

Patterns of primary succession on the foreland of Coleman Glacier, Washington, USA

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Abstract

Patterns of community development vary among studied glacier forelands around the world. However, there have been few studies of primary succession on glacial forelands in temperate regions of North America. We described patterns in community composition, vegetation cover, diversity, and vegetation heterogeneity during primary succession on the foreland of Coleman Glacier, in Washington State, USA. Community composition changed rapidly with high turnover between age classes. Cover increased through succession as expected. Species richness and diversity were highest in early succession at small scales and in late succession at larger scales. At small scales, heterogeneity decreased in early succession but increased in mature sites. At larger scales, heterogeneity reached its lowest point earlier in succession. These scale-dependent patterns in diversity and heterogeneity differ from results of other studies of glacier forelands. We hypothesize that these patterns arise due to the development of a dense canopy of the deciduous shrub *Alnus viridis* followed by a dense canopy of *Abies amabilis*, *Tsuga heterophylla*, and *Pseudotsuga menziesii*.

Introduction

Due to a significant increase in human disturbances to plant communities (Walker and del Moral 2003), it is becoming increasingly important to understand how plant communities respond to disturbance. Although primary succession occurs after natural disturbances on only a small fraction of the land surface of the earth, it frequently results from various forms of human disturbances. Site-specific factors can affect successional patterns in different ways, making it valuable to compare patterns among different sites (Drury and Nisbit 1973).

Community properties such as species composition, vegetation cover, species richness, diversity,

and vegetation heterogeneity should change as primary succession progresses. Plant cover and biomass increase through most successional sequences, usually leading to more intense competitive interactions between individuals.

Two major patterns of species diversity through succession have been suggested by both theory and observation (Peet 1992). First, diversity can increase asymptotically through succession (Odum 1969). As time passes, more species become established, until a balance between colonization and local extinction is reached. This pattern of increasing richness and diversity is very common in early primary succession (Matthews 1992) and has been observed or inferred over longer time scales in primary succession on volcanoes

(Whittaker et al. 1989) and glacier forelands (Reiners et al. 1971; Birks 1980). However, as biomass and cover increase later in succession, competitive dominance can lead to declines in richness and diversity (Connell 1978). This process results in the second pattern; a peak in diversity at an intermediate stage of succession, which has been observed in both secondary (Peet 1992) and primary succession (Matthews 1992).

As succession proceeds, the vegetation should become more similar to undisturbed surrounding vegetation. However, many factors, such as initial site conditions, landscape factors, and changes in environment through succession can influence the degree to which successional communities converge with surrounding undisturbed communities (Lepš and Rejmánek 1991). Later in succession, environmental control of the vegetation and intensity of species interactions are expected to increase (del Moral 1999). This should decrease heterogeneity in the vegetation within a site. Heterogeneity has been shown to decrease through early succession (Dlugosch and del Moral 1999; del Moral and Jones 2002), but increasing heterogeneity has also been described (Inouye et al. 1987).

The chronosequence approach (a space-for-time substitution) is often used to study succession. The drawback to this approach is that any differences in environmental or historical factors among sites can confound the effects of age. Studying primary succession on glacier forelands is less prone to the problems inherent in a chronosequence because they provide a gradient in terrain age at a single site (Matthews 1992). However, factors that vary across the foreland, such as elevation and distance from intact vegetation, can affect successional patterns, and must be considered (Fastie 1995).

Primary succession has been studied on glacier forelands around the world, although few studies have been conducted in Washington or British Columbia (but see Oliver et al. 1985; Jumpponen et al. 1998). High snowfall at high elevation combined with long growing seasons at low elevation allow the development of dense, structurally complex forests on glacier forelands in this area, a feature that is uncommon on forelands elsewhere.

This paper describes patterns of primary succession on the foreland of Coleman Glacier on Mount Baker in Washington State, USA. We addressed three questions: (1) how do vegetation

cover, richness, and diversity change through succession? (2) Does the vegetation become more similar to surrounding vegetation? (3) Does vegetation heterogeneity decrease through succession? We also analyzed factors other than terrain age, such as elevation and distance from intact vegetation, that may change with age and confound successional patterns. We expected that terrain age would be more important than these factors in controlling successional patterns.

Methods

Study site

Coleman Glacier is located on the northwest side of Mount Baker in northwestern Washington State (lat. N 48°48', long. W 121°51'). The foreland is in the *Abies amabilis* zone, while the slopes above the valley extend into the *Tsuga mertensiana* zone (Franklin and Dyrness 1988). These zones receive high annual precipitation, mostly as winter snowfall, but have relatively dry summers. The nearest meteorological station is at Glacier Ranger Station, 11 km northwest of and 1000 m lower than the glacier terminus. Average monthly high temperatures at that station range from 3.4 °C in January to 23.6 °C in August, but actual temperatures at the foreland are likely several degrees cooler than this due to the higher elevation. Average annual precipitation at Glacier Ranger Station is 180 cm, with only 16% of this precipitation falling in June–September (data from the National Oceanic and Atmospheric Administration). A spatial model (PRISM), which considers the effect of topography on precipitation, estimated annual precipitation of 292 cm on the foreland, again with 16% occurring from June–September (Daly et al. 1994, 1997).

