

Characterization of 'safe sites' for pioneers in primary succession on recently deglaciated terrain

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Summary

1 We characterized safe sites for individuals of five early colonizers (*Abies lasiocarpa*, *Juncus drummondii*, *J. mertensianus*, *Saxifraga ferruginea*, *S. tolmiei*) that had survived at least one growing season on the recently deglaciated forefront of the Lyman Glacier in the North Cascade Mountains, Washington, USA.

2 Sites with concave surfaces, coarse surface substrate and in the vicinity of large rocks were more likely to be colonized by pioneering plant species.

3 We speculate that the distribution of plants is determined by the presence of sites that facilitate seed trapping and protect seeds and seedlings from desiccation.

4 The data identify the abiotic factors that determine initial recruitment and spatial distribution of plants. Such controls precede biotic interactions in this primary successional sere.

Keywords: *Abies lasiocarpa*, *Juncus* spp., plant establishment, revegetation, *Saxifraga* spp.

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Introduction

Most studies on succession and successional mechanisms have concentrated either on biotic interactions (Connell & Slatyer 1977; Pickett *et al.* 1987; Matthews 1992; Chapin *et al.* 1994; Callaway 1995; Holmgren *et al.* 1997; Jumpponen *et al.* 1998) or on the ways in which abiotic changes are correlated with changes in plant communities (Crocker & Major 1955; Viereck 1966; Matthews & Whittaker 1987; Matthews 1992; Vetaas 1997; Frenot *et al.* 1998; Jumpponen *et al.* 1998). While both biotic and abiotic factors are critical at various stages in the development of plant communities, the early dynamics in primary successional habitats are under strictly abiotic control (Houle 1997). Such development of vegetation on newly formed or exposed substrate proceeds on raw parent material, rather than a developed or modified soil, and this is usually characterized by low nitrogen and

organic matter (Glenn-Lewin *et al.* 1992; Matthews 1992). Only as plants establish and modify their physical environment, do intra- and interspecific interactions between individual plants become more significant (Houle 1997). The role of abiotic factors in primary successional environments is also seen in the prevalence of wind-dispersed propagules, whose distribution is controlled by environmental factors after the seeds have been released from the seed source (Bigwood & Inouye 1988).

Although subtle differences in seed distribution and soil surface properties dramatically affect both establishment and survival of plants (Harper *et al.* 1965; Sheldon 1974; Hamrick & Lee 1987; Huenneke & Sharitz 1990), recruitment in primary successional systems has been little studied. Harper *et al.* (1961) proposed the term 'safe sites' to describe microsites suitable for germination and establishment. The importance of such sites and the abiotic factors characterizing them have been emphasized in primary succession (Matthews & Whittaker 1987; Svoboda & Henry 1987; Whittaker 1991; Frenot *et al.* 1998) but they have rarely been studied, despite the fact that such habitats are frequently characterized by harsh environmental conditions due to drought and/or exposure (Matthews 1992; Chapin 1993) that may

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induce early mortality of germinants (Chapin & Bliss 1989). The mechanisms of primary and secondary seed dispersal must also be considered as they govern the supply of seeds to safe sites.

The main objective of this study was to identify the characteristic microenvironment at safe sites suitable for initial plant colonization on the recently deglaciated forefront of the Lyman Glacier in the North Cascade Mountains, Washington, USA. The various factors that may govern seed dispersal and plant establishment were evaluated indirectly by characterizing the microenvironment around newly established plants *in situ*. Successful establishment depends on a site promoting the trapping of seeds or vegetative propagules, but although the existing seed bank is an essential component in plant recruitment and the resulting community, its composition may not be a good predictor of the distribution of plants able to survive and reproduce in that site (van der Valk 1992). Seed accumulation is only the first step towards successful seedling recruitment; the site must also provide conditions that support both germination and survival of some of the species present in the soil seed bank. Furthermore, one substrate or site may support high germination, while another may support high survivorship (Reader & Buck 1986; Huenneke & Sharitz 1990). In the initial stages of primary succession, the plants that actually establish must show success in all of seed trapping, seed germination and seedling establishment. We therefore located plants that had survived through at least one growing season on otherwise non-vegetated primary successional terrain close to the glacier terminus, and described their microsites to derive indicators that integrate all the requirements of a safe site.

