
VEGETATION CHRONOSEQUENCE NEAR EXIT GLACIER, KENAI FJORDS NATIONAL PARK, ALASKA

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ABSTRACT

The vegetation chronosequence near Exit Glacier in Kenai Fjords National Park has developed on an outwash plain deglaciated in the last 200 yr but which still actively floods much of the area deglaciated within the last 40 yr. This glacier is at the northern edge of the Harding Icefield and is the least isolated glacier within the Park. Vegetation cover, diversity, density, and plant sizes in several stands in each of seven successional stages were sampled using systematic points along line transects and belt transects. Seedlings were small, < 0.5 cm tall during their first year, and were subject to flooding during late summer and fall. *Populus trichocarpa* (black cottonwood) was an important species through the first 100 to 150 years after deglaciation and was the dominant early colonizer. The most extensive stands of *Alnus sinuata* (Sitka alder) occurred primarily in areas of repeated avalanche and rock slides and was also in the understory of Cottonwood stands. Although *Picea sitchensis* (Sitka spruce) and *Tsuga mertensiana* (mountain hemlock) seedlings were found on the outwash plain, these individuals probably did not survive to be mature trees. Although *P. sitchensis* established in the understory of *Populus trichocarpa* stands, and *T. mertensiana* colonized dead logs and organic soils in the Spruce - Cottonwood stage. In contrast, *A. sinuata* was the first colonizer near other glaciers that were more isolated from vegetation during the Little Ice Age.

INTRODUCTION

Although glacial retreats and the resultant vegetation colonization and development have been documented in many areas of Alaska and the world, little information had been available on the vegetation on the recently deglaciated terrain around Exit Glacier in Kenai Fjords National Park, Alaska. The site is intermediate between coastal glaciers which have forests dominated by *Tsuga* spp. (hemlock) and *Picea sitchensis* (Sitka spruce) (Cooper, 1930? (reprinted 1931); Cooper, 1931; Cooper, 1942; Crocker and Dickson, 1957; Chapin et al., 1994) and interior Alaska floodplains where Salicaceae (willows), including *Populus balsamifera* (balsam poplar), are major species in vegetation succession (Viereck, 1970; Helm et al., 1985; Walker et al., 1986; Viereck et al., 1993). The vegetation at Exit Glacier appears to differ from other chronosequences in more coastal areas in that *Populus trichocarpa* (black cottonwood) dominated much of the vegetation on the outwash plain through the first 100 to 150 yr of the chronosequence. Other studies reported stands dominated by *Picea sitchensis* (Sitka spruce) within 200 yr. Although *P. trichocarpa* occurred in the pioneer stage in Glacier Bay, *Dryas drummondii* (yellow-flowered avens) was more important (Schoenike, 1957-1958; Ugolini, 1968; Chapin et al., 1994). Scattered *P. trichocarpa* formed a "skyline" above the *Alnus sinuata* (Sitka alder) in the Alder stage at Glacier Bay (Ugolini, 1968). Cooper (1931) hypothesized that *P. trichocarpa* might be more common in fluvial succession, which was suggested by the remnants of an interglacial forest. He reported that no contemporary fluvial environments existed at that time to observe the fluvial succession directly.

Vegetation succession around different glaciers in coastal Alaska are similar, but each chronosequence has its unique characteristics, resulting from different environments, seed sources, and/or site histories. Indeed, the vegetation on the Exit-Glacier outwash plain differs from that near some other glaciers within Kenai Fjords National Park. The objectives of this study were to describe the vegetation on

various-aged surfaces on the recently deglaciated outwash plain of Exit Glacier and to observe seed dispersal and seedling survival.

STUDY AREA

Exit Glacier ($60^{\circ} 15' \text{ N } 149^{\circ} 30' \text{ W}$) is about 5 km long (1980's) and descends about 760 m from the Harding Icefield, one of the last great ice sheets of North America. Few other Alaskan coastal glaciers are readily accessible from the road system. Since the Kenai Fjords National Park was established in 1980, a 1-km paved trail was constructed in 1987 to within 400 m of the terminus, which is approximately the same location as in 1991-1993, the time of this study. Although Exit Glacier is a land-based glacier, it lies about 13 km air distance from Resurrection Bay, an arm of the Gulf of Alaska. Surrounding mountains are over 1000 m tall. The valley consists of an active floodplain still being colonized, slightly higher terraces which are above most recent flooding and which have been colonized since the retreat of 1950, and comparatively mature forests that were initiated prior to 1950. Since the valley itself is small, and succession on these riparian sites is slow, a vegetation chronosequence has not developed fully. Exit Glacier reached the Resurrection River in the mid 1700's (Ahlstrand, n.d.) at its farthest advance of the Little Ice Age. It probably joined another glacier at that time, but this study was confined to the National Park.