Soils near the foreland have developed as a mixture of volcanic ash and colluvium over glacial till (Goldin 1992; Boling et al. 1998). Under forest canopies the soil surface is covered by an organic horizon up to 30 cm thick. Soils are typically Spodosols or Andisols that have developed under acidic and cold conditions (Boling et al. 1998).

The terminus of the glacier was at an elevation of ~1300 m above sea level in 2000. Dendrochronological dating of moraines show that in ~1823 AD the terminus was at ~900 m, more than 2 km

beyond its current position (Heikkinen 1984). The 1823 moraine is within meters of an older moraine deposited in the early 16th century. Thus, the surface beyond this moraine has not been covered by ice for at least 500 years. The glacier has retreated since 1823, interrupted by several periods of advance during which moraines were deposited. A long period of advance occurred between 1947 and 1979, but the glacier had since retreated ~ 300 m (Harper 1993).

We divided the foreland into three age classes based on time since deglaciation: Age Class I = 0–24 years; Age Class II ≈ 70 –95 years; Age Class III ≈ 95 –180 years. These classes were bounded by dated moraines deposited in 1979, ~ 1908 , and ~ 1823 (Figure 1). A fourth age class consisted of terrain beyond the foreland but within 250 m of the moraine formed during the early 16th century. Each age class included a range of ages; within each age class surface age increased with distance from the glacier. However, it was not possible to determine the age of a given point within the age

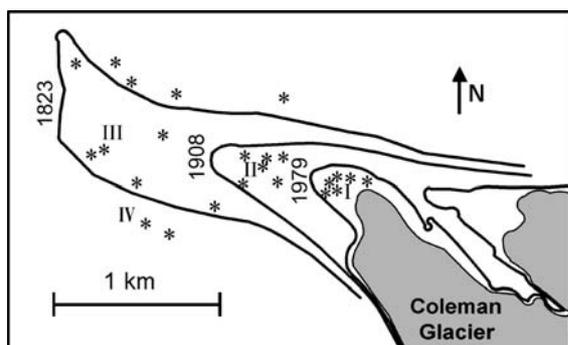


Figure 1. Map of Coleman Glacier foreland. Roman numerals identify age classes (see text) and lines indicate the position of the glacier in the year indicated. Stars indicate the approximate locations of the 100-m² plots.

class. Age Class III covers a wide range of ages, but most of the area within this age class is 150–180 years old.

Using ArcView 3.2 (ESRI 1999), with data from the USGS Digital Elevation Model (DEM) and maps from Heikkinen (1984), we summarized topographic information about each of the age classes (Table 1). While mean elevation was similar among age classes, much greater elevation range occurred in Age Classes III and IV, which extended from the valley floor to the surrounding ridges. Age Class II was more south-facing, while the other age classes contained both south- and north-facing slopes.

Field sampling

We located six 100 m² plots in each age class by randomly generating Universal Transverse Mercator (UTM) coordinates within the area of each age class (Figure 1). We then located these plots in the field in July and August of 2000 using the Global Positioning System. In ten randomly placed 1 m² quadrats within each plot, we measured percent cover of each species with individuals < 2 m tall. We estimated percent cover in the entire plot of each species with individuals > 2 m tall (canopy species). Nomenclature for vascular plants follows Kartesz (1999). Nomenclature for bryophytes follows Vitt et al. (1988).

For each plot we recorded location, elevation, slope, and aspect. Aspect was cosine transformed to give a range of values from -1 (south-facing) to 1 (north-facing). We also recorded a moisture index value for each plot based on topography: 1 = distant from surface water, 2 = a slope adjacent to surface water, and 3 = a depression

Table 1. Characteristics of age classes on the foreland of Coleman Glacier.

Age class	I	II	III	IV
Years since glaciation	0–23	70–94	94–179	> 500
Area (ha)	6.1	15.5	155.7	153.0
Mean aspect ^a	0.62 ± 0.50	-0.11 ± 0.86	0.14 ± 0.80	0.43 ± 0.62
Mean elevation (m)	1258 ± 39	1207 ± 53	1156 ± 143	1191 ± 216
Elevation range ^b (m)	142	237	698	913
Mean slope (%)	26.2 ± 9.2	23.2 ± 9.1	26.7 ± 10.4	24.1 ± 9.8

Numbers were calculated using GIS from the USGS Digital Elevation Model. Values are Mean \pm SD.

^aCosine transformed aspect.

