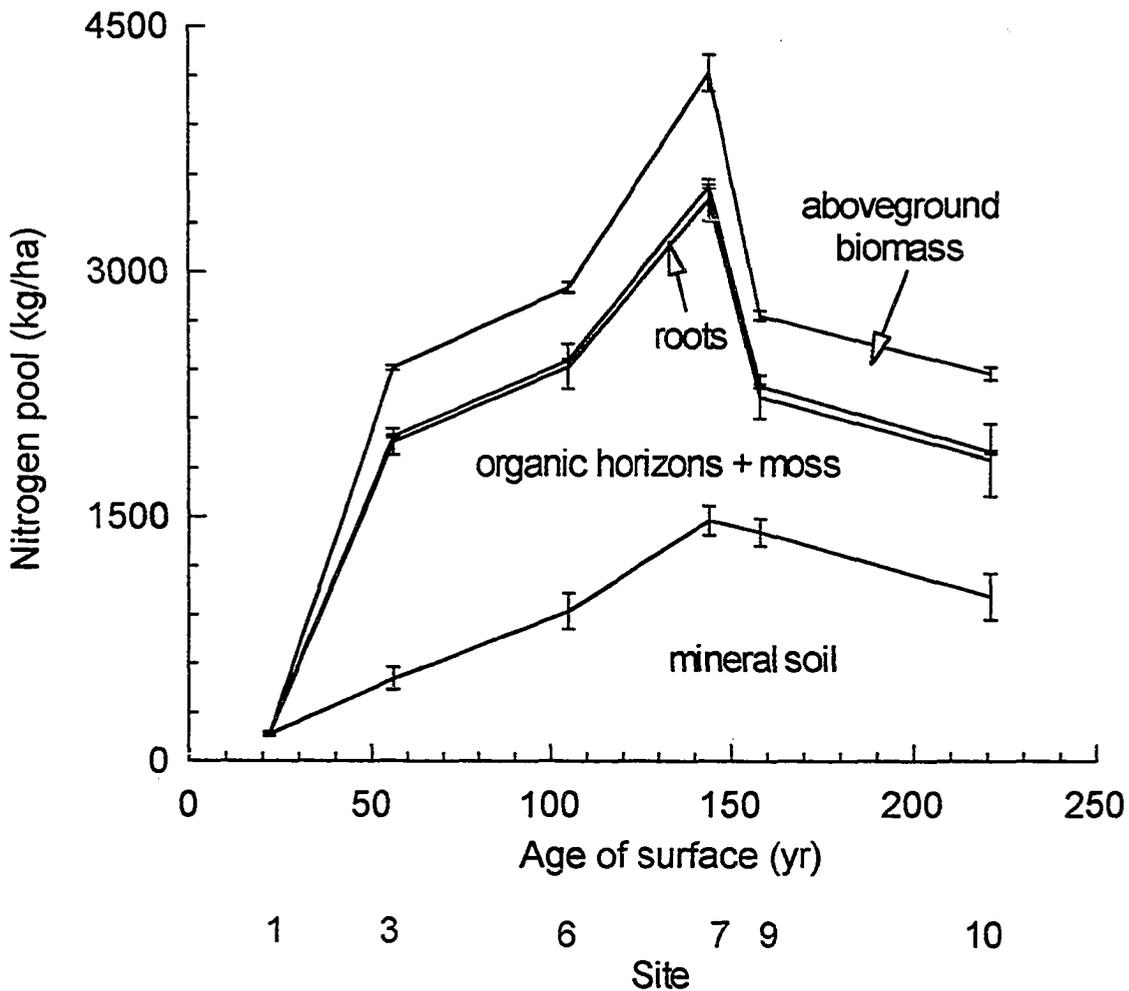


Fig 18. Total N pools in soil and biomass at six study sites. N pools in each component have been added to the cumulative underlying pool. Error bars are ± 1 SE of individual component pools ($n = 4$ to 6 pits/site for soils and roots, or 10 to 20 plots/site for vegetation). This spatial pattern across sites does not represent successional change.

DISCUSSION

At site 3, the measured increase in soil N between 1952 and 1989 is substantial (Fig. 19) and very similar to the increase inferred from the chronosequence (Crocker and Major 1955, Ugolini 1968, Bormann and Sidle 1990). The later successional decrease in soil N pools inferred from the chronosequence was not confirmed. Although the size of the N pool at site 7 was expected to decrease by about 15% to the pool size at sites 9 and 10 (Crocker and Major, 1955), it instead increased by more than 25% to a pool size larger than previously reported at any Glacier Bay site (Fig. 19). This result is consistent with the current abundance of N-fixing alder at site 7 compared to older sites, and with dendroecological stand reconstructions that indicate that N-fixing alder was an important and long-lived early successional species at site 7, but that long-lived shrub thickets were absent at all older sites (Chapter 1). This suggests that neither Crocker and Major's (1955) inferred decrease in total soil N of approximately 400 kg N/ha after age 100, nor the decrease of more than 1000 kg N/ha that could be inferred from this study, has occurred at any site. The inferred decrease is an artifact of a rapid increase in soil N at all sites where alder was an important early species (sites 3, 6, and 7), and a slower rate of N accumulation at all sites where alder was not important (sites 9 and 10, Fig. 20). The estimated N accumulation rate in soil at sites where alder is important is $3.6 \text{ g N m}^{-2} \text{ yr}^{-1}$ for the first 55 yr ($[\text{total soil N at site 3}] \div 55 \text{ yr}$), and $2.3 \text{ g N m}^{-2} \text{ yr}^{-1}$ averaged over the first 105 or 148 yr (at sites 6 or 7, respectively). Where shrub thickets have been less important, the N accumulation rates are $1.5 \text{ g N m}^{-2} \text{ yr}^{-1}$ for 153 yr (site 9), and $0.8 \text{ g N m}^{-2} \text{ yr}^{-1}$ for 221 yr (site 10).

This conclusion that soil N has accumulated more slowly at older sites is supported by results of the only two other soil N studies at Glacier Bay (Ugolini 1968, Bormann and Sidle 1990). At sites <100 yr old, three measurements by Ugolini (1968), and one measurement by Bormann and Sidle (1990) agree with the rate of soil N accumulation measured in the present study at sites where alder is important (Fig. 21). One measurement by Bormann and Sidle (1990) at a 110 yr old site where alder is important (site 6 of this study) appears to be inconsistent with the rapid N accumulation under alder (Fig. 21). However, the single 20 X 20 m plot at this site from which soil was