Total precipitation averaged over 150 cm per year (1990-1993), which is less than that received by other fjords along the Kenai Peninsula. The early growing season at Exit Glacier from May through late July, sometimes into August is dry. Winds blowing sand, seeds, and other matter across the unvegetated outwash plain off the glacier may be 20 to 30 km hr⁻¹ during warm weather. Most rain falls in late summer (starting with the fourth week of July) and autumn through the winter.

Exit Glacier Creek, which runs through the study area, drains the glacier as well as side slopes above both the glacier and deglaciated areas. The creek flows close to bank full or slightly above during the heavy rains of August when weather is also warm enough to melt the glacier. Water levels usually drop in the fall

prior to freeze-up unless the fall storms compensate. Both rain and snow fall in the winter. Fluvial processes dominate the most recently deglaciated portion of the outwash plain and probably have in the past also. Although the largely-unvegetated, recently deglaciated outwash plain is relatively dry during the early growing season and may be subjected to wind erosion and deposition, much of it has standing or moving water during the wet season. Ice that has calved from the glacier and become grounded on submerged gravel bars may divert water up some drainages and not others, thus creating microsites for seedling establishment. Approximately 5-10 cm of ice may form beneath the snow in winter.

METHODS

VEGETATION AND SOILS

Based on preliminary observations and descriptions from other studies, the chronosequence was divided into eight stages: (1) Barren, (2) Isolated plants, (3) Patchy, (4) Alder, (5) Cottonwood, (6) Sitka spruce - Cottonwood, (7) Sitka spruce, and (8) Sitka spruce - Mountain hemlock. At least three representative stands of each stage were sampled, except for Stages 1, 6, and 8 where only one was sampled and Stage 7 where no stands were found. The most emphasis was placed on stages 1 through 5 where changes occurred most rapidly as plants died or changed relative positions in the canopy.

Systematic points spaced 50 cm along a 20-m transect (Stages 1-5) or 30-m transect (Stages 6, 8) were used to sample cover. Longer transects were used in the late-successional forest because of the large tree sizes and scales of resultant vegetation patterns. A vertical line was projected downward and upward at each point, and all species encountered or "hit" by the projection were recorded. Three transects (sampling units) were randomly located within each stand. Where bare ground occurred, it was classified according to visual surface texture — rock, cobble, gravel, sand, and silt (which may have included fine sands). Data for life forms and other categories were calculated in the office by determining which life forms were encountered at each point. Total vascular cover was the surface covered by vascular plant

species. Total canopy cover was the cover provided by the three tree species or the tall shrub (*A. sinuata*), while total living cover included mosses and lichens.

Diversity was calculated using cover for vascular plant species in the reciprocal of Simpson's dominance index since it is most responsive to major species: $SR = (\sum_{i=1}^m p_i^2)^{-1}$ where p_i is the relative cover of vascular plant species i and m is the number of vascular plant species present (Simpson, 1949). This can be interpreted as an "effective" number of species (Hill, 1973). An evenness index was calculated by dividing the diversity index by the number of species m .

Density for major woody species (*Salix* spp., *Alnus sinuata*, *Populus trichocarpa*, *Picea sitchensis*, *Tsuga mertensiana*) in all vegetation types and the most important species in the earliest vegetation types was obtained by counting stems in belt transects adjacent to the cover transects. Low shrubs (< 1.5 m tall) and forbs were counted in 1-m wide plots alongside the cover transects. Tall shrubs (> 1.5 m tall) were counted in 2-m wide plots, and trees were counted in 5-m wide plots. Densities were converted from stems/plot to stems/ha using appropriate multipliers.

Two to four individuals of each species were selected near the end points of each transect and sampled for height, diameter (diameter-at-breast-height for trees, basal diameters for low shrubs), and age. Ages were estimated by counting rings on cores of larger individuals or cross-sections of smaller stems. External rings created by terminal bud-scale scars were counted on small *P. trichocarpa* where possible to avoid cutting individuals. One large and one small stem per transect were collected where possible to estimate the age range and to insure that small trees were young and not just stunted.

Composited soil samples were taken from the top 10 cm within most stands. Organic surface soils were separated from underlying mineral soils where both were present. Some sites had sufficient cobbles that these were removed with a crowbar to obtain sufficient material < 2-mm for analysis. Soil samples were returned to the laboratory, air-dried, and sieved to remove the fraction with particles > 2 mm in diameter. The fraction < 2 mm was analyzed for the following parameters: extractable N (NH_4^+ , NO_3^-) (2-N

KCl, (Bremner, 1982)), extractable P (Mehlich 3 if pH<7, (Mehlich, 1982) and Olsen's if pH > 7 (Olsen and Sommers, 1982), total N and P (digestion in H₂SO₄-H₂SeO₃, (Isaac and Johnson, 1976; Bremner and Mulvaney, 1982)), extractable K, Ca (Mehlich 3, (Mehlich, 1982)), cation exchange capacity (NH₄OAc, (Soil Conservation Service, 1984)), organic matter (loss on ignition, (Jackson, 1958)), and pH (paste, (Peech, 1965)). Soil particle size analysis was determined by the sand-sieve analysis technique.