Materials and methods

STUDY SITE

Lyman Glacier (48°10'N, 120°53'W; 1800 m above sea level) is retreating and over the past century has exposed a forefront extending 1100 m but with a drop in elevation of only about 60 m and without distinctive recessional moraines. The glacier and its forefront occupy a cirque and a north–south orientated, U-shaped valley bounded by cliffs that rise up to 600 m above the valley floor. The parent material of the forefront is a heterogeneous glacial till ranging from clay-sized particles to boulders intermingled with deposits of glacial–fluvial sediments (for a detailed description see Cázares 1992 and Jumpponen *et al.* 1998).

The vegetation on ridges and benches in areas adjacent to the forefront is in the ecotone between the upper parkland subzones of the *Abies lasiocarpa* zone and *Tsuga mertensiana* zone of the North Cascade Range (Franklin & Dyrness 1973). Succession on the glacier forefront can be divided into four vegetational

phases (Jumpponen *et al.* 1998): (i) a barren phase less than 20 years since exposure that lies closest to the glacier; (ii) a 20–30-year-old phase that is dominated by scattered individuals or small patches of the early seral species *Juncus drummondii*, *J. mertensianus*, *Luzula piperi*, *Saxifraga ferruginea* and *S. tolmiei* [the 'rawmark' community of Franklin & Dyrness (1973)]; (iii) a phase approximately 30–70 years old that is characterized by scattered shrubs (principally the willows *Salix phylicifolia* var. *planifolia* and *Salix commutata*) and occasional Pinaceae mixed with rawmark or low herbaceous communities (Franklin & Dyrness 1973) dominated by species of Cyperaceae, Juncaceae, Onagraceae, Saxifragaceae and Scrophulariaceae, with scattered individuals of other families; and (iv) a phase approximately 70–100 years old that is characterized by transition from low herbaceous to early stages of the heath shrub and lush meadow parkland communities containing individuals of *A. lasiocarpa*, *Larix lyallii* and *T. mertensiana* among patches dominated by several members of Ericaceae. Data for the current study were collected from an area that extends approximately 250 m from the current glacier terminus, which encompasses phase 1 and the transition between phases 1 and 2. We estimated that less than 1% of this area was vegetated, and what vegetation there was consisted of small, isolated individuals of a variety of species (Table 1).

SAMPLING AND DATA COLLECTION

To ensure correct identification of plant species other than *A. lasiocarpa* and the two distinctive *Saxifraga* spp., only plants in flower were recorded. Approximately 600 individual plants were located in the area of initial colonization (Table 1) and identified. A 10 cm × 10 cm area centred on each plant was defined as a safe site and this was characterized using the following parameters: distance from the glacier terminus, distance from a rock >20 cm in diameter, general topology (elevated, depressed or flat), position (slope, top or bottom), depth with respect to a imaginary 1-m² plane suspended from the highest surrounding points, surface contour (concave, convex, plateau), orientation of exposure (north, south, east, west), proportion of the surface covered by substrate particles <2 mm in diameter, and proportion of the surface covered by substrate particles >2 mm but <2 cm in diameter. A similar area was marked out 50 cm south of the vegetated site. If this area was non-vegetated, it was designated as a control site and the same variables were recorded. If this site was vegetated or plant recruitment was considered unlikely (e.g. if the area fell on bare rock or in standing water) an alternative control site was sought at a position obtained by 90° clockwise rotation. A control site was available within 50 cm of each safe site.