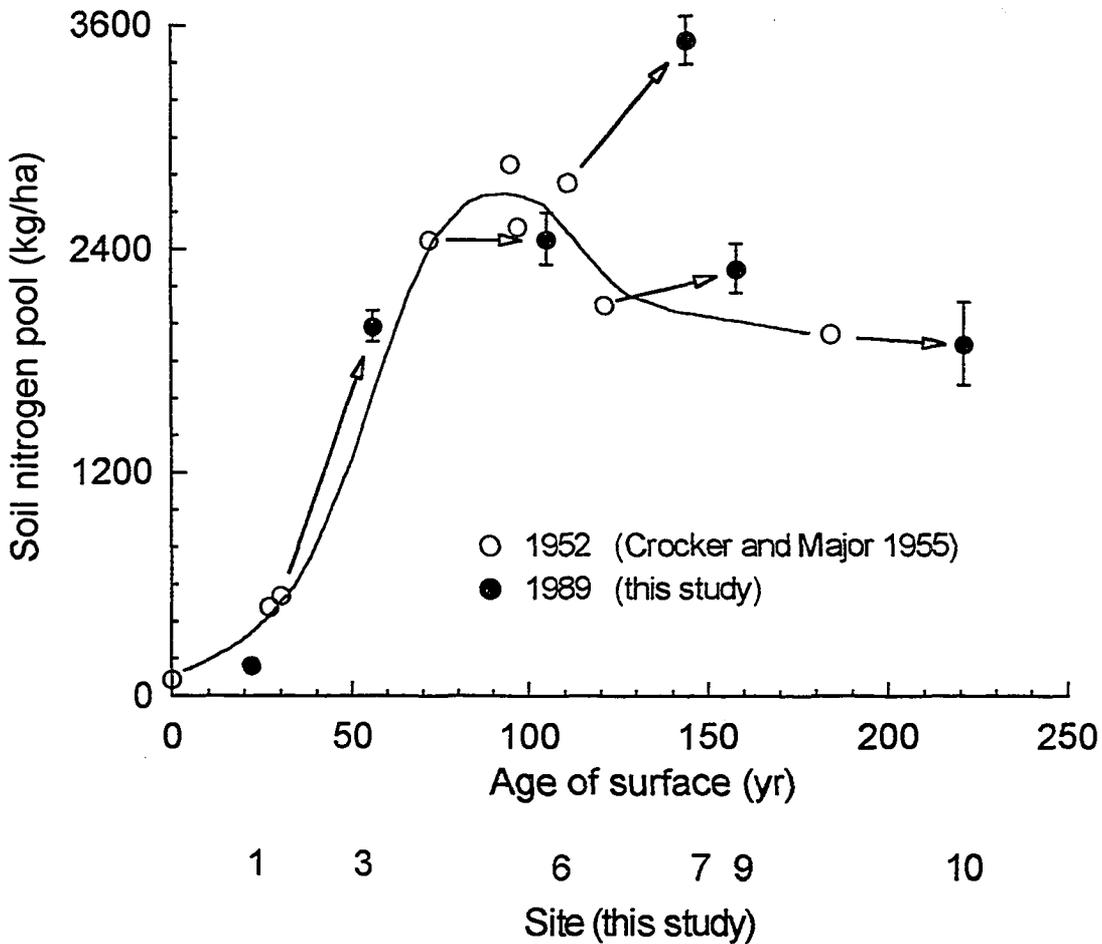


Fig 19. Total soil N at different aged sites at two times. Data are N pools in mineral plus organic soil horizons. Curved line is Crocker and Major's (1955) inference. Arrows connect measurements made at the same sites 37 yr apart. Error bars are ± 1 SE, $n = 4$ to 6 soil pits/site.

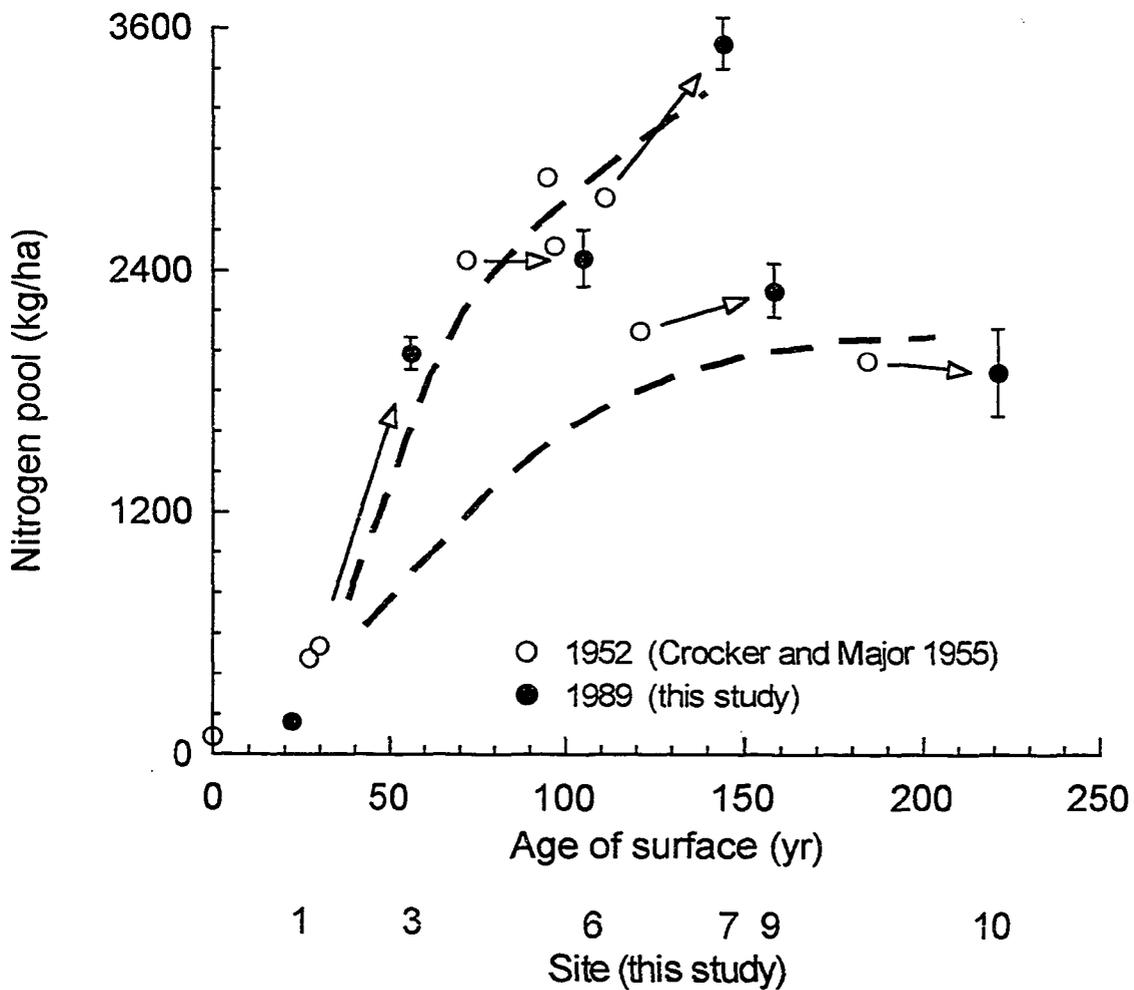


Fig 20. Two soil N accumulation curves. Each curve (dashed line) is hypothesized for a different part of the Glacier Bay chronosequence. The upper curve represents more rapid accumulation of soil N at sites where alder is an important and long-lived species in succession. The lower curve represents slower N accumulation at older sites where N-fixing shrubs have been less important. Data and symbols as in Fig. 19.