SEEDLING SURVIVAL

To determine seedling survival on the outwash plain, eight 20 cm x 50-cm plots were established in August 1992. Seedlings in eight plots were marked in 1992, but in September all seedlings were removed from five plots to ensure that seedlings observed in 1993 were new. New seedlings were extremely difficult to see since they were < 0.5 cm tall during their first year and 3-yr old plants were usually < 1 to 2 cm tall. The three plots with some seedlings remaining were used to estimate overwinter survival. The plots were checked approximately every two weeks beginning in June 1993, and new seedlings were marked with colored nails, a different color for each sample period. The number of surviving plants with each color nail was recorded during each sample period. Some seedlings were harvested as part of another study, but the survival percentage took this into account.

RESULTS

VEGETATION CHRONOSEQUENCE

Barren

The barren area was dotted by small seedlings of all the major woody plant species and *Epilobium latifolium* (dwarf fireweed), although the vast majority of seedlings were *Populus trichocarpa* and most woody seedlings were less than 1 to 3 cm tall. Plants were so scattered that none were encountered for either cover, density, or plant dimensions along the three transects. However, one 20 x 50-cm seedling plot contained over 30 seedlings. Seedlings concentrated in moist areas along drainages that had water only part

of the year. Lines of young plants frequently occurred along water marks in sloughs. Greater than 80% of the surface was covered by gravels or coarser materials (Table 1). Finer soil materials were located at the edges of small sloughs or other areas where they were deposited by slow-moving water. Only isolated fragments of moss (*Rhacomitrium* spp.) were observed in these stands, probably because of flood frequency. The "black crust" of Glacier Bay (Worley, 1973) was not observed here, possibly because of the continual redisturbance by flooding. Algae were abundant in some of the drainages, including some of our seedlings plots, when they flooded in August.

Isolated Plants

Plants in the Isolated Plant stage were sufficiently large to be readily observable, but were mostly scattered individuals of *P. trichocarpa*, *Salix sitchensis*, and *S. alaxensis* (Table 1). Many of these were sprouts off rhizomes of other plants. Gravel or coarser material covered 76% of the surface (Table 1). Cover of vascular plant species was only about 1%, but moss cover (mostly *Rhacomitrium* spp.) averaged 17% in these stands (Table 1). *Rhacomitrium* spp. has been reported to have nitrogen-fixing blue-green algae associated with it on Surtsey, Iceland (Henriksson et al., 1987). This was one of the most even stands and had Simpson's evenness near 0.94, with 1.0 being a perfectly even community. The extensive moss cover may be an indicator of reduced flooding events. *P. trichocarpa* had the greatest densities, and individuals averaged 30 cm tall and about 11 yr (Table 2).

Patchy

Size and density of plants were sufficiently large in the Patchy Stage (Stage 3) that clumps of vegetation were beginning to form. Moss covered over 50% of the surface and was still predominantly *Rhacomitrium* spp. The most common vascular plant species present was *P. trichocarpa* which provided over half the vascular plant cover (Table 1). Three species of willow were present as well as the *P. trichocarpa* (Table 1). Lichens, especially *Stereocaulon* spp., a nitrogen-fixing lichen, provided 5% cover,

although this was the only stage where lichens provided measurable ground cover. Over 50% of the stems counted were *P. trichocarpa* but *D. drummondii*, *E. latifolium*, and *S. sitchensis* were also important (Table 3). *P. trichocarpa* stems averaged 84 cm tall and 18 yr old (Table 3), similar to those measured by (Schoenike, 1957-1958). These stands appeared to average 8 yr older than the Isolated Plant stands although aging was only approximate because of sedimentation around plants. Diversity was about twice as great here as in the Isolated Plant Stage (2.5 vs 1.2) (Table 1), which resulted primarily from the greater species richness since evenness decreased.

Alder

These stands were dominated by *A. sinuata* (81% cover) which resulted in a low diversity of 1.4, because of the low evenness (0.32) (Table 1). These were the youngest stands where litter provided significant ground cover (Table 1). Although *A. sinuata* dominated the cover (Table 1), *P. trichocarpa* still contributed at least as many stems and was somewhat older (Table 4), which reflected its earlier establishment time. These stands were located mostly in areas of disturbance by rock avalanche chutes and along edges of other vegetation types.