Table 1 Plant species present and numbers recorded within the first 250 m from the Lyman Glacier terminus. Nomenclature follows Hitchcock & Cronquist (1973). Species with fewer than 20 observations were omitted from the analyses

| Family | Species | Observations |
|-----------------|--|--------------|
| Pinaceae | <i>Abies lasiocarpa</i> (Hook.) Nutt. | 43 |
| | <i>Pinus albicaulis</i> Engelm. | <20 |
| | <i>Pinus contorta</i> Dougl. | <20 |
| Compositae | <i>Antennaria lanata</i> (Hook) Greene | <20 |
| | <i>Hieracium gracile</i> Hook. | <20 |
| Ericaceae | <i>Phyllodoce empetriformis</i> (Sw.) D. Don | <20 |
| Onagraceae | <i>Epilobium alpinum</i> L. | <20 |
| | <i>Epilobium latifolium</i> L. | <20 |
| Juncaceae | <i>Juncus drummondii</i> E. Meyer | 102 |
| | <i>Juncus mertensianus</i> Bong. | 59 |
| | <i>Luzula piperi</i> (Cov.) Jones | <20 |
| Rosaceae | <i>Luetkia pectinata</i> (Pursh) Kuntze. | <20 |
| Caryophyllaceae | <i>Sagina saginoides</i> (L.) Britt. | <20 |
| Saxifragaceae | <i>Saxifraga ferruginea</i> Grah. | 295 |
| | <i>Saxifraga tolmiei</i> T. & G. | 41 |

STATISTICAL ANALYSES

Of the 15 species recorded, only five had more than 20 records of occurrence (Table 1) and these were analysed by logistic regression: sites with a plant represented an event, while the non-vegetated controls represented a non-event. The plant species were sampled at an equal frequency with their neighbouring non-vegetated control sites. As a result, species could not be used as a main effect but could only be incorporated into the interaction terms. Due to the overwhelming numbers of potential interaction terms (species \times environmental variable), the species were analysed separately. When a number of the measured variables was found to be correlated, all but one were omitted and four variables (Table 2) were thus selected for final analyses. A saturated model with two continuous variables (distance to a rock and proportion of coarse substrate), two categorical variables (surface contour, with plateau as the reference level, and topology, with position on a flat surface as the reference level), and all two-way interactions was fit on the Bernoulli-distributed, binary, presence/absence data. Only the main effects and two-way interactions were included in the saturated model

because of the vast number of potential interaction terms and the difficulties of interpretation of multi-level interactions. Saturated models were first compared to additive models with no interaction terms by drop-in-deviance tests (Ramsey & Shafer 1996). If the interactions were not significant at $\alpha = 0.05$, only additive models were studied further and an additive model with the lowest value of Q (McCullagh & Nelder 1989) was selected [$Q = D + 2qd$, where D = model deviance, q = number of explanatory parameters in the model, d = scaling parameter (due to Bernoulli distribution, here always 1)]. If drop-in-deviance tests showed saturated models significantly more informative at $\alpha = 0.05$ than the additive models, the 'best model' with interaction terms was again selected by minimizing the value of Q . Data were analysed in SAS using the GENMOD procedure (SAS 1997).

Results

The best logistic regression models describing safe sites for each five major plant species in a primary

Table 2 Description of the variables used in the final logistic regression analyses to characterize the safe sites for the early establishing plants in the primary successional habitat on the Lyman Glacier forefront. Parameter names used in Table 3 are displayed in parentheses

| Variable | Type | Description |
|---|-------------|---|
| 1 Distance from a rock (Distrock) | Continuous | Distance from the edge of a rock > 20 cm in diameter to the site centre |
| 2 Topology (Topology) | Categorical | Relative topology of site compared to topography of surrounding area within 1 m ² : elevated, depressed, or flat (reference level) |
| 3 Surface contour (Surface) | Categorical | Surface shape within the 10 \times 10 cm site: concave, convex or plateau (reference level) |
| 4 Proportion of coarse substrate (Coarse) | Continuous | Percentage of site covered with particles > 2 mm but < 2 cm in diameter. Pebbles > 2 cm in diameter were not considered as substrate |

