EARLY PRIMARY SUCCESSION ON A BARREN VOLCANIC PLAIN AT MOUNT ST. HELENS, WASHINGTON[1]

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The invasion pattern on a barren plain on the eastern flank of Mount St. Helens, Washington, devastated by the 1980 volcanic eruption was monitored between 1988 and 1992. All vascular plants on a grid consisting of 400 contiguous 100-square-meter quadrats were recorded with a cover score. The substrate was initially homogeneous, but significant heterogeneity had developed by 1988. Vascular plant species richness increased from 24 in 1988 to 41 in 1992. Mean species richness per quadrat increased from 0.44 to 5.71, mean cover increased from 0.04% to 0.51%, and mean diversity index (H') increased from 0.08 to 1.56. A variance/mean test of species richness pattern showed that invasion occurred sporadically since plots tended to have either several or no species. By 1992, mean species richness was more evenly distributed. Most seedlings continue to result from long-distance dispersal, but reproductive colonies of species are developing. Seedling distributions are controlled by microsites. Eleven common species strongly and similarly preferred safe-sites created by small rocks, undulations, or rills. However, many apparent safe-sites are empty, suggesting that seeds are scarce and that even the most favorable microsites are marginal. The niches of these species seem to overlap broadly. The Plains of Abraham is in the earliest stage of primary succession. The detailed invasion pattern permitted us to distinguish species still dependent on immigration from those now locally established. Pronounced microsite preferences emphasize that physical amelioration (e.g., nutrient input and erosion) must occur before further succession can commence. We have observed the early stages of succession where an inhospitable site is gradually and heterogeneously changed into a habitat where safe-sites do not limit succession, but where stochastic factors remain important.

Mount St. Helens, Washington, erupted violently on 18 May 1980, to create an array of devastated landscapes. This paper describes primary succession on a devastated plain distant from sources of most colonists.

Overall recovery patterns on Mount St. Helens were summarized by del Moral and Wood (1988, 1993) and del Moral and Bliss (in press). Recovery is strongly affected by the degree of initial destruction and by the degree of isolation. All new substrates were initially nutrient and organic matter deficient. Midsummer drought is common (del Moral and Bliss, in press). In isolated, devastated habitats, it appears that amelioration by weathering, erosion, and nutrient fallout must precede invasion.

Del Moral (1983a) summarized recovery of mildly impacted habitats. Any survivors led to rapid recovery. Del Moral and Clampitt (1985) used soil bioassays to discover physical amelioration. Growth of native species improved annually in substrates that had weathered in situ without plants growing in them. Wood and del Moral (1987) found a strong positive correlation between seed size and establishment success, but an inverse correlation between seed size and dispersal ability. These results implied that isolated, devastated sites recover slowly because well-dispersed species are rarely successful, while those that could establish rarely colonized.

Morris and Wood (1989) and Wood and Morris (1990) showed that the nitrogen-fixing *Lupinus lepidus* facilitated invasion only where lupines were sparse. Del Moral (1993) showed that most seedlings established on barren substrates in safe-sites and that colonization near lupines was usually delayed until lupines had died.

Del Moral and Bliss (in press) reviewed ecological and physiological succession mechanisms on volcanoes and contrasted succession on Mount St. Helens with conventional descriptions. Wood and del Moral (1988) described invasion and community structure on the Pumice Plains after 6 years.

Here we describe early primary succession on a barren plain and discuss factors that affect invasion and expansion. The Plains of Abraham received searing blasts but only modest pumice and tephra deposits. All plant life was obliterated and but few plants existed in 1987. The study site is several hundred meters from populations of most potential colonists. Our objective is to describe how species establish and expand on an isolated, homogeneous landscape. We will explore how habitat heterogeneity permits seedling establishment and discuss whether significant community development has occurred in 13 years.

MATERIALS AND METHODS

Study site—Mount St. Helens, southwestern Washington State, is at 46°12'N, 122°11'W. The Plains of Abraham is on its eastern flank, between 1,350 and 1,450 m. Before the eruption, the vegetation was sparse (Kruckeberg, 1987). Levels of extractable nutrients in 1989 were very low (del Moral and Bliss, in press). Timberline was 600 to 800 m below its climatic limit (Lawrence, 1938) before the eruption, and only scattered conifers then occurred. Although the fury of the 1980 eruption was directed northward, the study site was devastated by the blast and pyroclastic flows (Foxworthy and Hill, 1982). Several lahars (= mud flows) spawned by melting ice fields also impacted this plain. In September 1980, RdM inspected this site. It was

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TABLE 1. Species composition in 400 quadrats on the Plains of Abraham.[a]

Species	Authority	Frequency (%)	Cover score
Abies lasiocarpa	(Hook.) Nutt.	12.25	1.00
Agrostis diegoensis	Vasey	46.50	1.14
Anaphalis margaritacea	(L.) B. & H.	99.50	2.15
Arnica latifolia	Bong.	3.50	1.00
Carex limnophilla	Hermann	4.00	1.15
Carex mertensii	Prescott	4.50	1.18
Carex pachystachya	Cham.	22.00	1.02
Epilobium alpinum	L.	16.25	1.03
Epilobium angustifolium	L.	73.25	1.26
Hieracium albiflorum	Hook.	46.50	1.01
Hypochaeris radicata	L.	60.00	1.11
Juncus mertensianus	Bong	3.75	1.00
Juncus parryi	Engelm.	19.75	1.08
Luetkea pectinata	(Pursh.) Kuntze	30.00	1.03
Lupinus lepidus	Dougl.	2.50	1.50
Moss[b]	—	12.00	1.90
Penstemon cardwellii	Howell	34.00	1.11
Poa incurva	Scribn. & Will.	5.25	1.04
Salix commutata	Bebb	3.25	1.08
Saxifraga ferruginea	Grah.	7.50	1.17
Spraguea umbellata	Torr.	38.75	1.46

