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Effects of microsite conditions on seedling establishment on the foreland of Coleman Glacier, Washington

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Abstract

Questions: How do physical microsite conditions of microsites affect germination and seedling survival in different successional stages? Do different species germinate in similar microsites in a given successional stage?

Location: Coleman Glacier foreland, Mount Baker, Washington State, USA.

Methods: Two methods were used to characterize safe sites. 1. Grids of 300 10 cm × 10 cm plots were located in four different age classes on the foreland. 2. 105 pairs of plots, with and without seedlings of *Abies amabilis*, were located in each age class. For each plot we identified all seedlings and all individuals < 1 m tall. Microsite characteristics such as topography and presence of rocks or woody debris were noted for each plot. Microsite characteristics were compared between plots with and without each species. In addition we examined the effect of distance from seed sources on the presence of *Alnus viridis* seeds and seedlings in a newly disturbed area.

Results: In early successional sites, seedlings of several species were positively associated with depressions and presence of rocks, and negatively associated with ridges. Patterns were generally consistent among species. In later succession, seedlings were not significantly associated with any microsite characteristics. For *Alnus viridis*, seed density decreased with distance from seed sources but seedling density did not.

Conclusions: Because of harsh conditions in early succession, physical microsites are important, and most species have similar microsite requirements. In later succession, physical microsites characteristics are not as important and are more variable. Microsites appear to be more important than seed rain in controlling the distribution of *Alnus viridis* in early succession.

Keywords: *Abies amabilis*; *Alnus viridis*; Primary succession; Safe site.

Nomenclature: Kartesz (1999).

Introduction

Seed germination and plant establishment usually depend on the environmental conditions in the immediate vicinity of the seed or seedling (Grubb 1977). Due to small-scale environmental heterogeneity, some microsites are more favourable to seed germination or seedling establishment than others (Harper et al. 1965). These more favourable sites are called safe sites, defined as microsites that satisfy the criteria for germination and establishment in a given species (Harper et al. 1961).

Spatial distribution of safe sites can often determine where establishment occurs, strongly influencing colonization and successional patterns. Microsite conditions can affect patterns of seed germination and seedling establishment in many communities (e.g. Eldridge et al. 1991; Oswald & Neuenschwander 1993; Titus & del Moral 1998). Physical features such as topographical features, amount of litter, presence of rocks or woody debris, and soil texture are important characteristics of microsites that can affect seedling establishment. The presence of other vegetation can also create variation in microclimatic conditions and strongly influence seed recruitment, germination and establishment.

Because vegetation cover is low and soils are poorly developed in early primary succession, high temperature and lack of moisture often limit germination and seedling survival (del Moral & Bliss 1993; Stöcklin & Bäumler 1996; Lichter 2000). Because of these extreme environmental conditions, safe sites are particularly important in early succession (Matthews & Whittaker 1987; Whittaker 1991; Frenot et al. 1998).

Micro-topographic features, e.g. depressions, cracks, and rocks, can increase soil moisture and reduce soil temperatures by providing shade and trapping water (Harper et al. 1965; Jumpponen et al. 1999). The presence of existing vegetation can also ameliorate environmental extremes, facilitating germination. Facilitation has long been considered an important mechanism of succession (Clements 1916) particularly in extreme environments, such as early primary succession

(Connell & Slatyer 1977). In extreme environments, existing vegetation may act as ‘nurse plants’ and create safe sites by shading or by adding nutrients to the soil (Niering et al. 1963). Nitrogen-fixing plants, in particular, can provide facilitative effects (Walker et al. 2003). However, existing individuals may also compete for resources with new seedlings, so the importance of facilitation in succession is unclear (Chapin et al. 1994).

Both topographic features and existing vegetation can also create safe sites by trapping seeds (Tsuyuzaki et al. 1997; Jumpponen et al. 1999). This can lead to increased germination in these sites simply by increasing the number of seeds.