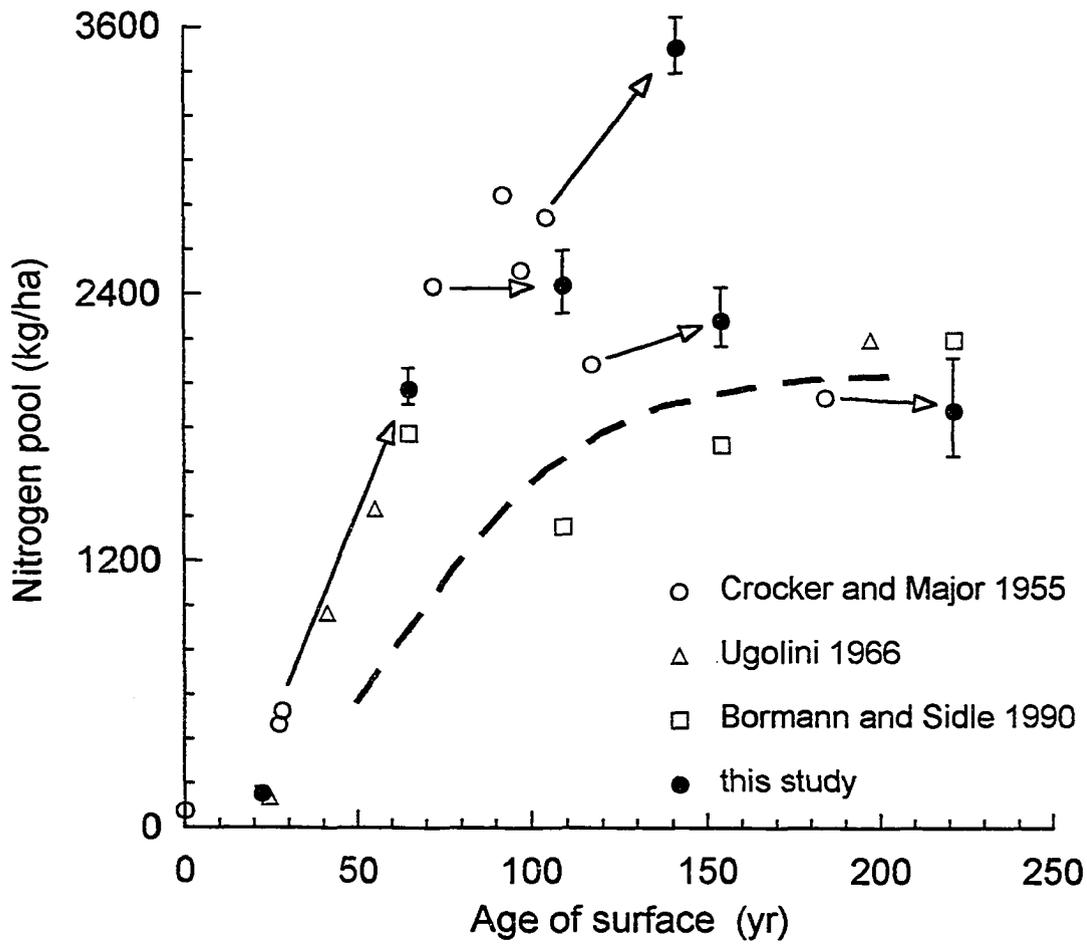


Fig 21. Total soil N pools from four independent studies at Glacier Bay. Only one of the two hypothesized N accumulation curves is shown. Data and symbols as in Figs. 19 and 20.

sampled by Bormann and Sidle is a small grove of spruce trees with a stand density higher than the current density of spruce at older sites where early shrub thickets were not important (Bormann and Sidle 1990). The distinct ring-width signature associated with emergence through a shrub thicket, which is found in 91.1% of the overstory spruce in 20 randomly located sampling plots surrounding this spruce grove (Chapter 1), is present in only 14.3% of the 21 overstory spruce in the small grove (C. Fastie unpublished). This suggests that this grove of spruce may be a young analog for the successional pathway typical of older sites at Glacier Bay where spruce invades densely and shrub thickets are short-lived, and would be the first documentation of such an analog in upper Glacier Bay. The relatively small pool of soil N measured at this site by Bormann and Sidle (1990) confirms a slower N accumulation rate in dense stands of spruce ($1.3 \text{ g N m}^{-2} \text{ yr}^{-1}$) than in adjacent stands of the same age with dense alder and scattered spruce ($2.3 \text{ g N m}^{-2} \text{ yr}^{-1}$).

There is additional evidence that the pattern of differences across the chronosequence does not represent successional change. Possible mechanisms for the inferred decrease in soil N pools from $3440 \pm 130 \text{ kg N/ha}$ at site 7 to $2233 \pm 130 \text{ kg N/ha}$ at site 9 (Fig. 18) are leaching loss, gaseous loss, and plant uptake of N. However, the inferred loss is at least an order of magnitude larger than can be explained by leaching or gaseous loss of N. Leaching of nitrate below the rooting zone of undisturbed forests is minimal (Vitousek et al. 1982), and stream loss of N in undisturbed stands rarely exceeds annual atmospheric inputs (Bormann and Likens 1979, Gosz 1981). Denitrification loss of N in undisturbed stands is also expected to be less than atmospheric inputs (Waring and Schlesinger 1985), because of low soil nitrate content and recalcitrant organic substrate (Klingensmith and Van Cleve 1993). Plant uptake cannot account for the inferred N loss between sites 7 and 9 because total plant N pools at both sites are less than half of the inferred loss (Fig 18). In addition, plant N pools at sites 9 and 10 are not larger than pools at site 7 (Fig. 16), so no inference of increasing plant N pools at the expense of soil N pools can be made. The lack of a reasonable mechanism for the inferred N loss is consistent with the conclusion that the inferred loss has not happened at any site and is an artifact of different rates of N accumulation at young and old sites at Glacier Bay.

The important differences between the successional pathways at young and old sites at Glacier Bay prohibits use of the entire 220 yr chronosequence to infer successional trends in tree growth, soil development, and the accumulation of nutrients in

soil and biomass. By excluding the oldest sites (sites 8, 9, and 10; Fig. 14), inference can be limited to that part of the chronosequence in which N-fixing shrubs have been important. However, black cottonwood is an important early tree species only at sites 1 through 4 (Chapter 1). Those young sites may differ from sites 5 through 7 in the success of Sitka spruce and in the within-stand distribution of biomass and nutrients. For example, the inferred decrease in cottonwood biomass between sites 4 and 5 (Fig. 22) has not happened at any site, but is an artifact of the increased early importance of cottonwood at sites deglaciated since 1900 (Chapter 1). It is therefore important to limit interpretation of even this shortened chronosequence to very general successional trends. For example, the pattern of succession from dominance by shrubs (mostly alder) to dominance by trees that can be inferred from this part of the chronosequence (Fig. 23) represents a general pattern of change that has happened at all of these sites. Similarly, the inferred pattern of change in N and P pools in biomass components of shrubs and trees (Figs. 24 and 25) is generally valid, although the inferred species-specific changes in nutrient pools are not (Figs. 16 and 17), because of the changed importance of cottonwood at sites deglaciated after 1900. Thus, even a shortened chronosequence including only sites where alder has been important must be interpreted with caution. Moreover, the information required to select the valid subset of chronosequence sites and to identify valid inferences from that truncated chronosequence came from an independent study of within-site successional histories (Chapter 1), and was otherwise unavailable.

Biomass accumulates faster at Glacier Bay than at primary succession sites on an interior Alaskan floodplain where there is a similar succession of dominance through *Salix*, *Alnus*, *Populus*, and *Picea* (Viereck et al. 1993). Nearly 300 Mg/ha of aboveground biomass is present after 150 yr at Glacier Bay (site 7) compared to about 200 Mg/ha in a white spruce forest of similar age on the Tanana River floodplain (Viereck et al. 1993, Yarie 1993). Soil N accumulates to about 2000 kg N/ha at age 50 to 100 yr in both Alaskan successions (Fig. 15, Walker 1989), but continues to accumulate rapidly only at Glacier Bay where 3440 ± 131 kg N/ha is present in soil after about 150 yr (Fig. 15). This difference is probably related to the different rates at which N-fixing shrubs are eliminated by the forest overstory. *Populus* and *Picea* begin to close the canopy above alder shrubs after age 75 to 100 yr on the Tanana River floodplain, but spruce are still