Cottonwood

P. trichocarpa dominated the Cottonwood stage, which was the most common stage at Exit Glacier (Table 1). This stage occupied much of the valley floor on sites deglaciated prior to 1950. The number of plant species (7.8) and diversity (2.4) was greater in the Cottonwood communities compared to the Alder (4.5, 1.4, respectively) (Table 1). Although the number of species averaged about twice that of the Patchy Stage stands, the dominance by *P. trichocarpa* and *A. sinuata* (almost 80% relative cover), resulted in a low evenness but a diversity similar to that of the Patchy Stage (Table 1). Cover of *Pyrola secunda* was greater than in the Alder stage, and *P. asarifolia* (liverleaf wintergreen) was also present in small quantities (Table 1). Other studies report *P. secunda* occurring later in succession (??). Both species had rhizomes

spreading through the litter. *E. angustifolium* (tall fireweed), rather than *E. latifolium*, was present in this stage. *Calamagrostis canadensis* (bluejoint reedgrass) also provided extensive cover in some Cottonwood stands, but this varied considerably among stands. Density of *P. trichocarpa* was lower in this stage as the individuals increased in size and the stands thinned (Table 5). *P. trichocarpa* ages averaged 43 yr while those of *A. sinuata* stems averaged 29 yr (Table 5). Larger *Picea sitchensis* averaged 33 yr while small ones averaged 8 yr, which indicated continuous recruitment of *P. sitchensis*. *T. mertensiana* averaged 11 yr in these stands, and thus established after *P. sitchensis*. *P. trichocarpa* regeneration was not evident and not expected because of the shade.

Spruce - Cottonwood

This was the oldest stage found on the outwash plain, and it occurred near the confluence of the Resurrection River, which was the extent of Exit Glacier over 200 yr ago. *Picea sitchensis* had almost twice as much cover as *Populus trichocarpa* in these stands (Table 1), indicating that it was probably an older stand within this stage, and most of the original *P. trichocarpa* were dead and decaying. Cover of *T. mertensiana* was still low (Table 1), and most *Tsuga* seedlings occurred on decaying logs. *Calamagrostis* cover decreased, and *Pyrola asarifolia* became more important. Other species present included *Echinopanax horridum* (devil's club). Density of the trees decreased as they matured and thinned (Table 6). Stems in this stand were old — 190 yr average for *Populus trichocarpa* and 197 yr average for *Picea sitchensis* (Table 6). *P. trichocarpa* trunks were frequently rotten in the center. Some of the older *A. sinuata* were 49 yr while younger stems were 22 yr. These ages indicate that *Picea sitchensis* may start becoming established permanently approximately during the Patchy Stage (Stage 3). The number of species increased to an average of 12, which compensated for the low evenness and resulted in an increased diversity of 4.72 (Table 1).

Spruce - Hemlock

The oldest stage sampled was that of the Spruce - Hemlock which was located on the slopes above the reach of recent glaciations. It was dominated by *Picea sitchensis* and *Tsuga mertensiana* with substantial cover by ferns and some *Echinopanax horridum*, which occurred in gullies or long stringers down the hillside (Table 1). The number of species decreased from the Spruce - Cottonwood stage although the evenness increased because of the more equitable distribution of cover among the trees and understory species (Table 1). Few plant species grew beneath the closed canopies. Densities of both tree species were similar (Table 7). Ages could not be obtained because the increment borers were too small, but this stand may have been at least several hundred years old. Many partially rotten trunks were on the ground, and these were as large as the living trunks that we tried to core.

SEEDLING SURVIVAL AND SEED DISPERSAL TIMING

The seedling survival study indicated that just over 60% of the 56 surviving seedlings marked in 1992 overwintered successfully. About 44% of all marked seedlings survived until the September 1993 period. Approximately half of those that survived the 1992-1993 winter survived their second growing season. July was the peak dispersal period. The majority of new seedlings during 1993 were observed on the July 28 observation date (60 seedlings) while 16 new seedling were marked on July 3 and 22 seedlings on July 14. All other periods had 5 or fewer new seedlings. The number of seedlings marked during this main dispersal period that survived to the end of the summer ranged from 56% for the July 14 group to 69% for the July 28 group. The greatest mortality came during the flooding season around August 15 - 22 when an average of 0.84 in of rainfall were received per day. Some plots were submerged for both of those sample periods so the exact time of mortality could not be determined on some plots. Plots that flooded tended to have greater mortalities than those that did not. Nearly 90% of the plants that had overwintered or were observed by July 3 survived whereas only 73% of those first observed on July 28 survived the

flooding. Data were pooled across all species since not all species could be identified because of their small size. Most seedlings that could be identified were *P. trichocarpa*.