Table 3 Logistic regression models characterizing the safe sites for the five plant species recorded in the primary successional site on the Lyman Glacier forefront. Odds ratio indicates the proportion of events compared to non-events (ratio between vegetated sites and non-vegetated sites under the condition defined by the parameter)

| Parameter | Odds-ratio | 95% confidence intervals | | $P(\chi^2, \text{d.f.} = 1)^*$ |
|--|------------|--------------------------|---------|--------------------------------|
| | | Lower | Upper | |
| <i>Saxifraga ferruginea</i> | | | | |
| Intercept | 0.0735 | 0.0358 | 0.1456 | 0.0001 |
| Distrock ($P = 0.0084, \chi^2, \text{d.f.} = 1$)† | 0.9828 | 0.9693 | 0.9956 | 0.0108 |
| Topology ($P = 0.0001, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Depressed | 1.0321 | 0.6163 | 1.7286 | 0.9041 |
| Elevated | 0.3967 | 0.2288 | 0.6861 | 0.0009 |
| Surface ($P = 0.0001, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Concave | 4.8423 | 3.0851 | 7.7014 | 0.0001 |
| Convex | 1.1181 | 0.6792 | 1.8415 | 0.6605 |
| Coarse ($P = 0.0001, \chi^2, \text{d.f.} = 1$)† | 1.0262 | 1.0192 | 1.0338 | 0.0001 |
| Deviance = 828.1043 | | | | |
| $Q = 842.1043$ | | | | |
| <i>Juncus drummondii</i> | | | | |
| Intercept | 0.1002 | 0.022 | 0.4119 | 0.0020 |
| Distrock ($P = 0.0001, \chi^2, \text{d.f.} = 1$)† | 0.7783 | 0.4119 | 0.9337 | 0.0203 |
| Topology ($P = 0.9708, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Depressed | 1.1164 | 0.6127 | 2.8982 | 0.8186 |
| Elevated | 1.1275 | 0.3583 | 3.61 | 0.8380 |
| Surface ($P = 0.0001, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Concave | 6.2227 | 3.2511 | 12.4547 | 0.0001 |
| Convex | 1.1443 | 0.4934 | 2.5777 | 0.7476 |
| Coarse ($P = 0.2035, \chi^2, \text{d.f.} = 2$) ^b | 1.009 | 0.995 | 1.0253 | 0.2335 |
| Distrock × topology ($P = 0.0153, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Distrock × depressed | 1.013 | 0.9456 | 1.1196 | 0.7543 |
| Distrock × elevated | 0.7686 | 0.5655 | 0.9602 | 0.0479 |
| Distrock × Coarse ($P = 0.0187, \chi^2, \text{d.f.} = 1$)† | 1.0022 | 1.0003 | 1.0047 | 0.0454 |
| Deviance = 378.9326 | | | | |
| $Q = 398.9326$ | | | | |
| <i>Abies lasiocarpa</i> | | | | |
| Intercept | 0.0092 | 0.0013 | 0.0494 | 0.0001 |
| Distrock ($P = 0.0001, \chi^2, \text{d.f.} = 1$)† | 0.9143 | 0.8553 | 0.9614 | 0.0024 |
| Topology ($P = 0.0901, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Depressed | 1.8791 | 0.5399 | 7.5754 | 0.3376 |
| Elevated | 0.7255 | 0.1802 | 3.2043 | 0.6553 |
| Surface ($P = 0.0001, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Concave | 5.9417 | 2.4269 | 16.4299 | 0.0002 |
| Convex | 0.5532 | 0.1131 | 2.1276 | 0.4138 |
| Coarse ($P = 0.0007, \chi^2, \text{d.f.} = 1$)† | 1.0263 | 1.0104 | 1.0450 | 0.0023 |
| Deviance = 207.7984 | | | | |
| $Q = 221.7984$ | | | | |
| <i>Juncus mertensianus</i> | | | | |
| Intercept | 0.0082 | 0.0015 | 0.0369 | 0.0001 |
| Distrock ($P = 0.0011, \chi^2, \text{d.f.} = 1$)† | 0.9498 | 0.9125 | 0.9816 | 0.0054 |
| Topology ($P = 0.0028, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Depressed | 2.8994 | 1.0341 | 9.483 | 0.0550 |
| Elevated | 0.8251 | 0.2428 | 3.0389 | 0.7615 |
| Surface ($P = 0.0001, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Concave | 4.0177 | 1.9568 | 8.6755 | 0.0002 |
| Convex | 0.4454 | 0.1184 | 1.3679 | 0.1847 |
| Coarse ($P = 0.0001, \chi^2, \text{d.f.} = 1$)† | 1.0288 | 1.0145 | 1.0453 | 0.0002 |
| Deviance = 269.9394 | | | | |
| $Q = 283.9394$ | | | | |