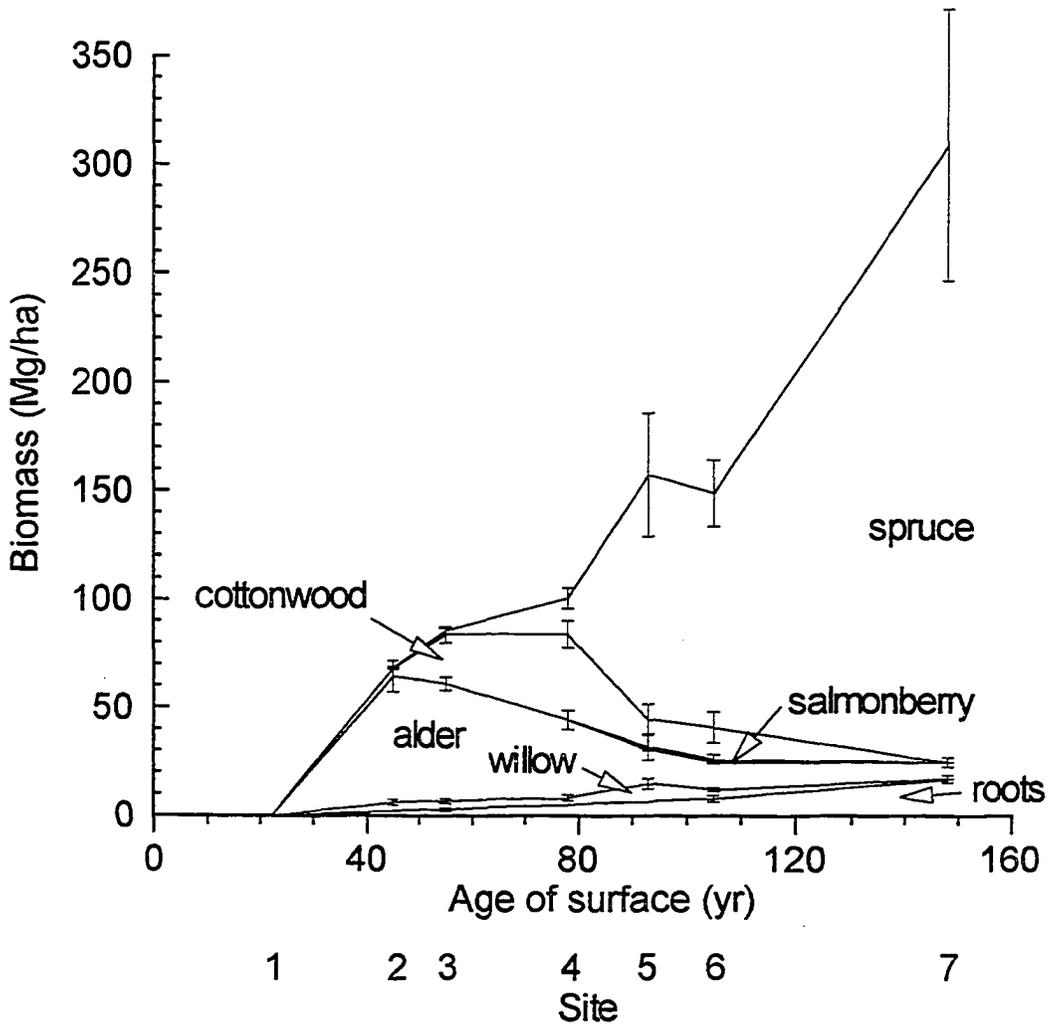


Fig. 22. Biomass of woody species at seven sites. Mass of each species is added to the cumulative pool below it. Error bars are ± 1 SE for individual species means, $n = 10$ to 20 plots/site, except $n = 4$ to 6 pits/site for roots. This spatial pattern across sites does not represent successional change.

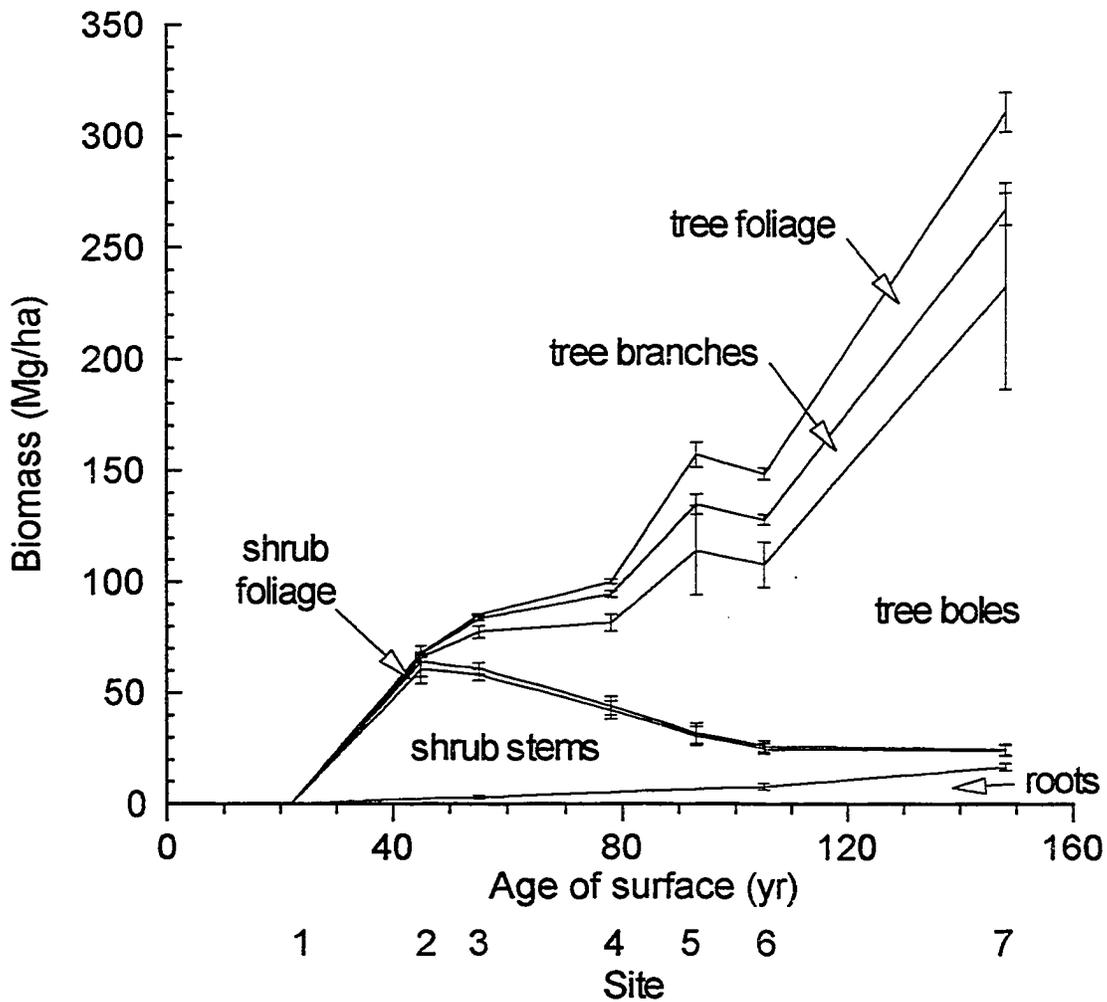


Fig 23. Biomass of woody-plant tissue at seven sites. The mass of each component is added to the cumulative pool below it. Error bars are ± 1 SE of individual component means, $n = 10$ to 20 plots/site, except $n = 4$ to 6 pits/site for roots.