The three species of Salicaceae dispersed seed during different, but overlapping, times during the growing season although the exact timing may vary with weather conditions, especially after a cold spring. Temperatures have been reported to affect timing of seed maturation in *Populus* (Schreiner, 1974). *Salix alaxensis* dispersed seed in early June 1993 (late May to late June) while *S. sitchensis* dispersed seed from early to mid-July. *P. trichocarpa* dispersed seed in mid July to early August. It dispersed seed slightly later than the other two Salicaceae (willow) species and closer to the initiation of late summer rains. The main dispersal time for these Salicaceae seemed to be a one to two-week period (approximately). *P. trichocarpa* and other willow seeds can be dispersed to high altitudes because of the plumes and their light weight. The Salicaceae seeds have short periods of viability, a few days for *Salix* spp. (Brinkman, 1974) and 2 to 4 wk for *P. trichocarpa* (Schreiner, 1974). Although these species require moisture for germination and initial establishment, flooding can damage seedlings (Brinkman, 1974; Schreiner, 1974). Dispersal closer to the rainy season may increase the chance of germination but increase the risk of flood mortality.

E. latifolium dispersed seeds late in the summer and early fall because of the number of areas and sites with different slopes and aspects where it was found. Some plants dispersed in mid-August while others have not yet bloomed.

Dryas drummondii was most common in the Patchy stage and somewhat less in the Isolated Plant stage. It formed mats up to 2 to 3 m in diameter but never averaged more than 1% cover, substantially less than that achieved in the Glacier Bay and other areas. Seeds were dispersed in August and September, a relatively long time compared to the Salicaceae. Although *D. drummondii* is a nitrogen-fixing plant species, we were unable to find any nodules, possibly because we could not dig deep enough in the gravels and cobbles without breaking the roots.

Although occasional seedlings of *A. sinuata* were found on the outwash plain it was not a major player in the early successional stages at Exit Glacier, in agreement with (Cooper, 1931)'s observations. However, it was the major early colonizer at many of the other glaciers in Kenai Fjords National Park where *P. trichocarpa* was not found. Many of the *Alnus* individuals at Exit Glacier were heavily nodulated. Germination of *A. sinuata* is frequently limited by moisture on disturbed sites (Mitchell and Mitchell, 1980) and may also require microorganisms such as mycorrhizal fungi and the nitrogen-fixing bacteria as suggested by (Helm and Carling, 1993).

SOILS

Soils in the various stages of the chronosequence were generally similar to those of other studies, but our substrates appeared coarser with > 50% of the sample being gravel in the early successional stages (Table 8), possibly as a result of wind, water, and frost action. Sand was the dominant soil particle size in the earliest stages (Barren through Patchy) and was greater in our study than others. We averaged about 90% sand whereas others averaged about 65% (Ugolini, 1968). The pH values initially were near neutral or higher ranging from 7.2 on the moraine adjacent to the glacier and the Patchy stage to 8.0 on the "Barren" portion of the outwash plain (Table 9). The pH dropped to 5.7 in the mineral soil in the Alder stage and remained near 6 through the Spruce - Cottonwood stage. The mineral soil in the Spruce - Hemlock stage had a pH of 4.5. Although extractable-N levels were high in organic layers in all stages with organic surface soils, the extractable-N levels in the mineral soils did not increase until the Cottonwood stage. Extractable P appeared greatest during mid-succession and in the organic layers. Extractable K was highly variable within the youngest stands. It was greatest with smaller particle sizes and probably with a reduction in flooding. The moraine soil had some of the higher K levels in mineral soils because it had more fines and was not being flushed by the river.

The total N concentration increased from 0.03% in the earliest stages to 0.08% in mineral soils in the Alder stage to 0.51% in the Spruce - Hemlock stage. Total P was similar throughout the chronosequence (Table 9). Organic matter and CEC also were low in the first three stages with some increase in the Alder stage, but the major increase occurred in the Cottonwood stage. Interestingly, the CEC on the moraine was greater than the CEC's in the other early stages, probably as a result of finer soil texture and lack of flooding.

COMPARISONS WITH OTHER KENAI FJORDS GLACIERS

Qualitative observations were made on vegetation species and colonization around other glaciers in Kenai Fjords during 1992 and 1993. Some glaciers were at tidewater and had little ground, except that to the sides, that had been deglaciated recently. Even where the glaciers had retreated far enough landward so that a floodplain existed, *Alnus sinuata* was the dominant early colonizing species, with newly germinated seedlings present in June. *Populus trichocarpa* was not found except for a few saplings in McCarty Fjord, at the south end of the Kenai Peninsula. Many of the other glaciers, including those at sea level, had more subalpine species. These were similar to some plant species observed on the slopes above Exit Glacier itself as compared with the outwash plain where our study concentrated. *A. sinuata* was abundant on the ridges, and numerous cones were found on the slopes. These other glaciers had wetter environments with the total precipitation increased southward along the coast (National Park Service, pers. comm.).

DISCUSSION

The chronosequence based at Kenai Fjords National Park differed from Glacier Bay in that *Populus trichocarpa* was a major colonizer rather than *Dryas drummondii*. Another difference was the emphasis on the outwash plain where fluvial actions were still active. Extensive alluvial flats did not occur at Glacier Bay during Cooper's studies, but apparently did during the interglacial period as stands of *P. trichocarpa*

were found in the remains of the interglacial forest of Muir Inlet (Cooper, 1931). Cooper used observations on the Stikine River in Alaska and British Columbia to document the early colonization by *P. trichocarpa*.