The following taxa occurred fewer than five times or were absent in 1992: *Achillea millefolium* L. ssp. *lanulosa* (Nutt.) Piper, *Agoseris aurantiaca* (Hook.) Greene, *Agrostis scabra* Willd., *Arenaria* sp., *Aster ledophyllus* Gray, *Athyrium distentifolium* Tausch, *Calamagrostis sesquiflora* (Trin.) Kawano, *Carex deweyana* Schw., *C. phaeocephala* Piper, *C. rossii* Boott, *Cryptograma crispa* (L.) R. Br., *Eriogonum pyrolifolium* Hook., *Hieracium gracile* Hook., *Lupinus latifolius* Agardh, *Luzula parviflora* (Ehrh.) Desv., *Pinus contorta* Dougl. var. *latifolia* Engelm., *Polystichum lonchitis* (L.) Roth, *Pseudotsuga menziesii* (Mirbel) Franco, *Rubus lasiococcus* Gray, *R. parviflorus* Nutt., *R. spectabilis* Pursh., *Senecio sylvaticus* L., *Stipa occidentalis* Thurb., *Trisetum spicatum* (L.) Richter, *Tsuga mertensiana* (Bong.) Carr., *Vaccinium membranaceum* Dougl., *V. parvifolium* Smith.

[a] Cover score = mean cover score of occupied plots.
[b] Mosses are not reproductive and have not been identified.

then covered by tephra and pockets of silt but dominated by pumice. Vascular plants were absent. Vegetation survived in the lee of the blast within 300 m of the study site. Such relicts are sources for potential colonists, although most in the study do not occur in the nearest remnants. A few individuals were found during reconnaissance in 1987. By then, erosion had removed all silt and tephra and had initiated shallow rills. The study site is nearly level.

The grid—The sampling protocol is that of Wood and del Moral (1988). Each July between 1988 and 1992 we sampled a permanently marked 100 × 400-m grid, composed of 10 × 10-m contiguous quadrats. Within each, each species was assigned a cover score: Class 1 = one to five plants; Class 2 = six to 20 plants; Class 3 = over 20 plants, or 0.25% to 0.5% cover; Class 4 = 0.51% to 1% cover; Class 5 = 1.01% to 2%; Class 6 = 2.01% to 4%; Class 7 = 5% to 8%; Class 8 = 9% to 16%; Class 9 = over 17%.

For each quadrat the total number of species (richness), the total cover score, an estimate of absolute cover, and a structure index based on the information theory diversity index (H', using cover scores, calculated as $-\Sigma\ p_i \ln$

p_i, where p_i is the proportion of the ith species in a sample) were determined annually. Because cover scores rather than actual cover were used, the index is not strictly a diversity measure, but it can be used for comparative purposes. For each species, the cover score was converted to an estimate of percent cover as follows: Class 1 was converted to 0.06% for small, delicate species, 0.09% for typical species, and 0.15% for prostrate species. Class 2 was converted to 0.09%, 0.15%, or 0.20%, respectively. The midpoint of the range was used for all other scores. These descriptors were compared between years using paired t-tests.

Community analysis—The data were analyzed by two-way indicator species analysis (TWINSPAN, Hill, 1979) in both 1991 and 1992. Cover scores were used directly as "pseudospecies," to mimic dominance values. Minimum group size was six quadrats, and up to six divisions specified. Final groups in 1992 are described by their dominant species. The number of contiguous members of each community type (CT) on the grid was determined by inspection. The mean cluster size of a particular CT was calculated. Results between years were compared to test the hypothesis that distinct CTs have developed.

Microsite preferences—Each individual encountered in the grid in 1990 was scored into one of these surface categories: smooth (consisting of even-sized pumice); small rocks (at least twice the size of local pumice); rill edges; drainages; and undulations. A plant that occurred in only one microsite was scored once for each cover score. If individuals occurred in two or more microsite types, a single occurrence was marked in each.

In order to estimate the proportion of each microsite class on the landscape, 1,038 1/4-m² quadrats were distributed at 2.5-m intervals along the 11 400-m transects that mark the grid. The microsite category of each quadrat was determined. If more than one microsite occurred, then quadrats were recorded in this order of preference: edges, drainages, undulations, rocks, and smooth surfaces. This procedure underestimates smooth surfaces. Surface type estimates were also made in each grid quadrat for descriptive purposes in 1988 and 1992. For each species, a χ^2 test was performed (Fienberg, 1977). The expected frequency assumes that species are distributed in microsites in the same proportion as the microsites occur.

Flowering—In order to determine if viable populations were developing on the grid, we noted any individuals flowering within a quadrat between 1990 and 1992. Data are the percentage of quadrats with flowering individuals, not the percentage of flowering individuals. This method greatly overestimates actual flowering abundance.

Species associations—At the scale of 100 m², with low densities, we predicted that species would be distributed randomly on the grid. This hypothesis was tested by testing for departures from random using 2 × 2 association tables among species of intermediate frequency. Thirteen taxa were neither too common nor too rare to test for mutual association.