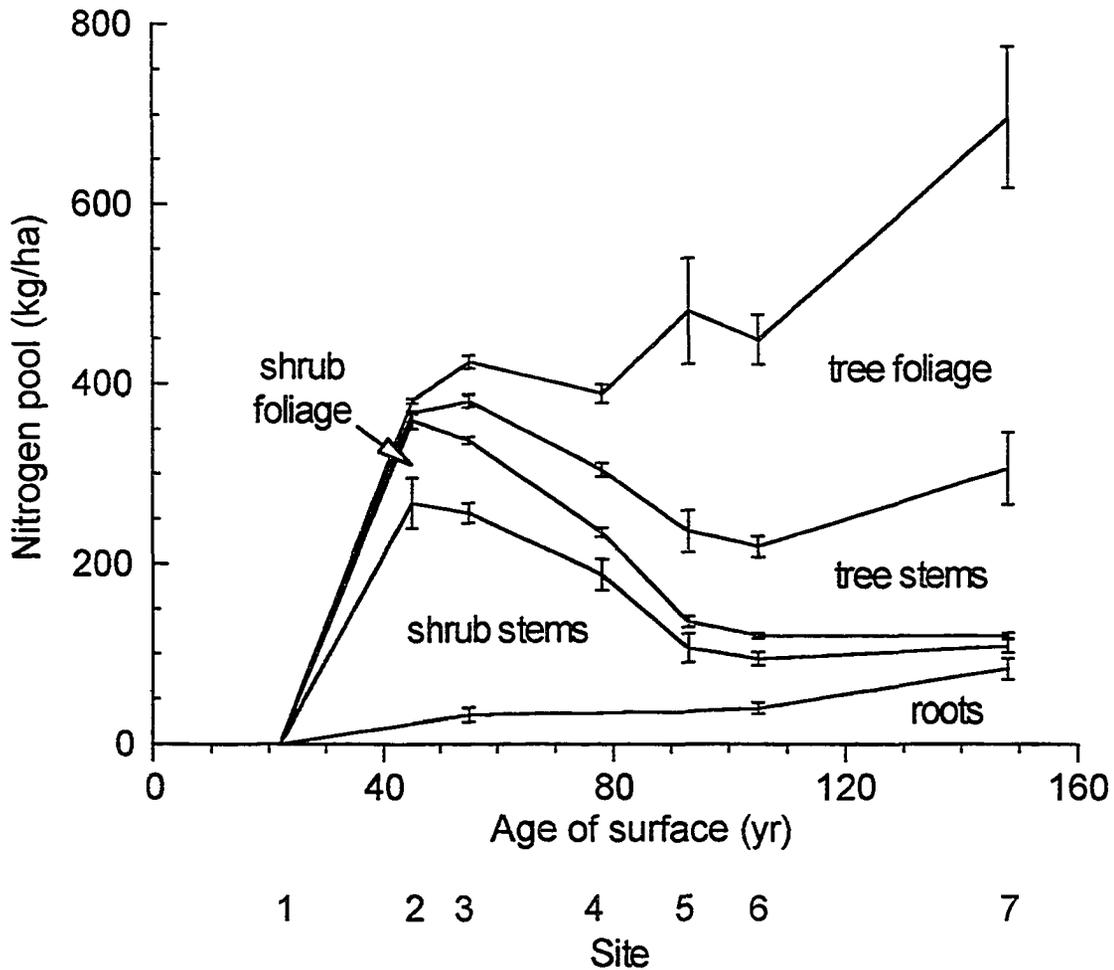


Fig. 24. N pools in biomass of trees and shrubs at seven sites. The N pool of each component is added to the cumulative pool below it. Error bars are ± 1 SE of individual component means, $n = 10$ to 20 plots/site, except $n = 4$ to 6 plots/site for roots.

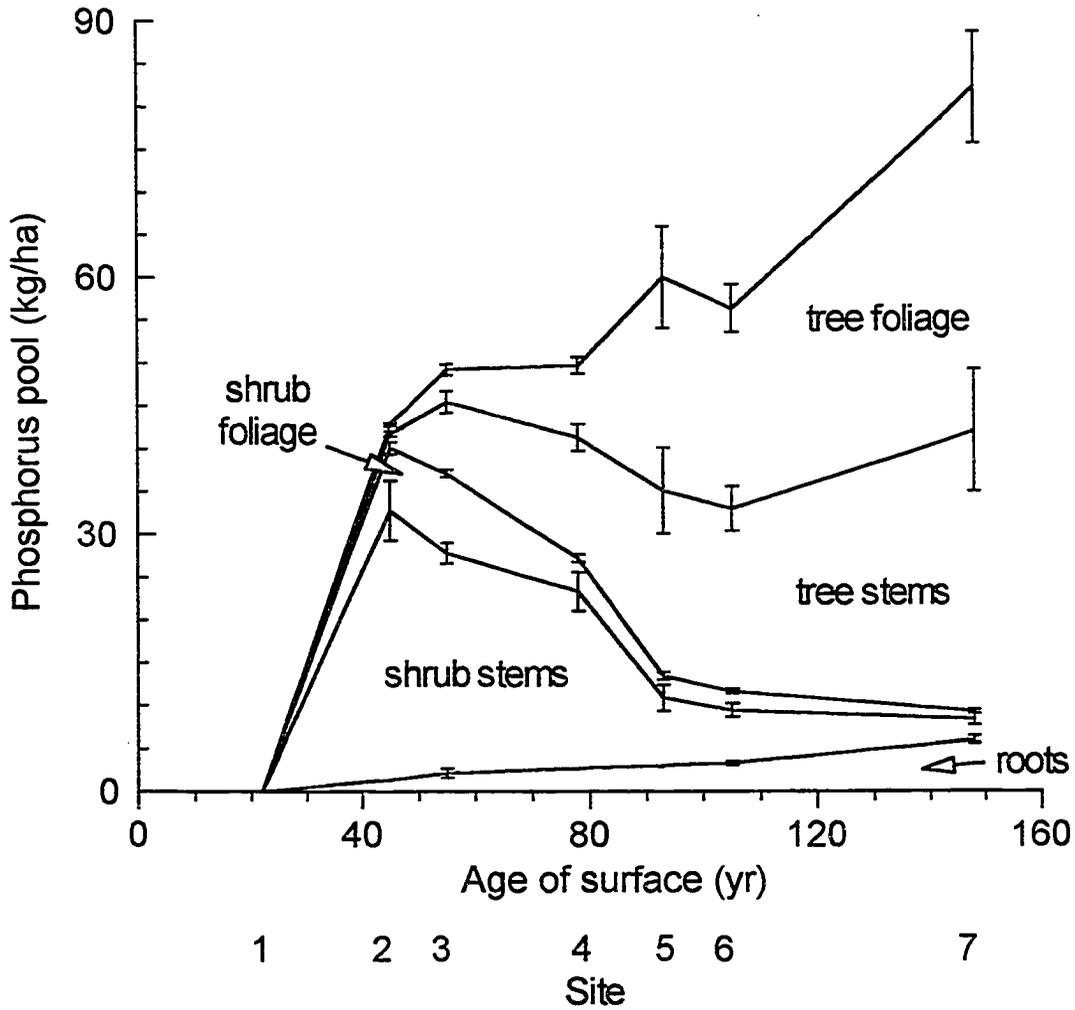


Fig. 25. P pools in biomass of trees and shrubs at seven sites. The P pool of each component is added to the cumulative pool below it. Error bars are ± 1 SE of individual component means, $n = 10$ to 20 plots/site, except $n = 4$ to 6 pits/site for roots.

scattered through a dense alder thicket after 150 yr (site 7) at Glacier Bay. The accumulation of soil N at Glacier Bay is similar to soil N accumulation in primary succession on other glacial deposits in southeastern Alaska (Crocker and Dickson 1957) and on volcanic ash in Hawaii (Vitousek et al. 1983), where soil N pools after two centuries were about 3200 kg/ha, and 3850 kg/ha, respectively. In contrast, primary successions without N-fixing vascular plants on mud flows in California (Dickson and Crocker 1953) and on lava flows in Hawaii (Vitousek et al. 1992) accumulated <500 kg N/ha in soil after one to two centuries. The accumulation of aboveground biomass after one or two centuries of secondary succession in five temperate coniferous forests in Washington, Oregon, and Japan (Fujimori 1971, Cole and Rapp 1981, Grier et al. 1981) exceeds that at Glacier Bay (site 8) by 15 to 300%, probably because of the intact soils at the start of secondary succession and a more moderate climate. The accumulation of N in biomass, which was measured in three of the above secondary succession studies (Cole and Rapp 1981), exceeds that at Glacier Bay (Fig. 16) by only 4 to 35%, emphasizing the extraordinary role of N-fixing shrubs at Glacier Bay. The largest biomass pool of P at Glacier Bay (site 8, Fig. 17) was larger than the P pool in two of the three temperate coniferous secondary succession stands.