The small size of the Exit Glacier valley limited the amount of replication available for some stages, especially the older stages. The chronosequence on the outwash plain has not reached the pure Spruce or later stages, probably because the valley has not been deglaciated long enough. The Spruce - Cottonwood stand, the oldest stand sampled on the outwash plain, was near the confluence of Exit Glacier Creek and the Resurrection River. Repeated initial disturbances may have resulted in slow initial colonization and vegetation development. Cooper (1931) felt that floodplain succession was probably slower than the chronosequences he described. The small size of the Exit Glacier valley, the dominance of the outwash plain between the valley walls, and repeated initial disturbances may account for fewer species here than at other glaciers. The slopes above the deglaciated portion of the outwash plain were predominantly cliffs, relatively inaccessible communities, or Spruce - Hemlock forest that was above the most recent glaciation. However, the vegetation on the slopes above the glacier itself was diverse and similar to that near some other glaciers in Kenai Fjords.

Initial colonization appeared most related to seed source since the most abundant seedlings were *Populus trichocarpa*, which was also the dominant tree species in the valley. (*Alnus sinuata* is the dominant early colonizer at other Kenai Fjords glaciers, where it was also the dominant species in the area.)

Timing of seed dispersal with respect to summer rains and flooding may affect plant germination and establishment. Some of the Salicaceae may disperse before there is significant moisture from rain. The substrates are too coarse to maintain moisture from snowmelt or rain for a significant period. *Salix alaxensis* dispersed early. It could establish along water courses or other sites with favorable moisture or during years with wet early growing seasons and dry late summers that had reduced flooding disturbance. Species that dispersed later may have better moisture but may not be established enough before high waters occur in August. Although seedlings of both *S. alaxensis* and *S. sitchensis* were found on the outwash

plain, *S. sitchensis* was more important in colonizing the outwash plain and surviving in the Isolated Plant and Patchy stages whereas *S. alaxensis* reached its best growth along drainages. *S. sitchensis* may be able to establish on the dry outwash plain more readily since it disperses closer to the rainy season but early enough to grow sufficiently to survive flooding. Although many other studies mention both species, *S. sitchensis* seemed to be present in more areas than *S. alaxensis* (??). The effect of timing of seed dispersal with respect to moisture availability and flooding has been reported on several riparian studies in Alaska (Viereck, 1970; Helm et al., 1985; Walker et al., 1986). *A. sinuata* seeds dispersed during the winter so early rains and snow melt would favor its establishment. Greater moisture at other locations may allow *A. sinuata* to establish on the youngest sites at those locations, but not on the Exit Glacier outwash plain where low moisture during late May and June may limit the germination.

Alder stands were the youngest ones that could be characterized by the dominant species but were not as common as expected from other studies. Most of the well-developed *A. sinuata* stands were near the runout of an avalanche-rock slide chute. Sites that have been deglaciated sufficiently long for *A. sinuata* to become established were still being actively flooded during many growing seasons. Other sites had already developed later successional vegetation except where the repeated disturbance of avalanches and rock slides maintains the vegetation in an earlier successional stage than it would be otherwise.

Changes in community composition were most rapid during early stages. Although initial establishment was slow, the dominance of various plant species changes relatively rapidly based on relative growth rates and longevity. Alder stands could develop within the first 40 yr if additional disturbances did not occur. As the longer-lived trees dominated, changes occurred more slowly until the next species dominated.

Changes in diversity were somewhat different from those at Glacier Bay (Reiners et al., 1971). They started with low evenness and increased over time, which was generally greater than ours throughout. They had a strong decrease in diversity in the ?? stage. We started with a relatively high evenness among the

earliest colonizers with no strong dominant. Our diversity decreased through the mid-successional stages as dominance by *A. sinuata* then mature *P. trichocarpa* decreased the evenness although richness increased. Diversities in the later stages were surprisingly similar. However, some of the diversity in the Spruce - Hemlock stand resulted from different species in the opening along gullies.

The dynamics of the outwash plain and our interest in early community development dictated that we divide this development into three stages similar to Ugolini (1968). The pioneer stage that other researchers refer to probably corresponds to our Isolated Plant (Stage 2) or Patchy (Stage 3) stages, which occur 10 to 20 years after "stabilization."

Picea sitchensis individuals did not contribute significant cover until the Cottonwood stage. The *T. mertensiana* was still only a minor species in the Spruce - Cottonwood stands, even though a seed source was not far away. Many young *T. mertensiana* did not occur until more organic soils or rotten logs were present for their establishment. Logs could raise the young plants above the competition with other plants on the forest floor (Deal et al., 1991).