RESULTS

Grid structure—*The general pattern*—There were no evident patterns that distinguished portions of the grid. It appears to be a sample of a single habitat with some heterogeneity. Table 1 summarizes 1992 frequency (percent) and mean cover score for the 21 most common species. All other ever-recorded species are listed in its footnote. *Anaphalis, Spraguea,* and mosses are the only common taxa with more than a few cases of cover scores greater than one. Most other species are represented by only a few individuals per quadrat.

Richness—The total number of species on the grid increased from 24 (1988) to 41 (1992), although 47 species have been encountered. In 1988, 156 quadrats had plants. Subsequent invasions have resulted in all 400 quadrats being occupied by 1992 (Table 2). Mean floristic richness increased steadily from 0.44 to 5.71 species (Table 2; Fig. 1). The increase of two species per plot between 1991 and 1992 may be due to the initiation of an exponential phase of development, but it is also possible that early snow melt and intermittent rains during June reduced seedling mortality. Each annual increase is highly significant ($P <$ 0.01, paired *t*-tests). Sometimes a species was lost from a quadrat, but in only 45 of 1,600 comparisons over 5 years did the number of species in a quadrat decline.

Cover—Figure 2 depicts the total cover score per quadrat, and Table 2 summarizes the changes by cover scores and derived percentages. Cover changes mimic the richness pattern because species usually have a cover score of 1. Mean cover increased from 0.04% to 0.51% by 1992. Mean cover scores increased from 0.46 in 1988 to 7.57 in 1992 (Table 2). Paired *t*-tests reveal all increases to be highly significant.

Diversity—Table 2 summarizes annual diversity changes. *H'* was initially very low, but it increased significantly to 0.68 in 1990 as a result of colonization. By 1992, most quadrats had at least two species, *H'* often exceeded 2.0, and the mean of 1.56 was significantly greater than in 1991.

Individual species distribution—Invasion and development of selected common species are shown in Figs. 3–8. A species cluster is defined by the number of contiguous quadrats occupied by a given species. By comparing the size and number of clusters from year to year, we obtained an objective measure of population spread
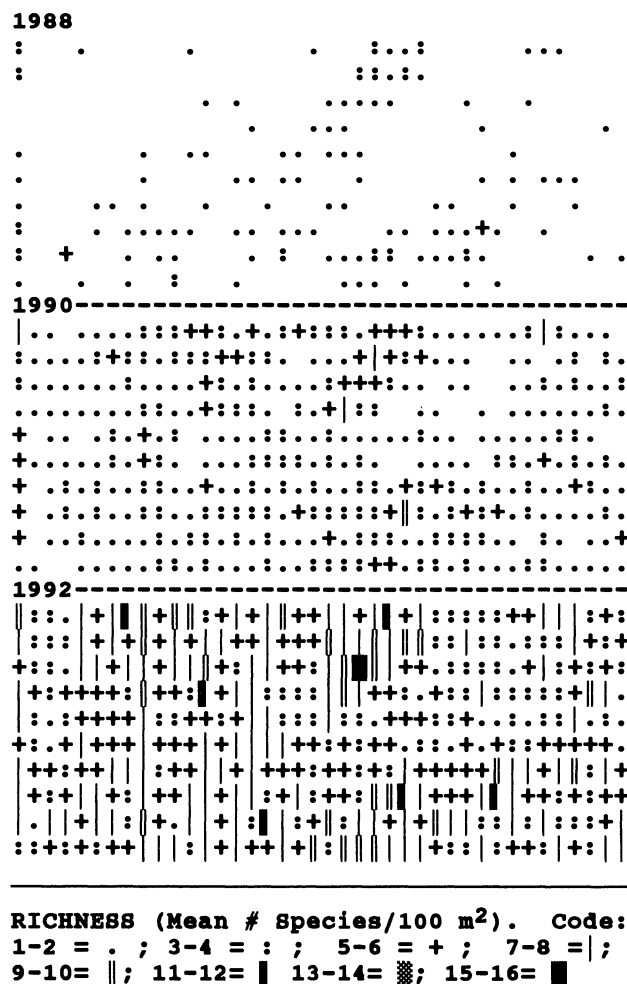

RICHNESS (Mean # Species/100 m²). Code:
1-2 = . ; 3-4 = : ; 5-6 = + ; 7-8 =| ;
9-10= || ; 11-12= | 13-14= ▓; 15-16= █

Fig. 1. Number of species per quadrat (richness) on the Plains of Abraham in a 10 × 40 grid of 100 m² contiguous quadrats: 1988, 1990, and 1992.

that can be used to infer the manner of invasion (Table 3). The percentages of plots with any flowering individual of a given species are summarized in Table 4.

Agrostis diegoensis—This grass occurred once in 1988, but by 1990 it occurred in scattered locations (Fig. 3). By 1991 it occurred throughout the grid in 51 small clusters (mean = 2.37), but by 1992 these had begun to coalesce. Flowering is variable (Table 4), but the population is maturing so that many flowering clones occur. Long-dis-

TABLE 2. Summary structural changes for the Plains of Abraham grid.

Parameter	1988	1989	1990	1991	1992
Total number of species	24	29	33	33	41
Richness (mean species #/plot)[a]	0.44	1.25	2.36	3.67	5.71
Variance/mean ratio[b]	1.52	1.45	1.01	0.86	0.81
Quadrats occupied (#)	156	270	367	396	400
Cover estimate (%)[a]	0.04	0.12	0.23	0.35	0.51
Cover score sum[a]	0.46	1.40	2.80	4.24	7.57
Diversity (*H'*)[a]	0.08	0.28	0.68	1.11	1.56

[a] Differences between all successive years are significant (paired *t*-test) with $P < 0.001$.
[b] Values <0.843 or >1.17 differ from 1.0 with $P < 0.01$.