Despite the identification of serious flaws in the Glacier Bay chronosequence, this study has confirmed the rapid accumulation of soil N under alder that has made Glacier Bay a classic example of facilitation by early successional N-fixing shrubs. This study has demonstrated that where alder is important N continues to accumulate rapidly in both soil and biomass for 150 yr (Fig. 18), 37 yr longer than had been previously documented. The potential facilitative effect of this N has not been addressed by this study, although spruce trees at sites where alder has been important consistently record greater radial trunk growth than at other sites (Chapter 1), an effect which could be attributed to facilitation by alder. However, at Glacier Bay, sites where alder is important consistently have fewer spruce trees than sites where alder is uncommon (Chapter 1). Thus, any possible response of spruce trees to facilitation by alder is confounded with the positive response to reduced competition among spruce. Because alder thickets inhibit the germination and establishment of spruce (Chapin et al. in press), the lower spruce stand density where alder is important may be a direct consequence of alder, and should be considered when determining whether there is a net facilitative

effect of alder on spruce. Plant ecologists have assumed that the large pools of soil N for which alder thickets are responsible can only benefit subsequent successional communities. But other possible consequences of long-term dominance by alder, including the reduced density of spruce and the associated differences in spruce crown architecture, canopy codominants, and understory species, should also be considered. Although there is an apparent long-term net facilitative effect of alder on *individual* spruce trees, a net effect of alder thickets on late successional *populations* of spruce has not been demonstrated.

CONCLUSIONS

Conclusions of the site-specific retrospective analysis (Chapter 1) are reinforced by estimates of current ecosystem pools of N and measured changes in soil N pools since 1952 (Chapter 2). Results of stand reconstructions indicate that Sitka spruce invaded densely at all sites deglaciated before 1840, and that thickets of N-fixing Sitka alder have been important only at younger sites. The inferred absence of long-lived communities of N-fixing shrubs at the oldest sites is confirmed by smaller ecosystem pools of N there than at younger sites where alder has been an important species. Directly measured changes in soil N between 1952 and 1989 at young sites confirm the widely cited accumulation of N under alder thickets, and demonstrate that N continues to accumulate for 150 years. Smaller soil N pools at older sites are not the result of loss or plant uptake of N, but of slower rates of N accumulation where early successional N-fixing shrubs are uncommon or short-lived.

The plant communities of different age that have developed in glacial deposits at Glacier Bay are not a single chronosequence, but are the product of at least three different successional pathways. Differences in the early seed rain to young terrain are probably responsible for the bay-length gradient in invasion of woody plants. Seed rain of Sitka spruce from old growth forests surrounding the southern end of Glacier Bay anchored one end of this gradient. With linear retreat of ice away from these forests, young terrain become progressively distant from this seed source, and the advancing front of successional vegetation, dominated by Sitka alder and other shrubs, became the primary source of seeds for new surfaces. Gradual shifts in the species composition of the advancing young successional community have altered the species composition of its seed output, and contributed to continuing changes in the composition of communities invading new surfaces.

The substantial pools of N and organic matter accumulating at sites dominated by Sitka alder are expected to have positive effects on the growth of plants in subsequent successional communities. But alder thickets also have negative effects on these later communities, including reducing the stand density of trees in mid- to late-successional forests. Thus, a definitive evaluation of the putative facilitative effect of alder thickets at Glacier Bay should include a sufficiently *long time scale* (> 100 yr), the *net* facilitative

effect (positive minus negative effects), and effects at the level of the *population* as well as of individuals.

REFERENCES CITED

- Aber, J. D. 1979. Foliage-height profiles and succession in northern hardwood forests. *Ecology* 60:19-23.
- Bard, G. 1952. Secondary succession on the Piedmont of New Jersey. *Ecological Monographs* 22:195-215.
- Bazzaz, F. A. 1968. Succession on abandoned fields in the Shawnee Hills, southern Illinois. *Ecology* 49:924-939.
- Birks, H. J. B. 1980. Modern pollen assemblages and vegetational history of the moraines of the Klutlan Glacier and its surroundings, Yukon Territory, Canada. *Quaternary Research* 14:101-129.
- Blundon, D. J., and M. R. T. Dale. 1990. Dinitrogen fixation (acetylene reduction) in primary succession near Mount Robson, British Columbia, Canada. *Arctic and Alpine Research* 22:255-263.
- Bormann, B. T. 1990. Diameter-based biomass regression models ignore large sapwood-related variation in Sitka spruce. *Canadian Journal of Forest Research* 20:1098-1104.
- Bormann, B. T., and R. C. Sidle. 1990. Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska (USA). *Journal of Ecology* 78:561-578.
- Bormann, F. H., and G. E. Likens. 1979. *Pattern and process in a forested ecosystem*. Springer-Verlag, New York.
- Brew, D. A. 1988. Plate-tectonic setting of Glacier Bay National Park and Preserve and of Admiralty Island National Monument, southeastern Alaska. Pages 1-5 in A. M. Milner and J. D. Wood, editors. *Proceedings of the second Glacier Bay Science Symposium*. U.S. Department of the Interior National Park Service, Anchorage.
- Brew, D. A., B. R. Johnson, D. Grybeck, A. Griscom, D. F. Barnes, A. L. Kimball, J. C. Still, and J. L. Rataj. 1978. Mineral resources of the Glacier Bay National Monument wilderness study area, Alaska. U.S. Geological Survey Open File Report 78-494.
- Calkin, P. E. 1988. Holocene glaciation of Alaska (and adjoining Yukon Territory, Canada). *Quaternary Science Reviews* 7:159.
- Cattelino, P. J., I. R. Noble, R. O. Slatyer, and S. R. Kessel. 1979. Predicting the multiple pathways of plant succession. *Environmental Management* 3:41-50.

Chapin, F. S., III, L. R. Walker, C. L. Fastie, and L. C. Sharman. in press. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs*.

Clements, F. E. 1916. *Plant Succession: An analysis of the development of vegetation*. Publication 242, Carnegie Institution of Washington, Washington, D. C.

Cole, D. W., and M. Rapp. 1981. Elemental cycling in forest ecosystems. Pages 341-409 in D. E. Reichle, editor. *Dynamic Principles of Forest Ecosystems*. Cambridge University Press, Cambridge.

Colinvaux, P. A. 1973. *Introduction to ecology*. John Wiley, London.

Collins, S. L., and D. E. Adams. 1983. Succession in grasslands: Thirty-two years of change in a central Oklahoma tallgrass prairie. *Vegetatio* 51:181-190.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119-1144.

Cooper, W. S. 1923a. The recent ecological history of Glacier Bay, Alaska: II. The present vegetation cycle. *Ecology* 4:223-246.

---. 1923b. The recent ecological history of Glacier Bay Alaska. III. Permanent quadrats at Glacier Bay: an initial report upon a long-period study. *Ecology* 4:355-365.

---. 1931. A third expedition to Glacier Bay, Alaska. *Ecology* 12:61-95.

---. 1939. A fourth expedition to Glacier Bay, Alaska. *Ecology* 20:130-155.

Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. I, II, III, IV. *Botanical Gazette* 27:95-117, 167-202, 281-308, 361-391.

Crocker, R. L. 1952. Soil genesis and the pedogenic factors. *Quarterly Review of Biology* 27(27):139-168.