The factors that control the distribution of a species can change through succession (Whittaker 1993). This can change the characteristics of microsites that are important for germination. On primary successional surfaces at Mount St. Helens, the importance of physical safe sites has declined with time (Titus & del Moral 1998). Microclimatic amelioration due to increased vegetation and soil organic matter allowed species to colonize a broader range of microsites. On a glacier foreland in the Swiss Alps, however, physical conditions were more important on older terrain that was located farther from the glacier and, therefore, was drier (Stöcklin & Bäumler 1996). While vegetation can facilitate germination in early succession, the dense vegetation of late succession can often inhibit germination and seedling survival (Chapin et al. 1994). In late succession, microsites that reduce competition or increase available light, such as those in canopy gaps or on logs, may be more important than physical microsite conditions that affect moisture or temperature (Eriksson & Ehrlén 1992).

Harper et al. (1961) hypothesized that different species have substantially different microsite requirements, which can lead to coexistence. This hypothesis has received strong support from some studies (Harper et al. 1965; Titus & del Moral 1998), while other studies found little variation among species (del Moral & Wood 1993; Jumpponen et al. 1999). Because different criteria are often used to characterize safe sites, comparisons among studies are problematic. In stressful environments, less variation in the characteristics of safe sites is expected among species than in more favourable environments because limiting resources will be more similar among species.

Glacier forelands provide the opportunity to study safe sites for different species on substrates in multiple successional stages. We examined the importance of microsite conditions along a chronosequence on the foreland of Coleman Glacier, in the Cascade Mountains of Washington, USA. This glacier has retreated during the past 180 years, creating a long successional sequence. The importance of microsites in plant establishment during primary succession has been studied in the Cascade Mountains both on volcanic substrates (del Moral & Wood 1993) and glacier forelands (Jumpponen et al. 1999), but these studies focused on early stages of succession. Few studies examine factors controlling seedling distribution throughout the successional sequence (Whittaker 1993; Chapin et al. 1994) and these few studies do not focus on microsite characteristics. We measured the distribution of seedlings in microsites throughout this succession over two years.

We addressed these major questions: 1. How do physical microsites affect the distribution of seedlings in different stages of succession? We hypothesized that the distribution of seedlings in early succession will be associated with microsites that can increase moisture availability, ameliorate temperature extremes, and trap seeds, but that these microsites will not affect seedling distribution in late succession. 2. Do different species germinate and grow in similar microsites in a given successional stage? We hypothesized that most species will grow in similar microsites in early succession but not in late succession. We addressed these questions by examining seedling distributions relative to microsites for the entire plant community and then by focusing on safe site characteristics for *Abies amabilis* and *Alnus viridis*, two common species.

Methods

Study site

Sampling was conducted on the foreland of Coleman Glacier, located on the northwest side of Mount Baker in NW Washington State (48º48' N, 121º51' W). The foreland is in the *Abies amabilis* zone while the slopes above the valley extend into the *Tsuga mertensiana* zone (Franklin & Dyrness 1988). Average annual precipitation on the foreland was estimated at 2920 mm using the PRISM model (Daly et al. 1994), with only 16% falling during the June-September growing season.

At the time of this study, the terminus of the glacier was at an elevation of ca. 1300 m a.s.l. Dendrochronological dating of conifers growing on moraines showed that ca.1823 AD the glacier terminus was more than 2 km beyond its current position (Heikkinen 1984). This 1823 moraine is within meters of a moraine from the early 16th century.

We divided the foreland into three age classes based on time since deglaciation: I = 0 - 24 a; II = ca. 70 - 95 a; III = 150 - 180 a (Fig. 1). These classes were bounded by dated moraines deposited in 1979, ca. 1908 and ca.1823. A fourth age class refers to terrain outside the foreland but within 250 m of the moraine from the early 16th

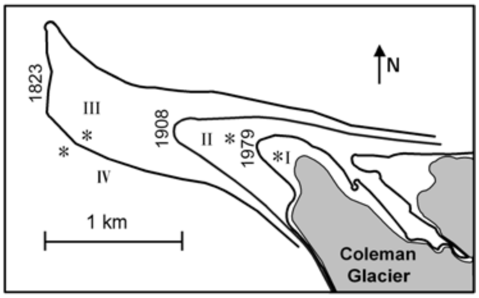

Fig. 1. Map of Coleman Glacier foreland. Roman numerals identify age classes (see text) and lines indicate the position of the glacier in the year indicated. Stars indicate the approximate locations of the grids and transects within each age class.