TABLE 3. Cluster statistics for the Plains of Abraham 1988, 1990, and 1992.[a]

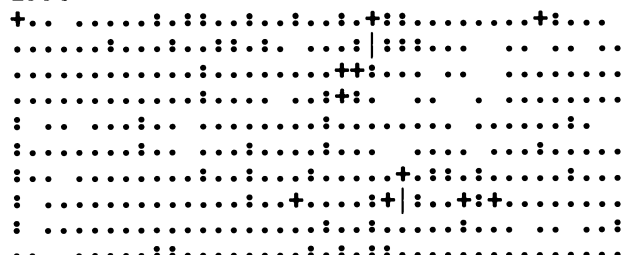| Species	1988		1990		1992	
	N	$\bar{X}$ (SD)	N	$\bar{X}$ (SD)	N	$\bar{X}$ (SD)
Abies lasiocarpa	17	1.41 (0.87)	21	1.67 (1.94)	26	1.85 (2.81)
Agrostis diegoensis	1	1.00 (0.00)	29	1.83 (1.37)	36	5.14 (19.4)
Anaphalis margaritacea	13	4.54 (3.93)	4	81.75 (160.2)	398	1.00 (0.00)
Carex mertensii	8	1.00 (0.00)	9	1.22 (0.67)	19	1.21 (0.53)
Carex pachystachya	0		11	1.46 (0.82)	56	1.59 (1.30)
Epilobium alpinum	7	1.00 (0.00)	6	1.33 (0.52)	38	1.68 (1.34)
Epilobium angustifolium	7	1.00 (0.00)	36	2.76 (3.99)	5	59.2 (99.3)
Hieracium albiflorum	5	1.20 (0.45)	50	2.04 (2.43)	34	5.53 (11.1)
Hypochaeris radicata	7	1.00 (0.00)	45	2.47 (2.97)	16	14.3 (29.4)
Juncus parryi	0		15	1.20 (0.41)	38	2.05 (1.99)
Luetkea pectinata	8	1.00 (0.00)	19	1.53 (1.17)	47	2.45 (2.56)
Penstemon cardwellii	2	1.00 (0.00)	18	1.58 (1.71)	44	3.11 (5.06)
Saxifraga ferruginea	0		3	1.33 (0.57)	19	1.58 (0.96)
Spraguea umbellata	1	1.00 (0.00)	16	1.50 (1.10)	26	6.54 (17.2)

[a] $\bar{X}$ (SD) is the mean number of 100 m² plots in the cluster (±SD); N = number of clusters; the total number of plots for a species is the product of N times X.

tance dispersal is poor (Wood and del Moral, 1987), but local dispersal is good. Seeds can blow along the ground, and it is difficult to determine sources of seedling recruitment. It is likely that both locally produced and introduced seeds are responsible for recent increases.
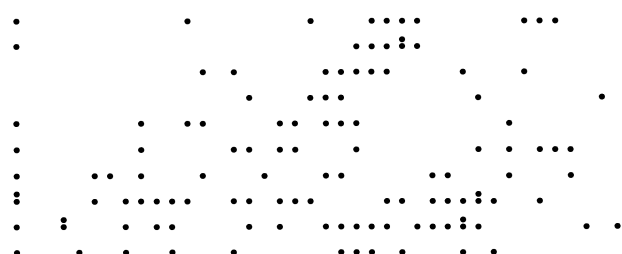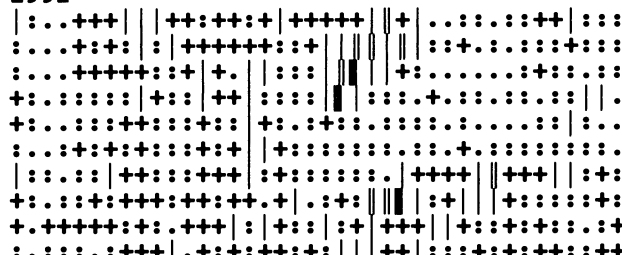

COVER (Sum of cover scores).   Code:
1-4 = . ;   5-7 = : ; 8-10 = +; 11-14= | ;
15-17= ‖; 18-20= █

Fig. 2. Total cover scores on the Plains of Abraham grid: 1988, 1990, and 1992.

Anaphalis margaritacea—This is the most abundant species (Fig. 4). In 1988, clusters were small. By 1990, much of the grid was occupied, and by 1991 there was a single cluster that expanded and became more dense in 1992 (Table 3). Further population growth will occur from expansion within each quadrat. Based on seed trap data, there is a moderate seed rain on the Plains of Abraham. Despite being the most common species on the grid, only 7.1% of trapped seeds were *Anaphalis* (del Moral and Bliss, in press). This suggests that it has a greater survival rate than other species. Only about 10% of quadrats had flowering *Anaphalis* through 1991, but this value increased dramatically in 1992 (Table 4). Until 1992, these individuals could only have contributed a small percentage of seedlings. Locally produced seedlings are an increasing fraction of those establishing on the site, but this population is not reproductively isolated.
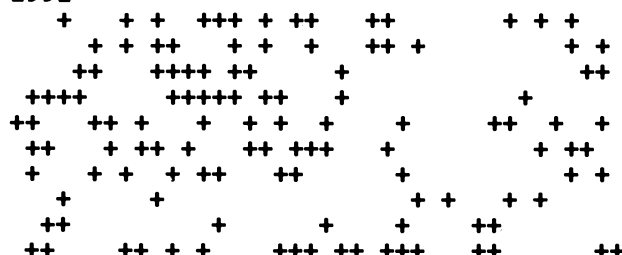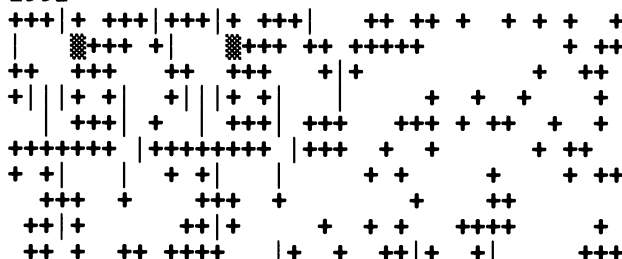
Cover Code: + = 1; | = 2;   █ = 3