---. 1959. The plant factor in soil formation. *Australian Journal of Science* 21:180-193.

Crocker, R. L., and B. A. Dickson. 1957. Soil development on the recessional moraines of the Herbert and Mendenhall glaciers, southeastern Alaska. *Journal of Ecology* 45:169-185.

Crocker, R. L., and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *Journal of Ecology* 43:427-448.

- Davis, M. B. 1981. Quaternary history and the stability of forest communities. Pages 132-153 in D. C. West, H. H. Shugart and D. B. Botkin, editors. *Forest succession: Concepts and application*. Springer-Verlag, New York.
- . 1983. Holocene vegetational history of the eastern United States. Pages 166-181 in H. E. Wright Jr., editor. *Late-Quaternary environments of the United States. Volume 2. The Holocene*. University of Minnesota Press, Minneapolis.
- Decker, H. F. 1966. Plants. Pages 73-96 in A. Mirskey, editor. *Soil development and ecological succession in a deglaciated area of Muir Inlet*. Institute of Polar Studies Report No. 20. Ohio State University, Columbus.
- del Moral, R., and L. C. Bliss. 1993. Mechanisms of primary succession: Insight resulting from the eruption of Mount St Helens. Pages 410 in M. Begon and A. H. Fitter, editors. *Advances in Ecological Research. Volume 24*. Academic Press, London.
- Dickson, B. A., and R. L. Crocker. 1953. A chronosequence of soils and vegetation near Mt. Shasta, California. II. The development of the forest floors and the carbon and nitrogen profiles of the soils. *Journal of Soil Science* 4:142-154.
- Field, W. O. 1947. Glacier recession in Muir Inlet, Glacier Bay, Alaska. *Geographical Review* 37:369-399.
- Fujimori, T. 1971. Primary productivity of a young *Tsuga heterophylla* stand and some speculations about biomass of forest communities on the Oregon coast. U.S Forest Service Research paper PNW-123.
- Gholz, H. L., C. C. Grier, A. G. Campbell, and A. T. Brown. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Research Paper No. 41. Forest Research Laboratory, Oregon State University, Corvallis, Oregon.
- Glaser, P. H. 1981. Transport and deposition of leaves and seeds on tundra: a late-glacial analog. *Arctic and Alpine Research* 13:173-182.
- Gleason, H. A. 1927. Further views on the succession concept. *Ecology* 8:299-326.
- Gorham, E., P. M. Vitousek, and W. A. Reiners. 1979. The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Annual Review of Ecology and Systematics* 10:53-84.
- Gosz, J. R. 1981. Nitrogen cycling in coniferous ecosystems. in F. E. Clark and T. Rosswall, editors. *Terrestrial nitrogen cycles*. *Ecological Bulletin* 33:405-426, .
- Greene, D. F., and E. A. Johnson. 1989. A model of wind dispersal of winged or plumed seeds. *Ecology* 70:339-347.

Grier, C. C., K. A. Vogt, M. R. Keyes, and R. L. Edmonds. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Canadian Journal of Forest Research* 11:155-167.

Grove, J. M. 1988. *The Little Ice Age*. Methuen, London.

Harper, J. L. 1977. *Population biology of plants*. Academic Press, San Diego.

Haselton, G. M. 1966. *Glacial geology of Muir Inlet, southeastern Alaska*. Institute of Polar Studies Report No. 18. University of Ohio, Columbus.

Henry, J. D., and J. M. A. Swan. 1974. Reconstructing forest history from live and dead plant material--an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55:772-783.

Holmes, R. L. 1992. *Dendrochronology program library: Installation and program manual*. Tucson, AZ.

Jack, W. H. 1971. The influence of tree spacing on Sitka spruce growth. *Irish Forestry* 28:13-33.

Jackson, S. T., R. P. Futyma, and D. A. Wilcox. 1988. A paleoecological test of a classical hydrosere in the Lake Michigan dunes. *Ecology* 69:928-936.

Jenny, H. 1941. *Factors of soil formation; a system of quantitative pedology*, 1st Edition. McGraw-Hill, New York.

---. 1958. Role of the plant factor in the pedogenic functions. *Ecology* 39:5-16.

---. 1961. Derivations of state factor equations of soils and ecosystems. *Proceedings of the Soil Science Society of America* 25:385-388.

---. 1980. *The soil resource: Origin and behavior*. Springer Verlag, New York.

Klingensmith, K. M., and K. Van Cleve. 1993. Denitrification and nitrogen fixation in floodplain successional soils along the Tanana River, interior Alaska. *Canadian Journal of Forest Research* 23:956-963.

Kramer, P. J., and T. T. Kozlowski. 1979. *Physiology of woody plants*. Academic Press, Orlando.

Lawrence, D. B. 1953. Development of vegetation and soil on deglaciated terrain of southeastern Alaska with special reference to the accumulation of nitrogen. University of Minnesota, Department of Botany, Minneapolis, Final Report, Office of Naval Research, Project NR 160-183.

---. 1958. Glaciers and vegetation in southeastern Alaska. *American Scientist* 46:89-122.

Lawrence, D. B., R. E. Schoenike, A. Quispel, and G. Bond. 1967. The role of *Dryas drummondii* in vegetation development following ice recession at Glacier Bay, Alaska, with special reference to its nitrogen fixation by root nodules. *Journal of Ecology* 55:793-813.

Loewe, F. 1966. Climate. Pages 19-28 in A. Mirskey, editor. Soil development and ecological succession in a deglaciated area of Muir Inlet, Southeast Alaska. Institute of Polar Studies Report No. 20. Ohio State University, Columbus.

Marks, P. L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecological Monographs* 44:73-88.

Matlack, G. R. 1989. Secondary dispersal of seed across snow in *Betula lenta*, a gap-colonizing tree species. *Journal of Ecology* 77:853-869.

Matthews, J. A. 1979. A study of the variability of some successional and climax plant assemblage-types using multiple discriminant analysis. *Journal of Ecology* 67:255-271.

---. 1992. The ecology of recently deglaciated terrain. Cambridge University Press, Cambridge.

McIntosh, R. P. 1981. Succession and ecological theory. Pages 10-23 in D. C. West, H. H. Shugart and D. B. Botkin, editors. Forest succession: Concepts and application. Springer-Verlag, New York.

Means, J. E., H. A. Hansen, G. J. Koerper, M. W. Klopsch, and P. B. Alaback. 1993. Software for computing plant biomass--Biopak users guide, editorial review draft. Pacific Northwest Forest and Range Experiment Station, Corvallis.

Mellor, A. 1987. A pedogenic investigation of some soil chronosequences on Neoglacial moraine ridges, southern Norway: examination of soil chemical data using principal components analysis. *Catena* 14:369-381.

Messer, A. C. 1988. Regional variations in rates of pedogenesis and the influence of climatic factors on moraine chronosequences, southern Norway. *Arctic and Alpine Research* 20:31-39.