Succession at Exit Glacier followed a combination of successional models. *Populus trichocarpa* was an initial colonizer and maintained itself through several successional stages at least 150 yr after deglaciation. Additional species arrived and departed within the lifetime of *P. trichocarpa* individuals. Hence, more overlap existed than indicated by the relay model. Although *Picea sitchensis* and *Tsuga mertensiana* seedlings were found in the youngest stages, these individuals usually did not mature from this stage, which corresponded to the thinking of (Cooper, 1923). Additional recruitment of *Picea sitchensis*, *Tsuga mertensiana*, and *Alnus sinuata* were needed to achieve the cover of later successional stages. All major species were found on the outwash plain, but patterns of establishment differed, making the initial floristics model inappropriate (Matthews, 1992). Species groups were not as distinct as the relay floristics model of Egler (1954).

Because of the extensive overlap of species in the different early and mid-successional stages, the initial floristic composition model (Egler, 1954) with its dependence on life cycles might be an appropriate model. However, the later stages of Exit Glacier chronosequence depend on reaction mechanisms or possibly facilitation, making the relay model more appropriate.

Similarly, the different processes within the facilitation, tolerance, and inhibition models of Connell and Slatyer (1977) affected community development at different stages. *Populus trichocarpa*, for example, shaded out some species (including itself), but the organic soils and dead logs eventually provided seed beds for *T. mertensiana*.

A geocological model proposed by Matthews (1992) which stresses the physical processes during the early stages of succession may be appropriate for the outwash plain where floods and winds blowing sands and silts are common. In the latter stages, biological processes become more important.

One intriguing question raised by comparing the vegetation chronosequence of the Kenai Fjords glaciers is why the other glaciers were dominated by *Alnus sinuata* and Exit Glacier by *Populus trichocarpa*. The wind-borne seeds of *P. trichocarpa* should reach distant areas more readily than *A. sinuata*. A few middle-aged *P. trichocarpa* were found in McCarty Fjord where this species could come through passes from the southern part of the Kenai Peninsula. However, in Northwestern Fjords, no *P. trichocarpa* have been found. This portion of Kenai Fjords has just been deglaciated in the last 41 years, is mid-way along the coast, and is surrounded by the tallest mountains. Hence, it was the most isolated portion of the Kenai Fjords. It is speculated that the *A. sinuata* may have been able to survive in refugia on the ridge crests during the recent glaciations, and hence the seed source was readily available. *P. trichocarpa* probably could not survive on these crests for one reason or another. The coastal points of land had already developed into conifer forests. Many of the herbaceous species found above the deglaciated areas at these other glaciers were similar to subalpine communities, and somewhat similar to those found at higher elevations above Exit Glacier proper. Many of these species were similar to those described in

other vegetation chronosequences. Additionally, Cooper (1942) noted two main types of vegetation near glaciers in the Prince William Sound area: one like the coastal forests and one dominated by *Alnus*. The latter were generally in areas that were close to their maximum advance and were very close to existing icefields. This would follow the same pattern in Kenai Fjords, where the other glaciers are closer to the main icefields.

Exact aging of sites was difficult because of the slow growth of seedlings, possible burial by sedimentation, litter buildup around the trunk, and the size of the increment bore handle which forces cores to be taken at least 20 cm above the ground. Ages may be underestimated by as much as 20 to 30 yr, similar to estimates of Viereck (1967). Based on excavations in the Isolated Plant and Patchy stages, sedimentation was not as extensive here as it was on the Susitna River in southcentral Alaska (Helm et al., 1985). Some "young" individuals of *P. trichocarpa* that we collected in the Patchy stage had nearly 20 terminal bud-scale scars (usually indicative of a year's growth) with essentially no elongation between these and were about 10 cm tall. *A. sinuata* ages were particularly difficult since the original stem would die but new stems arose from the same plant.

Seed traps placed around and distant from *P. trichocarpa* did not capture more seeds adjacent to a plant compared to traps away from plants. *E. latifolium* was small but appeared to provide a better deposition zone because of its bushiness next to the ground.

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TABLE 1
Cover of major species in various stages of vegetation chronosequence at Exit Glacier, Kenai Fjords National Park, 1991.