^bDifference between highest and lowest elevation within the age class.

with presence or signs of previous surface water. Distance from the edge of the foreland (and thus a potential source of colonists) was calculated using ArcView 3.2 (ESRI 1999). Soil samples were pooled from four samples collected at a depth of 5–15 cm in each plot. Soils were dried for 48 h at 105°, and then pH was determined for each composite sample. We measured percent organic matter based on loss on ignition after 8 h at 600 °C in a muffle furnace.

Statistical analysis

We assessed changes in community composition by comparing total percent cover of life forms and of dominant species among age classes. To examine patterns in cover and diversity, we calculated total cover (sum of cover of all species present), species richness, evenness, and H' (Shannon diversity) for each quadrat and each plot (McCune and Mefford 1999). Nearly every sample failed the Shapiro–Wilks normality test or the Bartlett's test for equality of variance, so we used the non-parametric Kruskal–Wallis test to compare age classes (Analytical Software 2001). For comparisons that were significant, we compared the means of age classes using the ranked sum test.

Patterns in species composition were summarized using Non-metric Multidimensional Scaling (NMS), with Sørensen's distance measure (PC-ORD, McCune and Mefford 1999). We used Monte Carlo simulations to determine the optimal dimensionality of the solution (cf. McCune and Grace 2002). NMS axis scores of each age class were then compared using a Kruskal–Wallis test followed by comparison of sample ranks. To assess the potential effects of age gradients within age classes on species composition, we calculated the correlation between distance from the glacier (which is strongly correlated with age) and NMS scores for all plots together and for plots in each age class.

Changes in composition among age classes was also determined by mean percent similarity (PS) among age classes at the 100 m² scale. We calculated PS among all pairs of plots using MVSP (Kovach 1998). PS between two age classes was calculated as the mean PS between all plots in one age class with all plots in the other age class.

We also used PS to assess changes in vegetation heterogeneity within age classes at two different scales: (1) Within-plot heterogeneity, the mean PS among all pairs of quadrats in the same plot and (2) among-plot heterogeneity, the mean PS among plots using mean cover of each species for the entire plot. For each scale, we compared mean PS among age classes using Kruskal–Wallis tests. Within-plot PS measures heterogeneity over short distances and among-plot PS measures changes in the vegetation over longer distances.

Because distance between plots can affect both diversity measures and heterogeneity, we calculated the mean geographic distances among plots for each age class. We used a Mantel test (McCune and Grace 2002) to compare the matrix of geographic distances between plots with the matrix of ecological distance (Sørensen distance = 1 – PS). We made this comparison for all plots together and for plots within each age class independently.

To assess what factors other than age could influence vegetation patterns, we compared the topographic and soil variables among age classes using Kruskal–Wallis tests followed by rank sum tests for significant results. Spearman correlations between NMS axis scores and topographic and soil variables were calculated to test for correlations between patterns in species composition and environmental variables. Spearman correlations were also used to test for correlation among environmental variables. Distance from the nearest foreland edge (source of potential colonizers) might have an effect on the vegetation that could confound effects of surface age. To test for this effect we calculated the Spearman correlation between distance from the foreland edge and plot richness and cover for all plots together and for each age class independently.

Results

Cover, richness, and diversity

Total ground layer cover increased from 25% in Age Class I to 101% in Age Class IV (Table 2A). Total vegetation cover (including canopy species) also increased from 25% in Age Class I to 169% in Age Class III (Table 2B). Total cover declined slightly in Age Class IV.

Table 2. Vegetation structure summarized by age class.

	<i>H</i>	<i>p</i>	I	II	III	IV
<i>A. Quadrats (n = 240)</i>						
Cover	58.74	< 0.0001	24.88 ^a	57.52 ^b	80.42 ^{bc}	100.58 ^c
Richness	66.56	< 0.0001	9.10 ^a	4.73 ^b	5.73 ^b	5.33 ^b
Evenness	9.45	0.024	0.66 ^{ab}	0.65 ^a	0.51 ^b	0.61 ^{ab}
Diversity (H')	29.79	< 0.0001	1.43 ^a	1.01 ^b	0.89 ^b	1.00 ^b
<i>B. Plots (n = 24)</i>						
Cover	13.63	0.004	24.89 ^a	156.80 ^b	169.36 ^b	146.64 ^{ab}
Richness	5.41	0.14	20.33	14.67	15.33	14.00
Evenness	0.96	0.81	0.63	0.59	0.60	0.64
Diversity (H')	3.03	0.39	1.89	1.58	1.61	1.63
<i>C. Age classes (n = 4)</i>						
Richness			33	23	38	39
Evenness			0.59	0.62	0.58	0.61
Diversity (H')			2.08	1.94	2.12	2.23

Quadrats include only ground layer, plots include canopy. Bold numbers indicates significant results of Kruskal–Wallis tests. Different superscript letters within a row indicate significant differences in the means as determined by ranked sum comparison ($\alpha = 0.05$).