- Miles, J. 1979. *Vegetation dynamics: Outline studies in Ecology*. Chapman & Hall, London.
- Miller, W. P., and D. M. Miller. 1987. A micro-pipette method for soil mechanical analysis. *Communications in soil science and plant analysis* 18:1-15.
- Mirskey, A., editor. 1966. *Soil development and ecological succession in a deglaciated area of Muir Inlet, Southeast Alaska*. Institute of Polar Studies Report No. 20. Ohio State University, Columbus.
- National Oceanic and Atmospheric Administration. 1990. *Climatological data, Alaska*. National Oceanic and Atmospheric Administration, Asheville, N. C.
- Neter, J. N., W. Wasserman, and M. H. Kutner. 1985. *Applied linear statistical models*, 2nd Edition. Irwin, Homewood, Illinois.
- Okubo, A., and S. A. Levin. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* 70:329-338.
- Olson, J. S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. *Botanical Gazette* 119:125-170.
- Ovenshine, A. T. 1968. Provenance of recent glacial ice in lower Glacier Bay, southeastern Alaska. *United States Geological Survey Professional Paper* 575-D:198-202.
- Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110-135 *in* G. E. Likens, editor. *Long-term studies in ecology: approaches and alternatives*. Springer-Verlag, New York.
- Pickett, S. T. A., and P. S. White, editors. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York.
- Reid, H. F. 1892. Studies of the Muir Glacier, Alaska. *National Geographic Magazine* 4:19-84.
- Reiners, W. A., I. A. Worley, and D. B. Lawrence. 1971. Plant diversity in a chronosequence at Glacier Bay, Alaska. *Ecology* 52:55-69.
- Richard, J. L. 1973. Dynamique de la végétation au bord du grand glacier d'Aletsch (Alpes suisses). *Bericht der Schweizerischen Botanischen Gesellschaft (Bern)* 83:159-174.
- Ritchie, J. C., and G. M. MacDonald. 1986. The patterns of post-glacial spread of white spruce. *Journal of Biogeography* 13:527-540.

Ryvarden, L. 1975. Studies in seed dispersal. II. Winter-dispersed species in Finse, Norway. *Norwegian Journal of Botany* 22:21-24.

SAS Institute Inc. 1989. SAS/STAT Users' Guide, Version 6, 4th Edition. SAS Institute Inc., Cary, NC.

Shelford, V. E. 1911. Ecological succession. *Biological Bulletin* 21:127-151.

Standish, J. T., G. H. Manning, and J. P. Demaerschalk. 1985. Development of biomass equations for British Columbia tree species. Informal report BC-X-264. Pacific Forestry Research Center. Canadian Forest Service.

Stephens, F. R. 1991 (1969). Primary ecosystems developing below receding glaciers in southeastern Alaska. Revised and edited unpublished report. *in* Watershed '91 Conference, April 16-17, 1991. U.S. Department of Agriculture Forest Service, Juneau.

Stevens, P. R., and T. W. Walker. 1970. The chronosequence concept and soil formation. *Quarterly Review of Biology* 45:333-350.

Swetnam, T. W., M. A. Thompson, and E. K. Sutherland. 1985. Agricultural Handbook No. 639: Spruce budworms handbook: Using dendrochronology to measure radial growth of defoliated trees. United States Forest Service, Washington, DC.

Tansley, A. G. 1939. *The British Islands and their vegetation*. Cambridge University Press, Cambridge.

Tarrant, R. F., and J. M. Trappe. 1971. The role of *Alnus* in improving the forest environment. *Plant and Soil Special Volume*:335-348.

Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, New Jersey.

Tisdale, E. W., M. A. Fosberg, and C. E. Poulton. 1966. Vegetation and soil development on a recently glaciated area near Mount Robson, British Columbia. *Ecology* 47:517-523.

Ugolini, F. C. 1966. Soils. Pages 20-72 *in* A. Mirskey, editor. Soil development and ecological succession in a deglaciated area of Muir Inlet, southeastern Alaska. Institute of Polar Studies Report No. 20. Ohio State University, Columbus.

---. 1968. Soil development and alder invasion in a recently deglaciated area of Glacier Bay, Alaska. Pages 115-140 *in* J. M. Trappe, J. F. Franklin, R. F. Tarrant and G. M. Hansen, editors. *Biology of alder, Proceedings of the Pacific Northwest Scientific Association Fortieth Annual Meeting*. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

- Ulrich, B., P. Benecke, W. F. Harris, P. K. Khanna, and R. Mayer. 1981. Soil Process. Pages 265-340 in D. E. Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge.
- Van Cleve, K., L. A. Viereck, G. M. Marion, J. Yarie, and C. T. Dyrness. 1993. Nitrogen mineralization and nitrification in successional ecosystems on the Tanana River floodplain, interior Alaska. *Canadian Journal of Forest Research* 23:970-978.
- Vancouver, G. 1798. A voyage of discovery to the North Pacific Ocean, and round the world; in which the coast of North-west America has been carefully examined and accurately surveyed. Volume 3. Robinson, London.
- Viereck, L. A. 1966. Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. *Ecological Monographs* 36:181-199.
- Viereck, L. A., C. T. Dyrness, and M. J. Foote. 1993. An overview of the vegetation and soils of the floodplain ecosystems of the Tanana River, interior Alaska. *Canadian Journal of Forest Research* 23:889-898.
- Vitousek, P. M., and L. R. Walker. 1987. Colonization, succession and resource availability: ecosystem-level interactions. Pages 207-224 in A. J. Gray, M. J. Crawley and P. J. Edwards, editors. Colonization, succession and stability. Blackwell Scientific Publications, Oxford.
- Vitousek, P. M., J. R. Gosz, C. C. Grier, J. M. Mellilo, and W. A. Reiners. 1982. A comparative analysis of potential nitrification and nitrate mobility on forest ecosystems. *Ecological Monographs* 52:155-177.
- Vitousek, P. M., K. Van Cleve, N. Balakrishnan, and D. Mueller-Dombois. 1983. Soil development and nitrogen turnover in montane rainforest soils on Hawaii. *Biotropica* 15:268-274.
- Vitousek, P. M., T. Fahey, D. W. Johnson, and M. J. Swift. 1988. Element interactions in forest ecosystems: succession, allometry and input-output budgets. *Biogeochemistry* 5:7-34.
- Vitousek, P. M., G. Aplet, D. Turner, and J. J. Lockwood. 1992. The Mauna Loa environmental matrix: Foliar and soil nutrients. *Oecologia* 89:372-382.
- Walker, D. 1970. Direction and rate in some British post-glacial hydroseres. Pages 117-139 in D. Walker and R. G. West, editors. Studies in the vegetational history of the British Isles. Cambridge University Press, Cambridge.
- Walker, L. R. 1989. Soil nitrogen changes during primary succession on a floodplain in Alaska, USA. *Arctic and Alpine Research* 21:341-349.

- Walker, L. R. 1993. Nitrogen fixers and species replacements in primary succession. Pages 249-272 *in* J. Miles and D. W. H. Walton, editors. Primary succession on land. Blackwell Scientific Publications, Oxford.
- Walker, L. R., J. C. Zasada, and F. S. Chapin III. 1986. The role of life history processes in primary succession on an Alaskan floodplain. *Ecology* **67**:1243-1253.
- Waring, R. H., and W. H. Schlesinger. 1985. Forest ecosystems concepts and management. Academic Press, Orlando.
- Warming, E. 1891. De psammophile vormationer i Danmark. Videnskabelige Meddelelser Fra den Naturhistorisk Forening i Kjobenhavn **1891**:153.
- Whittaker, R. J. 1989. The vegetation of the Storbreen gletschervorfeld, Jotunheimen, Norway. III. Vegetation-environment relationships. *Journal of Biogeography* **16**:413-433.
- . 1991. The vegetation of the Storbreen gletschervorfeld, Jotunheimen, Norway. IV. Short-term vegetation change. *Journal of Biogeography* **18**:41-52.
- Wilcox, D. A., and H. A. Simonin. 1987. A chronosequence of aquatic macrophyte communities in dune ponds. *Aquatic Botany* **28**:227-242.
- Willson, M. F. 1993. Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* **107/108**:261-280.
- Yarie, J. 1993. Effects of selected forest management practices on environmental parameters related to successional development on the Tanana River floodplain, interior Alaska. *Canadian Journal of Forest Research* **23**:1001-1014.
- Zedler, P. H., and F. G. Goff. 1973. Size-association analysis of forest successional trends in Wisconsin. *Ecological Monographs* **43**:79-94.