Fig. 3. Cover scores for *Agrostis diegoensis* on the Plains of Abraham grid, 1991 and 1992.

Fig. 4. Cover scores for *Anaphalis margaritacea* on the Plains of Abraham grid, 1988, 1990, and 1992.

Cover Code: + = 1; | = 2; ▓ = 3; ▓ = 4; ▓ = 5

Fig. 5. Cover scores for *Epilobium angustifolium* on the Plains of Abraham grid, 1989, 1990, and 1992.
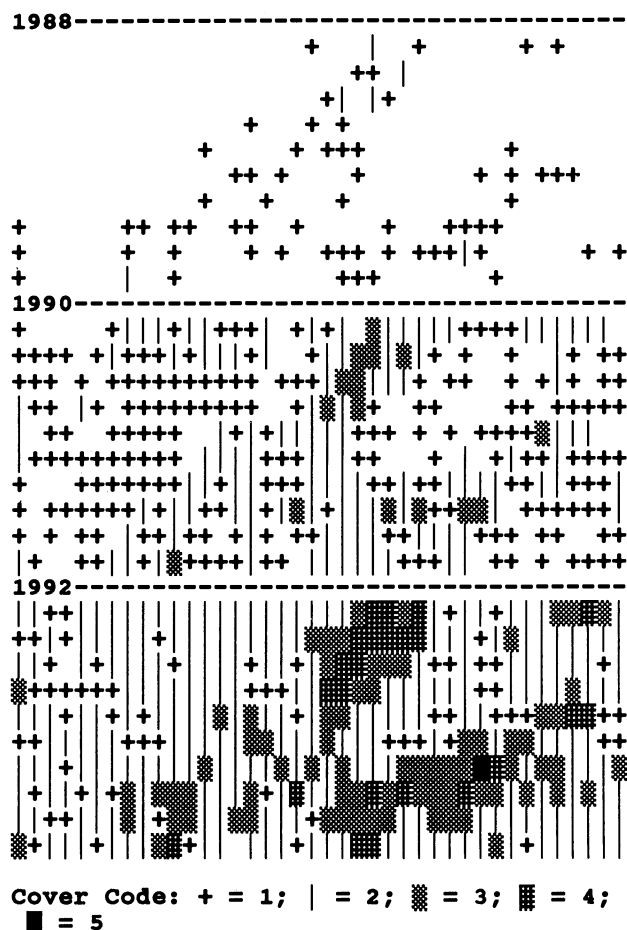
Cover Code: + = 1; | = 2; ▓ = 3

Epilobium angustifolium—Fireweed persists as suppressed seedling-sized plants (Fig. 5). Most individuals show severe nutrient stress symptoms (russet to copper-colored leaves). Virtually absent in 1988, it now occupies about half the grid. Clusters remained small in 1991, then expanded in 1992 (Table 3). The establishment pattern strongly suggests recruitment exclusively from the incoming seed rain. Only 6% of the quadrats had plants in flower in 1992 (Table 4), while over 60% of seeds found in traps are *Epilobium* (del Moral and Bliss, in press). High vagility, low flowering percentage, and very low seedling survival (Wood and del Moral, 1987; Wood and Morris, 1990) make it unlikely that more than a few recruits come from the grid. It may well be that *Epilobium* will persist without significant reproduction by chronic recruitment from surrounding habitats (the rescue effect, Shmida and Wilson, 1985).

Hieracium albiflorum—This excellent disperser can establish and set seed within 2 years. That only 1.35% of the seed trap sample was *Hieracium* reflects its relative density among wind-dispersed species. It occurs widely on the grid in gradually melding clusters (Fig. 6). Flowering is variable, but common, yet it is unlikely that many seedlings were produced on the grid since few seeds are

produced per flower, dispersal ability is great, strong winds can remove local seeds, and turnover rates are high.

Hypochaeris radicata—This alien species has excellent dispersal powers, but is near the limit of its cold tolerance (Turkington and Aarssen, 1983). Cluster size increased until 1991, when only 142 quadrats were occupied (Table

TABLE 4. Percentage of plots within which each species has at least one flowering individual in 1990, 1991, and 1992.