century. This age class has not been covered by ice for at least 500 years. The vegetation in Age Class I was predominantly herbaceous perennials mixed with the shrubs *Alnus viridis* and *Salix sitchensis* and seedlings of several conifer species (Jones 2003). A dense canopy of *Alnus viridis* (ca. 3-5 m in height) dominated Age Class II with an understorey of such shrub species as *Sambucus racemosa* and *Ribes lacustre*, a variety of herbaceous perennials, and scattered conifer saplings. In older parts of this age class, conifers contributed to the canopy. Age Class III was dominated by dense *Tsuga heterophylla* and *Abies amabilis* (>15 m in height). The understorey was sparse, dominated by several species of mosses. Beyond the foreland, Age Class IV had a more open conifer canopy. Understorey shrubs and herbs such as *Rubus* spp. and *Vaccinium* spp. were more common and mosses less common than in Age Class III.

Sampling and statistical analysis

We used three approaches to explore how microsite conditions affect establishment. First, in July-August 2001, we sampled 300 contiguous 10 cm × 10 cm plots in a 6 × 50 grid in each age class to allow pooling plots to examine larger-scale patterns (Jones 2003). The small plot size was chosen to characterize the environment in the immediate vicinity of the seedling. The location of each grid was determined randomly within a 0.25 ha (Age Classes I and II) or 1 ha (III and IV) area selected for accessibility. For each plot we recorded the presence and species of all seedlings. Seedlings were defined by size and lack of evidence of a previous year's growth. In addition, to understand the effects of microsite conditions on older plants, we recorded the presence of all species in each plot with individuals < 1 m tall. Analyses were conducted separately for seedlings and for all individuals. We also recorded characteristics of the physical conditions of each plot: topography (flat, depression, slope, or ridge); presence of any rock with ∅ ≥ 5 cm; and presence of woody debris ∅ ≥ 2 cm.

We used Fisher exact tests (Anon. 1997) to compare the abundance of each microsite type in plots with and without each species. This analysis was performed for every species with at least five, but not more than 295, occurrences in the 300 plots within an age class. Data were too sparse for analysis of rare species, whereas abundant species occur in all microsite types, making analysis meaningless.

The results of this first sampling approach showed that *Abies amabilis* was the only species present as a seedling in every age class. Therefore, we focused our second sampling effort in July-August 2002 on *Abies amabilis*. In Age Classes II, III, and IV we established seven line transects 3 m apart and 45 m long (Fig. 2). To space sample points along each transect we randomly located the points within every third meter along each transect (i.e. between 0 and 1 m, 3 and 4 m, 6 and 7 m, etc.). In Age Class I, stream disturbances and cliffs prevented the establishment of 45 m-long transects so we used 10 transects of varying length. All age classes had 105 sample points. We then located the *Abies amabilis* seedling nearest to each sample point. In a 10 cm × 10 cm area centred on the seedling, we recorded the identity of any other seedlings, estimated the percentage cover of each plant species (to the nearest 10%), and characterized the physical microsite, as described above. In Age Class I, we also recorded the percentage cover of gravel (> 0.5 cm and < 5 cm) and rock (≥ 5 cm). In Age Classes I, III and IV, we located a second 10 cm × 10 cm plot 50 cm to the west of each seedling as a control. If this plot contained an *Abies amabilis* seedling, we moved to 50 cm north of the original seedling. This design allowed comparison of vegetation and microsite characteristics between paired plots with and without *Abies amabilis* seedlings.

The density of *Abies* seedlings in Age Class II was very low. We found no seedlings within one meter on

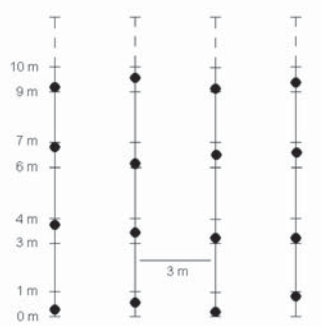

Fig. 2. Partial transect layout for 2002 microsite sampling. Vertical lines indicate parallel transects. ● indicate sample points randomly located within every third meter along each transect. The *Abies amabilis* seedling nearest each of the sample points was located for sampling.

either side of the first transect, so for this age class we sampled only the 10 cm × 10 cm plot surrounding each point. A few sample points in the other age classes did not have *Abies* seedlings within three meters, so those points were removed from the analysis. This resulted in from 100 to 105 pairs of plots (or single plots in Age Class II) for each age class.