Richness was higher in Age Class I (9.1 species/quadrat) than in any other age class at the 1 m² scale (Table 2A). It was also highest in Age Class I at the 100 m² scale (20.3 species/plot), but not significantly so. Total species richness, however, was higher in Age Classes III and IV (38 and 39 species) than in Age Classes I and II (33 and 23 species).

Diversity (H') at the 1 m² scale was higher in Age Class I (1.43) than in any other age class (Table 2A). Diversity and evenness at the 1 m² scale were lowest in Age Class III, which was dominated by mosses. There were no statistically significant differences in richness, diversity, or evenness at the 100 m² scale, although richness and diversity were both highest in Age Class I.

Species composition

Mean cover of common species varied among age classes (Table 3). Total cover was low in Age Class I, and was comprised predominately of herbaceous perennials mixed with young individuals of *Alnus viridis*, *Salix sitchensis*, and various conifers (Table 3). *Alnus viridis* became more common farther from the glacier in Age Class I. Age Class II was dominated by a canopy of *A. viridis* with an understory of several shrubs (e.g. *Sambucus racemosa* and *Ribes lacustre*) and herbaceous perennials, and scattered, but taller, conifers. In older parts of this age class, conifers formed part of

the canopy and dead *A. viridis* individuals were common. Age Class III was dominated by *Tsuga heterophylla* and *Abies amabilis*. The understory was sparse, dominated by several species of moss including *Rhytidiopsis robusta*, *Rhytidiadelphus loreus*, and *Hylocomium splendens*. Shrub and herbaceous understory species were locally abundant. Beyond the foreland, Age Class IV also had a conifer canopy but with more openings (Table 4). Many of the species were those found in Age Class III, but in Age Class IV shrubs and herbs such as *Rubus* spp. and *Vaccinium* spp. were more common and mosses less common.

The one-dimensional solution for NMS was optimal. NMS axis scores (reflecting species composition) for plots in Age Classes I and II were different from each other and from all other ages, but scores of Age Classes III and IV did not differ significantly from each other (Figure 2). NMS axis scores were strongly correlated with distance from the glacier for all plots together ($r = 0.93$, $p < 0.0001$) and for plots within Age Class II ($r = 0.94$, $p = 0.002$).

There was high species turnover between Age Classes I and II. Of the 33 species present in Age Class I, only six, including *A. viridis* and four conifer species, were present in other age classes. The change in species composition between Age Classes II and III was less drastic, with 70% of the species present in Age Class II also present in Age Classes III or IV. However the abundance of these species changed dramatically.

Table 3. Mean percent cover of common species by age class.

Species	Age class			
	I	II	III	IV
Trees	0.25	38.04	91.5	65.84
<i>Abies amabilis</i> (Dougl. Ex Loud.) Dougl. ex Forbes	0.06	6.55	37.5	20
<i>Abies lasiocarpa</i> (Hook.) Nutt.	0.01	2.83	0	0
<i>Pseudotsuga menziesii</i> (Mirbel) Franco	0.08	0.83	5.33	1.67
<i>Tsuga heterophylla</i> (Raf.) Sarg.	0.10	22.5	47	44.17
<i>Tsuga mertensiana</i> (Bong.) Carr.	0	5.33	1.67	0
Shrubs	15.66	92.24	11.75	36.4
<i>Alnus viridis</i> (Vill.) Lam. & DC.	9.36	72.5	1.17	0
<i>Menziesia ferruginea</i> Sm.	0	0	0.22	2.91
<i>Oplopanax horridus</i> Miq.	0	0	4.28	4.17
<i>Ribes lacustre</i> (Pers.) Poir.	0	8.34	0.05	0.01
<i>Rubus pedatus</i> Sm.	0	0	2.37	4.84
<i>Rubus spectabilis</i> Pursh	0	0	2.18	7.18
<i>Salix sitchensis</i> Sanson ex Bong.	6.30	0	0	0
<i>Sambucus racemosa</i> L.	0	11.4	0	0
<i>Sorbus sitchensis</i> M. Roemer	0	0	0	1
<i>Vaccinium membranaceum</i> Dougl. ex Torr.	0	0	0.37	2.72
<i>Vaccinium ovalifolium</i> Sm.	0	0	1.11	13.47
Forbs	4.19	15.64	6.36	1.95
<i>Anaphalis margaritacea</i> (L.) Benth.	1.02	0	0	0
<i>Chamerion latifolium</i> (L.) Holub	1.27	0	0	0
<i>Claytonia sibirica</i> L.	0	12	0	0.90
<i>Maianthemum stellatum</i> (L.) Link	0	0	1.26	0.01
<i>Tiarella trifoliata</i> L. var. <i>trifoliata</i>	0	0	2.62	0.13
Graminoids	2.77	0.05	0.12	0.2
<i>Agrostis scabra</i> Willd.	1.07	0	0	0
Ferns and Allies	0.02	1.19	9.68	6.09
<i>Athyrium filix-femina</i> (L.) Roth	0	0.87	4.47	3.3
<i>Gymnocarpium dryopteris</i> (L.) Newman	0	0	1.98	1.73
<i>Polystichum munitum</i> (Kaulfuss) K. Presl	0	0.32	2.93	0.54
Mosses and Liverworts	2.2	9.99	50.01	37.81
<i>Hylocomium splendens</i> (Hedw.) Schimp. in B.S.G.	0	0	2.4	0.45
<i>Hypnum</i> sp. Hedw.	0	4.13	1.15	4.86
<i>Polytrichum commune</i> Hedw.	0	3	0.08	0
<i>Racomitrium canescens</i> (Hedw.) Brid.	1.80	0	0	0
<i>Rhizomnium nudum</i> (Britt. & Williams) T. Kop.	0	0	5.10	1.83
<i>Rhytidiopsis robusta</i> (Hook.) Broth. ^a	0	2.73	41.18	30.6