Table 3—continued

| Parameter | Odds-ratio | 95% confidence intervals | | $P(\chi^2, \text{d.f.} = 1)^*$ |
|--|------------|--------------------------|---------|--------------------------------|
| | | Lower | Upper | |
| <i>Saxifraga tolmiei</i> | | | | |
| Intercept | 0.0147 | 0.0018 | 0.0916 | 0.0001 |
| Distrock ($P = 0.0002, \chi^2, \text{d.f.} = 1$)† | 0.8146 | 0.0916 | 0.9973 | 0.1748 |
| Topology ($P = 0.1960, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Depressed | 2.8705 | 0.5109 | 14.5647 | 0.1702 |
| Elevated | 1.2678 | 0.2488 | 7.1642 | 0.7770 |
| Surface ($P = 0.8089, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Concave | 1.4154 | 0.4659 | 4.4044 | 0.5426 |
| Convex | 1.0219 | 0.1457 | 8.1507 | 0.9824 |
| Coarse ($P = 0.0010, \chi^2, \text{d.f.} = 1$)† | 1.0253 | 1.0095 | 1.0440 | 0.0033 |
| Distrock × surface ($P = 0.0123, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Distrock × concave | 1.2119 | 1.0227 | 1.5863 | 0.0797 |
| Distrock × convex | 0.6924 | 0.1692 | 1.2834 | 0.4175 |
| Distrock × topology ($P = 0.8543, \chi^2, \text{d.f.} = 2$)† | – | – | – | – |
| Distrock × depressed | 0.9991 | 0.7964 | 1.601 | 0.9950 |
| Distrock × elevated | 0.9628 | 0.7179 | 1.5571 | 0.8119 |
| Deviance = 206.9117 | | | | |
| $Q = 228.9117$ | | | | |

* Type 1 analysis; significance of the parameter as sole explainer of variation; set of previous parameters does not affect the parameter significance.

† Type 3 analysis; significance of the parameter after accounting for all the previous parameters in the model.

successional system on a retreating glacier forefront are displayed in Table 3.

Three species (*A. lasiocarpa*, *J. mertensianus* and *S. ferruginea*) were most likely to occur close to large (> 20 cm) rocks. An increase in the distance from such a rock decreased the recruitment probability of these species, as indicated by odds ratios significantly less than 1 (Table 3). For *J. drummondii* increase in the distance from a rock substantially decreased the probability for recruitment in elevated positions (which are unlikely locations for recruitment, except close to large rocks), while no such effect was visible in depressed positions. Other parameters, such as coarse substrate for *J. drummondii* or concave surfaces for *S. tolmiei*, also facilitated recruitment, and when these were present the rock effect was minimal or non-existent. For example, coarse substrate interacted with distance from rocks for *J. drummondii*: the presence of coarse substrate overrode the effects of being distant from a substantial obstruction and proximity to a rock compensated for too little coarse substrate.

Although included in the models for all species, topology did not significantly affect recruitment of either *A. lasiocarpa* or *S. tolmiei* (type 3 analysis $P = 0.0901$ and 0.1960 , respectively). Recruitment of *J. mertensianus* may be more likely in the depressions than in flat positions (type 1 analysis $P = 0.0550$), whereas *S. ferruginea* recruitment was substantially less likely in the elevated positions than on flats or depressions that did not differ from each other (type 1 analysis $P = 0.0009$; Table 3). For *J. drummondii*, topology interacted with distance to large rocks as described above.