To test for associations between microsite characteristics and distribution of each species except *Abies amabilis*, we used data only from the 'control plots' because those containing *Abies* seedlings were chosen due to the presence of *Abies* and were a biased sample. For *Abies* analysis we used all plots. As above, we eliminated all rare (less than five occurrences) and common (absent in less than five plots) species from analysis. We used Fisher exact tests for association with rocks or logs and χ^2 tests for topography (Anon. 1997) since there were more than two categories (i.e. flat, depression, slope, ridge). For *Abies* seedlings, we used Wilcoxon signed rank tests (Anon. 2001) to compare percent gravel, percent rock, percent litter, richness, total cover, and cover of common species (frequency > 20%) between plots with and without *Abies* seedlings. For comparisons of richness and cover, *Abies* seedlings were not included.

We used Multi-Response Permutation Procedures (MRPP) with Sørensen's distance (McCune & Mefford 1999) to test for a difference in vegetation composition between plots with and without *Abies* seedlings. This procedure determines whether plots with *Abies* seedlings are more similar to each other than would be expected by chance (McCune & Grace 2002). Effect size is measured by *A* (the chance-corrected, within-group agreement).

The third sampling approach was devised to study the effects of seed rain density on seedling establishment and to consider the effects of microsite conditions on seed trapping. This approach also investigated the effect of distance from a colonization source on the density of the seed rain. The seeds of *Alnus viridis*, the most common species in Age Classes I and II, are dispersed in late fall, often after the first snowfall. The seeds are blown across the snow and can concentrate in depressions in the snow surface. In November 2001, we counted *Alnus* seeds on the surface of the snow at varying distances from seed sources in an area within Age Class II that had been denuded by a flood in the summer of 2001. This flood produced a large area with no remnant vegetation or organic soil (similar to the surface immediately following glacial retreat), and with an abrupt edge of mature individuals of *Alnus viridis*. We counted the number of seeds in a 40cm × 40cm quadrat every 2.5 m along three 30 m-long transects extending from the edge of the *Alnus* thicket. We also recorded the topography of the snow surface in the quadrat. To compare the distribution of *Alnus* seeds and seedlings, we sampled five 30 m-long transects in the same area during September 2002. We counted the number of *Alnus* seedlings in 1-m^2 quadrats every 2.5 m along these transects and noted the topographical position of the seedlings.

We calculated the mean number of *Alnus* seeds and seedlings at each distance from the edge of the flood disturbance and calculated the Spearman rank correlation of number with distance. For seeds, we compared mean number of seeds per quadrat among topographic classes using a Kruskal-Wallis test. We observed that the majority of *Alnus* seedlings were under overhanging rocks or on north-facing slopes, so we calculated the percentage of seedlings on north-facing slopes, under overhanging rocks, or neither. We compared the proportion of the seedlings in quadrats with north-facing slopes with the proportion of quadrats with north-facing slopes using the Fisher exact test.

Results

A total of 55 species were sampled in the study plots (App. 1). Of these, 24 species were present as seedlings (App. 2). Although many of the same species were present as seedlings in both the 2001 and 2002 sampling, the frequency of many species varied greatly between the sampling regimes.

Physical microsite conditions

Topography affected the distribution of seedlings for many species in Age Classes I and II in 2001 (Table 1). In Age Class I, *Deschampsia elongata* was more common in depressions and on flat ground and less common on ridges than expected by chance. *Epilobium anagallidifolium* and *Montia parvifolia* were also more common in depressions. *Saxifraga ferruginea* was more common next to rocks and less common on ridges than expected by chance. In Age Class II, *Claytonia sibirica* was less common on slopes and more common in depressions, and *Stellaria crispa* was more common on slopes. In Age Classes I an II, *Abies amabilis* was not common enough for analysis. There were no significant results for any seedlings in Age Classes III and IV.

The patterns of associations between species and microsite characteristics were different for all individuals than for seedlings alone (Table 2). Several species were less common than expected by chance on ridges in Age Class I, but only *Montia parvifolia* was more common than expected in depressions. In Age Class II several species were less common than expected by chance in depressions. There were species with significant positive and negative results for flat terrain throughout succession. Some species were associated positively and some negatively with the presence of litter or woody debris. Several species were positively associated with the presence of rocks in Age Classes I-III. Many species were positively associated with slope in Age Classes II and IV, but this is likely a result of topographical breaks in the grids in these age classes. All of the slope plots were grouped together at one end of the grid and several species were present only on the slopes. Because many of the individuals of these species were larger than the plot size, a single individual was present in multiple quadrats.