All species with greater than 1% cover in any age class are listed. Totals by growth form (in bold) include rare species.

^aThese values also include cover of *Rhytidiadelphus loreus* (Hedw.) Warnst. because the two species were not differentiated until after sampling was conducted

Table 4. Characteristics of the canopy (individuals >2 m in height) by age class.

Canopy	Age class			
	I	II	III	IV
Conifer cover (%)	0	38	91.5	65.8
<i>Alnus</i> cover (%)	0	72.5	1.2	0
Total canopy cover (%)	0	110.5	92.7	65.8
SD (of total canopy)	–	19.9	20.1	22.7

PS between Age Class I and all other age classes were very low (Table 5). Vegetation in Age Class III was the most similar to the mature vegetation in Age Class IV.

Heterogeneity

Mean within-plot PS was higher later in succession, with a high of 50.6% for plots in Age Class

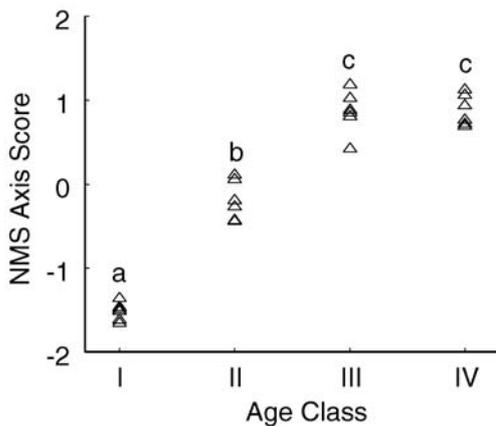


Figure 2. NMS axis scores of plots by age class. Each triangle represents the NMS axis score for a 100-m² plot. Different letters indicate significant differences in mean axis score among age classes as determined by comparison of ranks following a Kruskal–Wallis test ($\alpha = 0.05$).

Table 5. Mean among-plot PS by age class.

Age classes	Mean PS	SE
I–I	52.97 ^a	3.811
II–II	57.59 ^a	3.565
III–III	47.34 ^{ab}	4.274
IV–IV	44.56 ^{abc}	4.550
III–IV	47.41 ^a	2.906
II–III	17.54 ^{cd}	2.540
I–II	10.27 ^d	0.6179
II–IV	18.68 ^{bcd}	2.618
I–III	1.381 ^e	0.4549
I–IV	0.2178 ^e	0.0272

Roman numerals indicate age classes being compared. PS values were compared with a Kruskal–Wallis test ($H = 222.3$, $p < 0.0001$). Different superscript letters within columns represent significant differences as determined by comparison of ranks ($\alpha = 0.05$).

III (Figure 3; Kruskal–Wallis test: $H = 72.46$, $p < 0.0001$). Among-plot similarity was not significantly different among age classes ($H = 6.77$, $p = 0.08$). Unlike within-plot similarity, among-plot similarity was high in Age Class I.

Mean geographic distance among plots was much higher in Age Classes III and IV than in Age Classes I and II (Table 6) because of the larger area in these age classes. Mantel tests indicated significant ($p < 0.05$) correlations between geographical distance and ecological distance for

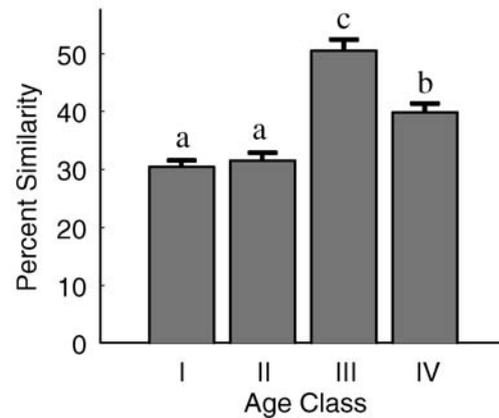


Figure 3. Mean within-plot PS by age class. Error bars indicate standard error. Different letters indicate significant differences among age classes as determined by comparison of ranks following a Kruskal–Wallis test ($\alpha = 0.05$).

all of the plots combined and for Age Class II, but not for the other age classes (Table 6).