	1990		1991		1992	
Species	N	% Flowering	N	% Flowering	N	% Flowering
Agrostis diegoensis	53	49.1	121	7.2	185	61.6
Anaphalis margaritacea	327	13.1	371	8.9	398	29.9
Carex mertensii	6	33.3	18	33.0	22	27.3
Carex pachystachya	16	31.2	42	17.9	89	15.7
Epilobium angustifolium	112	0.9	204	2.0	98	6.08
Hieracium albiflorum	102	52.0	168	28.3	188	59.6
Hypochaeris radicata	110	65.5	142	28.8	294	50.7
Juncus parryi	18	77.8	40	74.4	78	64.1
Luetkea pectinata	28	25.0	63	20.0	115	15.7
Lupinus lepidus	7	100.0	10	90.0	10	90.0
Penstemon cardwellii	30	3.3	80	21.3	137	33.6
Poa incurva	4	0.0	11	36.4	24	54.2
Saxifraga ferruginea	5	80.0	18	82.3	30	77.2
Spraguea umbellata	24	66.7	59	72.9	157	72.0

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1988------------------------------------

                    +

            +                   +
                +           ++

1991--------------------------------------
  +  +++ ++++  +++  +  ++++ +        +
  +++ +   +++++     +  +++ + +        +
  +    +  + ++++       ++            +   +
       ++  + +|+   +++            + +
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1992--------------------------------------
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  +   +  ++ +   +      +++        + + +
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Fig. 6.   Cover scores for *Hieracium albiflorum* on the Plains of Abraham grid, 1988, 1991, and 1992.

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1988------------------------------------
                    +
                      +
                  +
              +

                    +     +
                      +

1991--------------------------------------
    ++++++    +   +    +++       +++
  ++  + +++  + ++    + +++ +      +
  +    +   +  + +    |||+              +
    +       +++++ ++  ++++              +
  +  + + +++     +    +    ++      +++
  +  +++ +++ ++ +       + + +  +
    + +   +   +       ++++ +++++ ++++
      + +     ++ ++    ++++  +++    + ++
      +++++++       + ++++++   ++ +    ++
        + + + + ++    + ++   |  +
1992--------------------------------------
    +||+++  +      ++ +++|     ++    +
  ++ +++++  + +  ++ ++++|||+++++ ++ ++++ +
  +    +++  + ++   ||++|+++       ++   ++
  +  ++++++ + ++++  +++|+++ + +   + ++|
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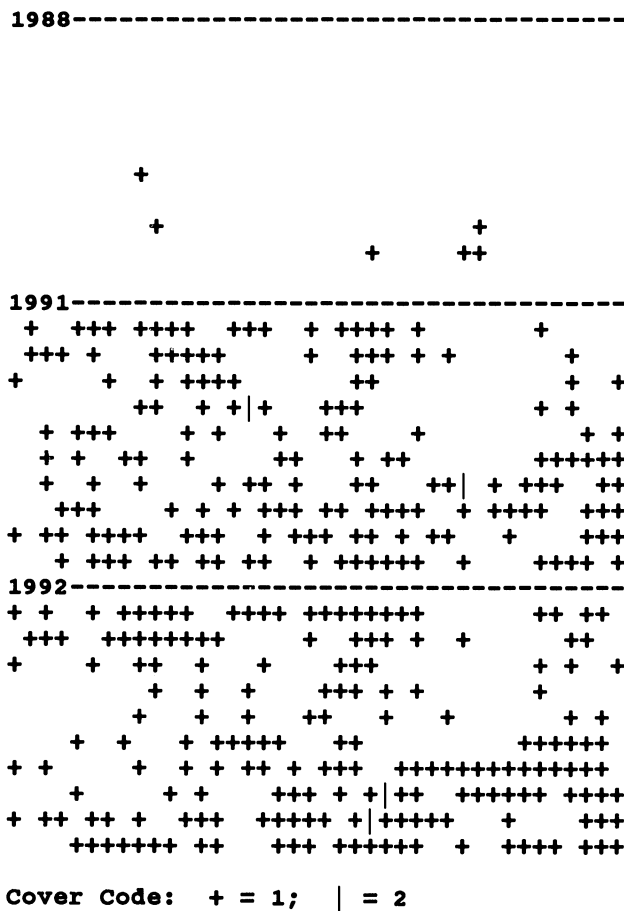
Fig. 7.   Cover scores for *Hypochaeris radicata* on the Plains of Abraham grid, 1988, 1991, and 1992.

3). This changed dramatically in 1992 when 240 quadrats had been invaded and cluster size increased. There remained 16 clusters with 60% of the grid filled, suggesting a population derived from a general seed rain. Low nutrients, surface drought, and low temperatures limit seedling success (Wood and del Moral, 1987; Morris and Wood, 1989). Many plants flower. Nearly two-thirds of the plots had flowering individuals in 1990 and 1992 (Table 4). The population density expanded explosively between 1991 and 1992, yet the grid produced few seeds. *Hypochaeris* constituted 16.7% of seeds in traps, demonstrating its invasion potential, but seedling survival is usually low (Wood and del Moral, 1987). These observations lead us to conclude that most seedlings are derived from immigrants (Fig. 7). The relatively few flowering plants contribute little to the developing population.