Seedlings were uncommon in the 2002 plots. Only *Abies amabilis*, *Epilobium anagallidifolium*, *Montia parvifolia*, *Claytonia sibirica* and *Tsuga heterophylla* were sufficiently common for analysis. Of these, only *Abies amabilis* seedlings were associated with any microsite characteristics in the 2002 data. When we included all individuals of a species, *Hypnum* spec., a moss that grows on rocks and logs, was positively associated with rocks in Age Class II and with woody debris in Age Class IV ($p < 0.01$). *Tiarella trifoliata* was negatively associated with woody debris in Age Class IV ($p < 0.05$). *Claytonia sibirica* tended to be more common on flat terrain and less common on slopes and ridges in Age Class II ($\chi^2 = 13.57$; $p = 0.0036$).

Abies amabilis analysis

Microsite characteristics of plots with and without *Abies amabilis* seedlings differed only in Age Class I. *Abies* seedlings were more common in depressions and near rocks and less commonly found on ridges than expected by chance (Table 3A-B). In addition, mean total percentage cover, percent cover of the moss *Racomitrium canescens*, and species richness were higher in the plots containing *Abies* seedlings (Table 3C). No comparisons were significant in Age Classes III or IV for topography ($\chi^2 \leq 2.85$; $p \geq 0.42$), presence of rocks or woody debris ($p \geq 0.14$), or characteristics of the existing vegetation ($p \geq 0.10$). Results from MRPP showed no difference in species composition between plots with and without *Abies* seedlings (all $p > 0.35$). Chance-corrected within-group agreement (A) ranged from -1.28×10^{-4} in Age Class I to -3.38×10^{-3} in Class III. Similarity within groups did not deviate from chance expectation.

Table 1. Association of seedlings with microsite characteristics for 2001 data. Significant results of two-tailed Fisher exact test are indicated by + and – ($p < 0.05$) or + + and – – ($p < 0.01$). Empty columns indicate that the microsite was not present or was always present in the age class. Only species present in five or more plots are included.

	Rock	Wood	Flat	Depr.	Ridge	Slope	Litter
Age Class I							
Agrostis scabra	0		0	0	0		
Chamerion latifolium	0		0	0	0		
Deschampsia elongata	0		+	+	–		
Epilobium anagallidifolium	0		0	+	0		
Montia parvifolia	0		0	+ +	0		
Saxifraga ferruginea	+		0	0	– –		
Age Class II							
Claytonia sibirica	0	0	0	+ +		– –	0
Stellaria crispa	0	0	0	0		+ +	0
Age Class III							
Abies amabilis	0	0	0	0			0
Age Class IV							
Abies amabilis			0			0	
Rubus pedatus			0			0	
Vaccinium ovalifolium			0			0	

Alnus viridis analysis

Numbers of *Alnus viridis* seeds on the snow surface decreased with distance from the edge of the disturbed area (Fig. 3); $r = -0.65$; $p < 0.0001$) but numbers of seedlings did not ($r = -0.16$; $p = 0.36$). The number of seeds differed among topographical classes (Kruskal-Wallis test: $H = 13.18$; $p = 0.0043$), with more seeds in

Table 2. Association of species (all individuals) with microsite characteristics for 2001 data. Significant results of two-tailed Fisher exact test are indicated by + and – ($p < 0.05$) or + + and – – ($p < 0.01$). Empty columns indicate that the microsite was not present or was always present in the age class. Only species present in five or more plots are included.