Surface contour was a significant parameter in explaining the presence of most species. While convex and plateau surfaces did not differ, concave surfaces had substantially higher odds for recruitment of *A. lasiocarpa*, *J. drummondii*, *J. mertensianus* and *S. ferruginea* (Table 3). For *S. tolmiei*, surface characteristics interacted with distance from large rocks and no clear conclusions were possible, although it appears that concave surfaces were less advantageous when located near a substantial physical obstruction. However, this *S. tolmiei* data set contained the fewest observations and therefore might be less reliable.

Increase in coarse substrate also usually enhanced plant recruitment. An increase in surface coverage by coarse substrate (> 2 mm in diameter) resulted in an increase in recruitment probability for *A. lasiocarpa*, *J. mertensianus*, *S. ferruginea* and *S. tolmiei*. For *J. drummondii*, however, as described above, substrate interacted with distance from substantial rocks. The pattern was similar to the interaction of surface characteristics with distance to rocks for *S. tolmiei* (Table 3).

Discussion

The data presented here indicate that the spatial distribution of the first plants to colonize a primary successional glacier forefront is not random. Successful establishment and survival of plant individuals occurs only in safe sites and these can be characterized simply by their physical attributes.

Concave surfaces had substantially greater overall plant recruitment than convex or plateau surfaces.

The five species analysed depend primarily on wind dispersal. Spatial variation in seed rain and the non-uniform distribution of sites where seeds become trapped result in a soil seed bank with a strongly clustered spatial distribution (Ryvarden 1971; Rabinowitz & Rapp 1980; Reichman 1984; Price & Reichman 1987; Bigwood & Inouye 1988). Small depressions and concave surfaces provide a 'wind shadow' where surface wind velocities are lower and surface water flow may slow or stop, leading to substantial seed accumulation as a result of horizontal seed movement (Reichman 1984). Depressions appear to be effective collectors of seeds undergoing either primary and secondary dispersal (Reichman 1984; Matlack 1989).

Besides trapping seeds from transient populations, shallow depressions may also provide greater moisture than the surrounding soils and thus enhance seed germination, particularly in environments where surface desiccation may be a major factor (Watt 1919). Early successional sites are characterized by intense radiation at the soil surface, which results in extreme fluctuations in soil temperature and rapid drying of surface soils (Chapin 1993). The importance of protection against water loss and desiccation has been emphasized for successful germination and establishment (Harper *et al.* 1965; Sheldon 1974; Hamrick & Lee 1987). Drought may, indeed, be the major cause of seedling mortality during the first year after germination in primary succession (Chapin & Bliss 1989). Seed trapping that leads to the clustering of seeds in small depressions or other locations where germination and survival are likely to be enhanced would result in a strong effect similar to that observed here. In a controlled study of microsites, in which heterogeneity was created experimentally, Harper *et al.* (1965) concluded that the majority of seedlings of two *Plantago* spp. emerged in depressions or near obstructions. It is likely that the promotion of germination will be more important since the conditions for plant survival and growth are generally less restrictive than those for germination. Provided that the emerging radicle is able to penetrate the soil surface, the likelihood of subsequent establishment is high (Sheldon 1974).

Plant occurrence was generally higher near large rocks, especially in locations where occurrence was otherwise unlikely. Livingston (1972) pointed out that *Juniperus communis* established more frequently near rocks in New England pastures and suggested that this might be a result of faecal deposition of seeds by robins resting on rocks after feeding on juniper berries, as well as to greater moisture levels due to a 'microwatershed' created by the rocks. Fowler (1986, 1988) similarly observed increased survival and growth near rocks and interpreted this to result mainly from reduced evaporation, but did not acknowledge the 'microwatershed' effect. We assume both to be important at our study site as extended periods of drought may occur annually in the glacier

forefront and water retention is poor due to low organic matter content. Furthermore, rocks may create points for mountain dew to accumulate and thus further improve moisture conditions in the absence of precipitation. We have also observed on several occasions that snow adjacent to elevated rocks melts earlier, resulting in a lengthening of the short growing season at the Lyman Glacier forefront. The rock effect was, however, minimal or non-existent in the presence of other recruitment-facilitating parameters (coarse substrate, for *J. drummondii*; concave surfaces, for *S. tolmiei*), suggesting that the effect of rocks was similarly mediated via enhanced seed trapping and burial.