Spraguea umbellata—The single *Spraguea* on the grid in 1988 died. A successful invasion commenced in 1989 (Fig. 8). This species can expand quickly once it arrives. Although cluster size remains small (Table 3), several lines of evidence suggest that local individuals contribute greatly to recruitment. Wood and del Moral (1987) demonstrated that *Spraguea* was an adept pioneer, but that its long-distance dispersal powers are limited. While it bears winged fruits, these are fairly heavy, lose seeds easily, and are not airborne. About 70% of the quadrats contain flow-
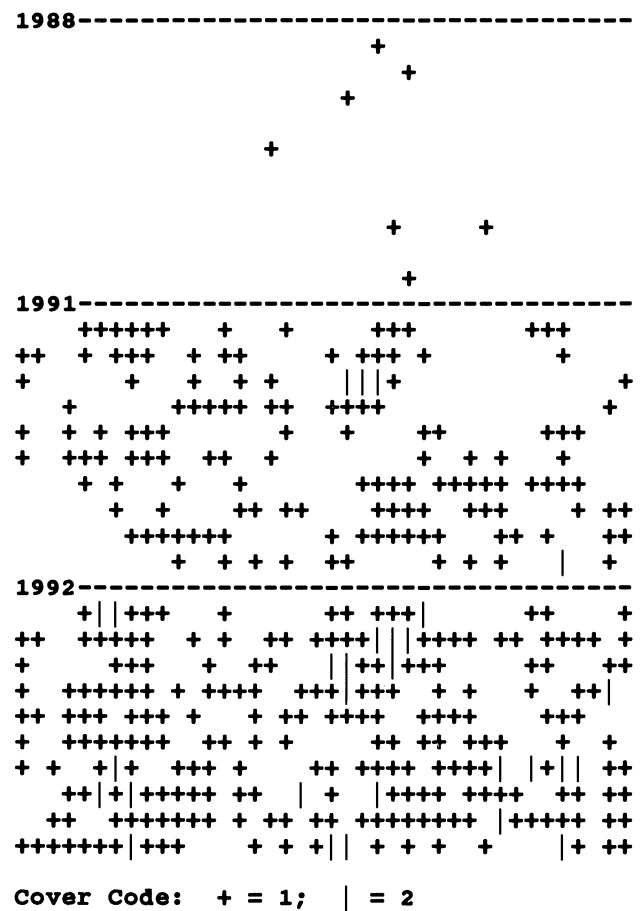
ering individuals (Table 4) and these are frequently surrounded by young plants. Finally, this species has become locally abundant in those sites where it appeared in 1990. High densities in localized quadrats are not predicted for populations dependent on incoming seeds.

Other species—*Juncus parryi* has become common and flowers often (Table 4). Seeds are tiny and easily borne across the landscape. It was absent from the grid in 1988 and 1989. We cannot easily determine whether colonists in 1991 were derived locally or from afar. Cluster size has increased despite the increase in cluster number.

Most remaining species show patterns of gradual spread within the grid and gradual increase within quadrats. *Carex mertensii* and *Carex pachystachya* are relatively common species that occur in seed traps. The seeds are relatively heavy, and although winged, their long-distance dispersal ability is not proven. These species occur across the grid. It is likely that most recruitment now occurs from already established individuals.

Lupinus lepidus, a prominent species in other devastated sites on Mount St. Helens, occurs only in a few quadrats from which it has failed to expand. Despite its nitrogen-fixing ability, dispersal limitations and surface severity appear to have precluded its spread. In contrast, *Saxifraga ferruginea* appears poised to make a major expansion. It occurs in small, widely distributed clusters,
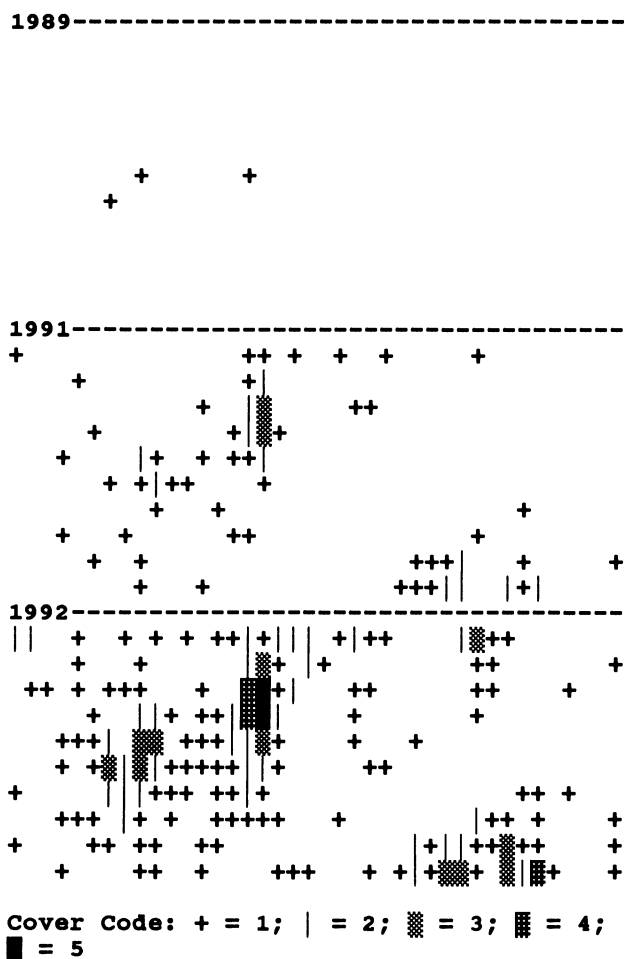
Fig. 8.   Cover scores for *Spraguea umbellata* on the Plains of Abraham grid, 1989, 1991, and 1992.

probably derived from beyond the grid. Most occupied plots contain flowering individuals and numerous seedlings.

The seed rain also included several Asteraceae absent from the grid. Alien species such as *Cirsium* spp. and

Lactuca sp. have yet to establish under the conditions of the Plains of Abraham, although they are common on the Pyroclastic Plains (Wood and del Moral, 1988).

Species associations—We hypothesized that because each quadrat had an equal opportunity to be invaded and because all contain many apparently unexploited microsites, species associations should be random.

Table 5 shows the 13 species that in 1992 occurred in from 24 (*Poa*) to 294 (*Epilobium*) quadrats. At the 5% confidence level, we would expect to encounter about four nonrandom associations among the 78 comparisons, but there are 16 significant associations ($P < 0.05$), of which 15 are positive. Only *Abies,* a species that is never among the first invaders, shows a consistent pattern with six positive associations. No species is anywhere dense. We infer that microsites are not homogeneously distributed on the Plains of Abraham and that some quadrats may be qualitatively better than others.