	Rock	Wood	Flat	Depr.	Ridge	Slope	Litter
Age Class I							
Agrostis scabra	0		0	0	–		
Chamerion latifolium	0		0	0	0		
Deschampsia elongata	0		+ +	0	– –		
Epilobium anagallidifolium	0		0	0	0		
Montia parvifolia	0		0	+ +	0		
Poa arctica	0		0	0	0		
Poa spec.	0		0	0	0		
Polytrichum spec.	0		0	0	– –		
Racomitrium canescens	0		0	0	– –		
Salix sitchensis	+		0	0	0		
Saxifraga ferruginea	+ +		0	0	– –		
Age Class II							
Alnus viridis	+	0	0	0		0	0
Galium triflorum	0	0	– –	0		+ +	0
Heracleum maximum	+	0	0	0		0	0
Osmorhiza berteroi	0	0	0	0		+ +	0
Polystichum munitum	0	+	0	0		0	0
Ribes lacustre	0	–	– –	+ +		+ +	0
Rhytidiopsis robusta	+ +	+	–	–		+	– –
Sambucus racemosa	0	0	0	0		0	– –
Stellaria crispa	0	0	0	– –		+ +	0
Age Class III							
Hypnum spec.	0	0	– –	0			–
Polytrichum commune	+ +	0	0	0			0
Rhytidiopsis robusta	0	0	+ +	0			+ +
Age Class IV							
Abies amabilis			0			0	
Clintonia uniflora			0			0	
Menziesia ferruginea			– –			+ +	
Rubus pedatus			+			–	
Vaccinium ovalifolium			– –			+ +	

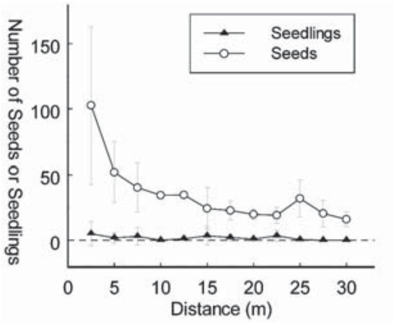

Fig. 3. Effect of distance from adults on number of seeds (per 0.2 m^2) and seedlings (per 1 m^2) of *Alnus viridis*. Error bars indicate ± 1 standard deviation.

depressions than on flat surfaces or slopes. The number of seeds on ridges was not significantly different from any other class. Of the 105 seedlings sampled, 77.1% were under overhanging rocks and 62.9% were on north-facing slopes. Only four seedlings were neither under overhangs nor on north-facing slopes. Only 32% of the sampled quadrats were on north-facing slopes. A significantly higher proportion of seedlings were found on north-facing slopes than would be expected based on the proportion of quadrats that contained north-facing slopes (Fisher exact test: $p = 0.0002$).

Table 3. Comparison of plots with and without *Abies amabilis* seedlings: Age Class I. Statistics are reported for χ^2 (A), Fisher exact (B), and Wilcoxon signed rank (C) tests. Significant ($p < 0.05$) results are in bold. The + and - columns indicate plots where *Abies* seedlings are present and absent respectively. Numbers in these columns indicate observed number of plots with expected values in parentheses (A), observed number of plots (B) and mean values for plots (C).

	Abies amabilis seedlings			
A	+	–	χ^2	p
Topography			**13.74**	**0.0033**
Flat	17 (18)	19 (18)	0.121	
Ridge	0 (3)	6 (3)	6.001	
Slope	58 (62)	66 (62)	0.521	
Depression	26 (18)	10 (18)	7.121	
B	+	–	Diff. in ratios	p
Rock	94	78	**0.158**	**0.0025**
No rock	7	23		
Woody debris	-	-	-	-
No woody debris	-	-		
C	+	–	Z	p
Percent gravel	30.5	30.3	0.07	0.94
Percent rock	39.9	35.4	0.99	0.32
Percent litter	1.93	1.19	0.82	0.41
Percent cover	34.9	28.5	**4.02**	**0.0027**
Species richness	2.35	1.74	**2.99**	**0.0001**
Alnus viridis cover	11.6	12.6	–0.01	0.99
Racomitrium canescens cover	6.24	3.61	**2.98**	**0.0029**

Discussion

The results of this study highlight the importance of microsite conditions for colonization in primary succession. Physical microsite conditions affected the distribution of seedlings and established plants early in succession. In older age classes, however, effects of physical microsite conditions declined for seedlings and changed for adult plants. In addition, microsites appeared to have similar effect on species (i.e. either positive or negative for all affected species) early in succession, but effects of microsites later in succession were more variable.