	Barren		Isolated		Patchy		Alder		Cottonwood		Spruce-Cottonwood		Spruce-Hemlock	
	n=3		n=16		n=17		n=4		n=13		n=3		n=3	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Surface	100	0	90	5	83	4	27	15	2	1				
Gravel	76	3	68	6	66	4	1	1						
Sand	16	5	3	1										
Silt	4	4	0	0										
Ground			17	5	63	3	84	9	99	0	99	1	99	1
Mosses			17	5	57	3	13	8	25	4	33	7	26	7
Lichens					5	2			0	0	1	1		
Litter					2	1	77	13	94	3	94	3	89	4
Forbs					2	1	1	1	12	4	13	4	3	1
<i>Epilobium latifolium</i>					1	1								
<i>Epilobium angustifolium</i>									1	1				
<i>Pyrola secunda</i>							1	1	7	2	1	1		
<i>Pyrola asarifolia</i>									1	1	9	5		
<i>Pyrola</i> spp.									0	0				
<i>Moneses uniflora</i>									0	0	1	1		
Shrubs			0	0	3	1	9	4	10	5	4	1	12	5
<i>Salix alaxensis</i>			0	0	1	0	4	4	9	6				
<i>Salix sitchensis</i>			0	0	1	0	5	1	1	1				
<i>Dryas drummondii</i>					1	1								
<i>Alnus sinuata</i>					0	0	81	9	48	7	28	13	3	2
Trees			1	0	6	1	6	3	73	5	44	4	86	5
<i>Populus trichocarpa</i>			1	0	6	1	6	3	73	5	18	1		
<i>Picea sitchensis</i>									2	1	33	6	44	18
<i>Tsuga mertensiana</i>											1	1	48	22
Total Vascular Plant Cover			1	1	10	2	88	6	93	3	70	7	97	1
Total Canopy Cover			1	0	6	1	84	6	85	4	59	5	87	5
Total Living Plant Cover			17	5	67	3	93	3	95	2	85	5	99	1
Number of Species			1.3		3.6		4.5		7.8		12.0		7.0	
Simpson's Evenness			0.94		0.70		0.32		0.40		0.39		0.66	
Simpson's Diversity			1.20		2.52		1.40		2.74		4.72		4.60	

TABLE 2
Dimensions and ages of species in Isolated Plant stage 2, Exit Glacier, 1991.

16 transects	n	Height (cm)		Age (yr)		Density (stems/ha)	
		Mean	SE	Mean	SE	Mean	SE
Cottonwood < 2m		30	5	11	1	3500	788
Feltleaf willow		44	8			156	75
Sitka willow		9	0			250	102
Avens		5	1			94	50
Dwarf fireweed		6	1			750	296

Table 4
Dimensions and ages of species in Alder Stage 4, Exit Glacier, 1991.

4 transects	n	Height (m)		Basal Diameter (cm)		Age (yr)		Density (stems/ha)	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Cottonwood < 2m								3375	2249
Cottonwood > 2m*		4	1	5	0	20	2	100	71
Alder		4	0	5	0	14	2	2250	957
Feltleaf willow		5	0	5	0	21	0	500	354
Sitka willow		3	1	5	2	15	2	250	144

*Basal diameter is actually DBH (diameter-at-breast-height)

Tables 8, 9.
Soils characteristics in chronosequence at Exit Glacier, summer 1991 and 1993

	Count	pH	EC (mmhos/cm)	NH4 (ppm)	NO3 (ppm)	Ext N (ppm)	Ext P (ppm)	Ext K (ppm)	Tot_N (%)	Tot_P (%)	OM (%)	CEC	Gravel (%)	Sand (%)	Silt (%)	Clay (%)
Moraine	2	7.63	0.17	1.5	1.1	2.6	4	68	0.04	0.08	1.29	2.90	53.80	61.2	24.0	14.8
Barren	3	8.01	0.21	7.0	0.7	7.7	3	16	0.03	0.08	1.27	0.72	57.77	90.4	6.2	3.4
Isolated	5	7.39	0.19	4.2	1.8	6.0	5	9	0.04	0.07	1.62	0.66	51.85	94.9	3.2	1.9
Patchy	5	7.23	0.10	4.0	1.2	5.2	6	9	0.03	0.06	1.74	0.87	63.86	97.1	1.3	1.6
Alder-Mineral	3	5.72	0.15	2.0	2.4	4.4	9	32	0.08	0.09	1.62	2.09	32.10	74.0	14.0	12.0
Alder Organic	2	5.11	0.40	39.0	66.0	105.0	15	136	0.52	0.09	20.25	48.18	0.00	88.4	10.0	1.6
Cottonwood Mineral	3	5.97	0.21	12.3	7.0	19.3	5	53	0.49	0.08	4.73	5.62	63.29	82.8	10.7	6.6
Cottonwood Organic	1	5.76	0.19	91.0	7.0	98.0	21	344	1.58	0.08		102.07	0.00			
Spruce-Cottonwood	1	6.32		2.0	1.0	3.0	4	46	0.13	0.11	3.76	5.52		65.6	28.0	6.4
Spruce-Hemlock Mineral	1	4.50		12.0	7.0	19.0	2	58	0.51	0.10	16.59	27.99		57.6	40.0	2.4
Spruce-Hemlock Organic	1	3.84		87.0	8.0	95.0	20	240	1.23	0.12	57.17	82.49		94.0	3.6	2.4

Table 8 will be texture, Table 9 will be rest. I needed to break it down to put std err in without getting too unwieldy.