Environmental factors potentially influencing succession

Several of the topographical variables differed significantly among age classes (Table 7). Mean elevation declined from Age Classes I to III, although elevation in Age Class IV was similar to Age Class I. The elevation of plots in Age Class III were lower than those in Age Class I. Distance from plots to the nearest foreland edge decreased from Age Class I to III. There were no significant differences among age classes in slope, aspect, or moisture class. Soil organic matter increased from Age Class I to Age Class IV. Soil pH was higher in Age Class I than in any other age class.

Several topographical and soil variables were also correlated with the NMS axis scores

Table 6. Effects of distance on similarity between plots.

Age class	Mean distance (m)	r (Mantel statistic)	p
All Plots	945	0.501	0.001
I	142	−0.081	0.532
II	102	0.662	0.010
III	732	−0.136	0.409
IV	857	−0.205	0.206

Mantel statistic calculated by comparing matrix of geographical distance with Sorensen distance.

Table 7. Comparisons of topographical and soil variables among age classes.

	H	p	I	II	III	IV
Aspect ^a	4.94	0.18	0.20 ± 0.86	-0.58 ± 0.75	0.16 ± 0.90	-0.03 ± 0.96
Distance ^b (m)	15.2	0.0005	433.2 ^a ± 40.5	315.9 ^{ab} ± 42.6	98.4 ^b ± 48.8	-
Elevation (m)	10.7	0.014	1254 ^a ± 54	1190 ^{ab} ± 64	1082 ^b ± 412	1237 ^{ab} ± 573
Moisture Index ^c	1.71	0.63	1.50 ± 0.84	1.33 ± 0.52	1.83 ± 0.75	1.67 ± 0.82
Organic Matter (%)	16.2	0.001	0.58 ^a ± 0.01	4.84 ^{ab} ± 0.04	20.47 ^b ± 0.32	25.17 ^b ± 0.23
PH	11.7	0.008	5.60 ^a ± 0.38	4.63 ^b ± 0.54	4.67 ^{ab} ± 0.39	4.57 ^b ± 0.44
Slope (°)	1.79	0.62	18.67 ± 8.59	16.50 ± 10.37	18.67 ± 12.91	12.67 ± 4.54

Values are means ± SD. Values in bold are significant results of Kruskal–Wallis tests at $\alpha = 0.05$. Different superscript letters within a row indicate significantly different means among age classes as determined by rank sum comparison ($\alpha = 0.05$).

^aCosine-transformed aspect.

^bDistance from edge of foreland.

^cbased on topography: 3 = depression with surface water; 2 = slope adjacent to water; 1 = distant from water.

(Table 8). Age class and organic matter were positively correlated with NMS scores, and distance from foreland edge and pH were negatively correlated. There are strong correlations among these variables (Table 9).

There was a significant correlation between total cover and distance from the foreland edge for all of the plots together (Spearman $r = -0.70$; $p = 0.002$), but not for plots within any age class ($p > 0.41$ for all age classes). There were no significant correlations between distance from the foreland edge and species richness ($p > 0.17$).

Discussion

Most studied glacier forelands are located at high latitudes and/or elevations and develop simple communities (Matthews 1992). Many forelands are in treeless areas, but there are exceptions (e.g. at Glacier Bay, Alaska). The less extreme conditions on the foreland of Coleman Glacier allowed

Table 8. Correlations of environmental variables with NMS axis scores.

Variable	r	p
Age class	0.87	<0.0001
Aspect ^a	-0.02	0.92
Distance ^a	-0.93	<0.0001
Elevation	-0.38	0.07
Moisture class ^a	0.33	0.12
Slope	0.07	0.73
Organic Matter	0.69	0.0003
PH	-0.44	0.03

^aSee Table 7 for definitions.

Bold indicates significant Spearman correlations.

Table 9. Correlations among environmental variables.

	Age	Distance	Elevation	O. M. ^a
Distance	-0.94			
Elevation	NS	0.678		
O.M. ^a	0.82	-0.717	NS	
pH	-0.59	0.647	0.471	-0.643

^asoil organic matter.

All values are Spearman rank correlations that are significant at $\alpha = 0.05$. NS = not significant.

a structurally complex forest community to develop, and this has affected patterns of community development.

Several successional stages were present on this foreland. An initial herb-dominated stage was followed by dominance by *Alnus viridis*. Conifers colonized early but grew slowly during the pioneer and *Alnus* stages. Very few seedlings of woody species germinated under the dense *Alnus* canopy, but the existing conifers continued to grow. After ~100 years the *Alnus* senesced and was replaced by a dense stand of conifers. Finally, beyond the foreland, an uneven-aged, more open conifer canopy allowed a well-developed understory.