Physical conditions of microsites are important in early succession where few plants have established. Although not all species in Age Class I were significantly associated with physical characteristics of microsites, about 75% of the seedling species (including both *Abies amabilis* and *Alnus viridis*), and 64% of the species of older plants studied were significantly associated with one or more specific microsite characteristics. Seedlings were more common in depressions and near rocks and less common on ridges, as found on other glacier forelands (Stöcklin & Bäumler 1996; Jumpponen et al. 1999; Erschbamer & Niederfriniger-Schlag 2001). These microsites can increase soil moisture, reduce surface temperatures, and trap seeds. However, patterns of *Alnus viridis* colonization indicate that more seeds (such as in areas nearer to colonization sources) do not necessarily translate into more seedlings. Even close to adult plants, where seed density was high, seedlings were restricted to specific microsites, so seed trapping is probably less important.

There is some suggestion of facilitation in early succession, as *Abies amabilis* seedlings were more commonly found where plant cover and richness were higher, even when *Abies* itself was removed from the analysis. However, this could be due to species clustering in suitable microsites. The distribution of *Abies amabilis* was not positively associated with the nitrogen-fixing shrub *Alnus viridis.* Many shrubs, even N-fixing shrubs, have been shown to have both inhibitory and facilitative effects on seedlings growing beneath them, thereby obscuring patterns (Chapin et al. 1994; Jumpponen et al. 1998).

The importance of microsites later in succession is less clear. Seedlings were not positively associated with any microsite in Age Classes III and IV in either sample year. Very few species had seedlings that were common in these age classes, but even those that were common, such as *Abies amabilis*, appear to be randomly distributed relative to the microsite characteristics measured. With increased canopy cover, small-scale variation in temperature and moisture is often reduced (Vetaas 1994; del Moral 1999). In addition, canopy cover can act to reduce temperature extremes and increase moisture, potentially reducing the role of physical microsites in controlling germination.

Other studies have found that microsites that increase light availability or reduce competition can increase germination in late successional habitats (Eriksson & Ehrlén 1992; Oswald & Neuenschwander 1993), but it is not clear that the physical microsite characteristics measured in this study have a consistent effect on light availability and competition. In mature forests in the region, seedlings of some species have been found to germinate primarily on logs or other elevated surfaces because of reduced competition from understorey plants (Harmon & Franklin 1989; Lusk & Kelly 2003). This was not found in the current study, but there were no logs in the grid in Age Class IV. Decaying logs with seedlings growing on them were present in areas of Age Class IV but they were patchily distributed. Too few plots in the transect area were associated with logs to adequately address this issue.

The presence of existing vegetation can also inhibit germination and survival (Chapin et al. 1994). Seedlings of *Abies amabilis*, however, were not associated with lower cover or richness in Age Class III or Age Class IV. There was also no evidence for facilitation of *Abies amabilis* in late succession, suggesting that the tolerance model may be most applicable at this stage (Connell & Slatyer 1977). *Abies amabilis* is a shade-tolerant species that can germinate on many different types of substrates and therefore may not be strongly influenced by small variation in light levels (Klinka et al. 1990). Other potential characteristics of mature forest microsites, such as canopy gaps and patches of mineral soil from uprooted trees (Harmon & Franklin 1989), were not considered in this study.

We also asked whether different species occurred in similar microsites. Although we did not explicitly test for differences in microsite association among species, the results suggest some general patterns. Species responded similarly to microsites in Age Class I. If a microsite characteristic had a positive or negative effect on a given species, the direction of the effect was the same in all other species that were significantly associated with that same characteristic. Several other studies of microsites in early primary succession have also found little variation among species (del Moral & Wood 1993; Jumpponen et al. 1999). Environmental conditions were sufficiently harsh in early succession that seedlings of most species were restricted to similar microsites (i.e. those that provided significant amelioration of stressful conditions). In cases where environmental conditions are less stressful, species may respond differently to microsites even in early primary succession (Whittaker 1993).

Later in succession, however, species tended to occur in different microsites. In Age Classes II–IV, certain characteristics of microsites were positively associated with some species and negatively associated with other species. Similar variation in species response to microsites occurs in other mature temperate forests (Duncan 1993; Lusk & Kelly 2003). This variation in species responses to microsites could result from increased variation among species in resource use in later succession (Whittaker 1993).

This study confirms that physical microsites such as depressions and rocks are important as safe sites in early primary succession on this glacier foreland. However, results also suggest that these characteristics are not important as safe sites in later succession. Other microsite characteristics may be more important in these later stages of succession. Since factors that affect the distribution of species often vary by successional stage (Whittaker 1993), further study is necessary to understand how safe sites change through succession.

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