There are several likely factors involved in the greater occurrence of plants with greater amounts of coarse substrate. Like the small-scale depressions of the concave surfaces, coarse substrate contains seed trapping cavities between the particles. Coarse substrate also allows partial burial between the particles, improving the moisture retention around the seed and increasing the likelihood of successful germination. Surface water flow would move small seeds into the minute cavities and cracks in the surface and further percolate through the surface substrate with vertical flow (Bigwood & Inouye 1988). The protection offered by the cavities and the associated seed burial are essential for seeds to remain viable (Enright & Lamont 1989). Hamrick & Lee (1987) concluded that optimal conditions for successful establishment and survival were provided by small irregularities in the soil surface, particularly in areas prone to desiccation. Such burial may ensure that seeds remain viable but dormant until conditions are favourable for successful germination (Stamp 1989). Although seed predation was not measured directly, seed burial further reduces the likelihood of seed discovery by predators (Enright & Lamont 1989). Coarse substrate may also increase the likelihood of radicle penetration and seed anchorage because smooth and compacted surfaces provide few possibilities for successful penetration of the surface by the emerging radicle (Sheldon 1974). The substrate at the glacier forefront is mainly glaciofluvial silt intermingled with some coarser fragments. When desiccated, the silt frequently forms cemented crusts, precluding seed trapping and radicle penetration. Finally, needle ice formation occurs on the forefront in autumn if hard frost precedes a snow cover, and frost heaving is then a hazard to small plants. We observed that the needle ice formed mostly on silt surfaces but not where pebbles or gravel provided a surface mulch.

Topology had no significant effect on *A. lasiocarpa*, *J. drummondii* or *S. tolmiei* recruitment, although *S. ferruginea* recruitment was less likely in the elevated positions. Plant occurrence was therefore less dependent on topography relative to the surroundings than on parameters describing the microsite itself.

Although our design allowed no direct evaluation of differences between the plant species, it is notable

that the safe site characteristics appeared to be remarkably similar for all five plant species studied. The pattern of establishment depended both on differential seed dispersal and spatial distribution of the seed bank, as well as on species-specific responses in germination and survival (Reader & Buck 1986; Price & Reichman 1987). Seed size and seed morphology have been described as important factors in dispersal and distribution (Rabinowitz & Rapp 1981; Reichman 1984; Peart & Clifford 1987) and are believed to be partly responsible for the floristic diversity and spatial distribution of plants (Sheldon 1974; Chapin 1993). Most of the species we encountered were wind dispersed but not all had small seeds. Our detailed characterizations of safe site requirements involved one large seeded species with wings (*A. lasiocarpa*), although the remaining four species had small seeds with no such devices. Based on both field and laboratory experiments with four sympatric *Erodium* species, Stamp (1989) suggested that variation in seed size may mainly account for the ability to take advantage of different seasonal conditions even if species do not colonize different microsites.

Early stages in the life cycle (seed dispersal, seed distribution, germination, etc.) seem more important than subsequent stages in determining the distribution and abundance of plants (Reader & Buck 1986). Hamrick & Lee (1987) concluded similarly that greatest mortality occurs between dispersal and establishment. Distribution of plants in primary successional systems is therefore expected to be determined by the abiotic microenvironment that governs seed trapping, successful germination and establishment. Given the potential importance of drought-induced mortality (Chapin & Bliss 1989), safe sites have received surprisingly little attention in studies of primary succession. In this paper, our intention is to draw attention to the patterns of initial plant colonization as an essential mechanism in defining the plant distribution and spatial community structure in a primary successional habitat. We hope to initiate further interest in the abiotic factors preceding the biotic interactions and mechanisms in primary succession.

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