These successional stages were similar to those found on forelands at Glacier Bay, Alaska (Chapin et al. 1994), although the Coleman Glacier foreland lacked a dwarf shrub stage. The development of a dense, even-aged conifer canopy with a poorly developed understory dominated by mosses (Age Class III) is consistent with other studies of primary (Oliver et al. 1985) and secondary succession (Alaback 1982) in northwestern North America. The dramatic

changes in species composition between Age Classes I and II and between Age Classes II and III were accompanied, and potentially caused, by the development of dense canopies of *Abies viridis* and conifers, respectively. However, the existence of gaps in terrain age between age classes could increase apparent turnover. Although Age Classes III and IV were structurally different, there was high overlap in species composition between them. Similarity between the two age classes was higher than among plots within Age Class IV.

Although vegetation cover increased, diversity and richness at small scales decreased during succession. The initial accumulation of species that has been found in many studies of primary succession (Matthews 1992; Walker and del Moral 2003) was not found on this foreland. The rate of species accumulation can be dependent on the isolation of the site. At many primary successional sites this accumulation has occurred over the first 20–40 years (Zollitsch 1969 as cited in Birks 1980; Matthews 1992). In more isolated primary succession sites, such as forelands at Glacier Bay (Reiners et al. 1971) and newly created islands (Rydin and Borgegård 1988; Whittaker et al. 1989), species accumulation can continue for more than a century.

On the Coleman Glacier foreland, there were ample sources of propagules for pioneer plants, both on the ridges above the foreland and along stream channels and other disturbed sites in older parts of the foreland. The availability of propagules led to a rapid accumulation of species even on the youngest terrain. At the same time, there was a gap in age between the first two age classes. Age Class I covered the range from 1 to 24 years while Age Class II was at least 70 years old. Because of the combination of rapid species accumulation and the constraints of the dating system, species accumulation over the first few decades would be difficult to detect.

Other studies of primary succession on glacier forelands have found peaks in species richness early in succession (Persson 1964; Zollitsch 1969 as cited in Elven and Ryvarden 1975; Matthews 1992). Because this study did not detect the initial accumulation of species, a peak in early succession would appear simply as a decline in species through succession.

Several factors could have caused a peak in richness and diversity within Age Class I. First, on

this site species turnover between age classes was very high, preventing overlap of early and late successional species, which could lead to a peak in diversity in mid-succession (Roberts and Gilliam 1995). Second, the development of a dense canopy often corresponds to a decrease in richness and diversity. A study of primary succession on a glacier foreland near the present study site also found strong decreases in diversity after canopy closure (Oliver et al. 1985). Studies of secondary succession in the northwestern United States (Halpern and Spies 1995) and elsewhere (Peet 1978; Christensen and Peet 1984) have demonstrated similar effects. However these studies also showed an increase in diversity as forests matured, which was not found at this site. Because a dense canopy is present in all age classes except Age Class I, canopy development could explain the reduced diversity in these age classes.

In contrast to small-scale patterns, overall species richness in age classes peaked late in succession. However, the greater overall richness late in succession could be due to increased distance between plots sampled in these ages. While similarity in species composition often declines with increasing distance (del Moral 1998), there were no significant associations between ecological and geographic distances in Age Classes III and IV. Increasing variability in environmental and topographical conditions among plots could also have led to increased richness late in succession. Of the variables recorded, only elevation had greater variability between plots in Age Classes III and IV. Since Age Classes III and IV included plots at lower elevations than younger classes, species present only at low elevations may have increased the sampled species richness in these age classes.

Various factors can affect vegetation heterogeneity. As vegetation develops, species patterns are more likely to be controlled by environmental conditions and species interactions than by stochastic events such as dispersal. This should lead to a decrease in heterogeneity as succession proceeds. In addition the development of a dense canopy can reduce variation in environmental conditions and lead to reduced compositional heterogeneity (Vetaas 1994; del Moral 1999). However, variation in canopy structure can create a heterogeneous light environment and maintain heterogeneity in the understory vegetation. In addition, variation in initial site conditions can

persist through succession and maintain heterogeneity throughout succession (Elgersma 1998; Walker and del Moral 2003).

Heterogeneity within plots decreased through early succession, as has been found in other studies of vegetation heterogeneity in primary succession (del Moral and Jones 2002; del Moral and Ellis 2004). Heterogeneity was lowest in Age Class III where conifer canopy cover was highest, then increased again in Age Class IV where average canopy cover was only 65%, providing a greater range of light environments within plots. In addition, the understory in Age Class III was dominated by *Rhytidiopsis robusta* and had the lowest evenness in quadrats, which would lead to lower heterogeneity. Although Age Class II had high canopy cover, it was a mixed canopy of deciduous *Alnus viridis* and evergreen conifers. This mixed canopy maintained a higher level of heterogeneity within plots in this age class.

Unlike within plot heterogeneity, among plot heterogeneity did not decrease through succession. Although canopy cover was high in Age Class III, it was variable among plots (Table 4). Also, topographic differences among sites can maintain heterogeneity (del Moral and Jones 2002). Elevation is much more variable in Age Classes III and IV, although variability in slope and aspect was consistent among age classes. This could increase the heterogeneity in these age classes and counteract the effects of increased canopy cover and species interactions.

Reduced among-plot similarity in Age Classes III and IV could also be due to greater distance between plots. Stochastic differences in dispersal are more likely as plots are farther apart. However, the correlation between geographic and ecological distance was only significant for Age Class II. This result is surprising, because the plots in Age Class II were close together. This result may have been due to the gradient in terrain age within Age Class II, which affected species composition. Age Class II was the only age class with a strong correlation between distance from the glacier and NMS axis score; in areas of the age class closest to the glacier there were only scattered conifers among dense *Alnus*, while areas farther from the glacier contained an even mixture of *Alnus* and conifers.

Factors other than age may affect patterns of vegetation between age classes. Differences in

topographical factors among age classes could influence the successional patterns differently at each site, invalidating the assumptions of the chronosequence approach. However, many of the measured topographical variables were not significantly different among age classes. The significant changes in soil variables such as pH and organic matter were expected as a result of vegetation and soil development. The increase in organic matter and decrease in pH were similar to those found at 18 glacier forelands in Norway (Messer 1988) and at Glacier Bay (Chapin et al. 1994).

The two significant variables that could affect vegetation patterns and that are independent of age were elevation and distance from the foreland edge (i.e. colonization source). Elevation was not significantly correlated with NMS axis scores, which suggests that it did not strongly influence vegetation patterns. If distance from the edge of the foreland were important in determining vegetation patterns, richness and cover should be lower farther from the edge within the same age class, but they were not. The negative correlation between cover and distance from the foreland edge for all of the plots together can be attributed to the increase in cover through succession, since late-successional plots are also closer to the foreland edge. Although elevation and distance from the foreland edge probably have some effect on the vegetation, these results suggest that they have far less influence than time since disturbance.

This study reinforces several important concepts about patterns of primary succession. First, the spatial scale of the foreland can have important consequences for interpreting patterns of succession. On this small glacier foreland, many species were able to colonize rapidly after glacial retreat, shortening the species accumulation phase of primary succession. Seedlings of the dominant late successional conifer species were able to colonize rapidly, as on other forelands in the region (Oliver et al. 1985) and in early stages of glacial retreat at Glacier Bay (Cooper 1923). However, as newly exposed terrain at Glacier Bay became increasingly remote from sources of conifer seeds, colonization was delayed (Reiners et al. 1971; Chapin et al. 1994). Differences in conifer colonization can lead to alternative successional pathways (Fastie 1995).

Second, this study suggests the importance of canopy development in successional patterns. At

this site, development of a deciduous shrub canopy was accompanied by major changes in species composition. This was followed by a conversion to an evergreen conifer canopy that was accompanied by further change in ground layer composition. Because of the restrictions of the dating system, more detailed study of the effects of canopy development on patterns of primary succession was not possible at this site. Permanent plot and experimental studies are needed to understand the role of canopy development in primary succession.

Third, this study shows how the constraints of the dating system in a chronosequence can affect the ability to detect successional patterns. Most chronosequence studies are restricted by the ages that are available, but the effects may vary depending on the specifics of the chronosequence chosen. In this case, the available dating system inhibited our ability to examine species accumulation and canopy development. It is necessary to consider the limitations of specific chronosequences in studies of primary succession.

Finally, comparisons of primary succession on this site with studies of secondary succession in the region suggest that patterns of forest development are similar. In both cases relatively even-aged conifer stands with species-poor understories develop, followed by thinning and the development of more diverse understory communities. There are, however, at least two major differences. In secondary succession many understory species survive the disturbance and are present in all stages of succession (Halpern and Spies 1995) whereas here species turnover among age classes was large. Also, canopy development in secondary succession occurs within 25–50 years after the disturbance (Alaback 1982; Halpern and Spies 1995), while during primary succession forest development is slower. Dense conifer forests developed only after more than 100 years both at this site and at another nearby foreland (Oliver et al. 1985). This slower rate is probably due to the initial lack of nutrients and slow soil development in primary succession (Prach et al. 1993).

Patterns of primary succession are affected by site-specific factors. Although many aspects of primary succession on the foreland of Coleman Glacier are similar to other glacier forelands, site factors such as spatial scale, canopy development, and regional climate affected patterns on this site.

Further study of the effects of these factors on community development is needed.

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