Community patterns—We identified 12 ad hoc CTs in 1991 and 1992 using TWINSPAN (Table 6). CT composition and descriptions varied between years, and the classification of quadrats differed greatly. Only 186 of 400 quadrats were similarly classified in the 2 years. This degree of lability and the sparseness of the vegetation suggest that detailed analysis of this classification is as yet unwarranted.

Anaphalis dominates each type. Characteristic species or co-dominants fall into one of the three classes: small-seeded, wind-dispersed species (*Epilobium, Hypochaeris* and *Hieracium*); diffuse, rhizomatous species (*Agrostis, Juncus*); and dense, spreading species (*Penstemon, Luetkea, Saxifraga,* moss).

Microsite studies—The relationship between seedling establishment and microsites on the grid was determined from the distribution of seedlings in microsites. Joint occurrences were compared to our estimate of the proportion of each microsite on the landscape (Table 7). Patterns are obvious and very highly statistically significant. *Anaphalis margaritacea* rarely occurs on smooth, exposed sites or in drainages. Healthy individuals typi-

TABLE 5.   Species associations for species common on the grid. Symbols represent positive (+) or negative (−) associations at the 5%, 1% or 0.1% confidence levels, based on Yates' corrected chi-square.

Species: Number of plots:	Abla[a] (47)	Agdi (185)	Capa (89)	Epan (294)	Hial (188)	Hyra (240)	Jupa (78)	Lupe (115)	Moss (49)	Peca (137)	Poin (24)	Safe (30)
Agrostis diegonensis	ns[b]											
Carex pachystachya	ns	ns										
Epilobium angustifolium	ns	ns	ns									
Hieracium albiflorum	++	ns	ns	ns								
Hypochaeris radicata	++	ns	ns	ns	ns							
Juncus parryi	ns	ns	ns	ns	ns	ns						
Luetkea pectinata	ns	−	ns	ns	+	ns	ns					
Moss	+	ns	ns	+++	ns	++	ns	++				
Penstemon cardwellii	++	ns	+	ns	ns	ns	ns	ns	ns			
Poa incurva	ns	ns	+	ns	ns	ns	ns	ns	ns	ns		
Saxifraga ferruginea	++	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
Spraguea umbellata[c]	+++	++	ns	ns	ns	ns	++	ns	+	ns	ns	ns

[a] Abla = *Abies lasiocarpa.*
[b] Not significant.
[c] Number of *Spraguea* plots = 157.

TABLE 6. Characteristics and spatial patterns of community types on the Plains of Abraham grid.

CT	Characteristic species	N	C	$\bar{X}$	SD
A	Anaphalis-moss/Hypochaeris-Epilobium-Hieracium	42	8	7.62	5.90
B	Anaphalis/Hypochaeris-Epilobium	28	12	3.42	1.51
C	Anaphalis-Luetkea/Epilobium-Agrostis	29	19	1.47	1.66
D	Anaphalis/Epilobium-Luetkea	32	19	1.89	1.66
E	Anaphalis/Spraguea-Luetkea	10	9	1.11	0.33
F	Anaphalis/Epilobium	68	26	2.85	3.03
G	Anaphalis-Agrostis/Epilobium-Hypochaeris	30	24	1.29	0.69
H	Anaphalis-Spraguea/Epilobium	32	11	2.63	2.34
I	Anaphalis-Penstemon/Spraguea-Epilobium-Juncus	41	22	1.86	1.78
J	Anaphalis/Penstemon-Saxifraga-Epilobium	19	13	1.38	0.65
K	Anaphalis-Penstemon/Agrostis-Epilobium	52	28	1.82	1.83
L	Anaphalis-Spraguea/Epilobium alpinum	12	6	2.00	1.55

[a] CT = community type; N = number of quadrats; C = number of clusters; $\bar{X}$ = mean size of cluster; SD = standard deviation of cluster size.

TABLE 7. Microsite analysis for the Plains of Abraham, 1990; values are number of times species was observed in each microsite and number expected based on the estimated proportion of microsites on the landscape; chi-square is for 2 × 5 contingency tables.

	Microsites				
Species	Smooth	Rocky	Edge	Undulating	Drainage
Anaphalis margaritacea (χ^2 = 1682.2 P $\ll$ 0.0001)					
Observed	16	247	112	56	5
Expected	303.9	49.7	15.76	34.9	31.8
Epilobium angustifolium (χ^2 = 604.98 P $\ll$ 0.0001)					
Observed	1	70	40	10	1
Expected	85.0	13.9	4.4	9.8	8.9
Hypochaeris radicata (χ^2 = 488.34 P $\ll$ 0.0001)					
Observed	5	69	32	10	2
Expected	82.2	13.5	4.2	9.4	8.6
Hieracium albiflorum (χ^2 = 532.69 P $\ll$ 0.0001)					
Observed	8	90	8	8	0
Expected	79.5	13.0	4.1	9.1	8.3
Agrostis diegoensis (χ^2 = 265.29 P $\ll$ 0.0001)					
Observed	2	43	4	4	0
Expected	36.9	6.0	1.9	4.2	3.9
Abies lasiocarpa (χ^2 = 133.29 P $\ll$ 0.0001)					
Observed	3	24	2	3	0
Expected	22.3	3.6	1.1	2.6	2.33
Juncus parryi (χ^2 = 52.62 P $\ll$ 0.0001)					
Observed	3	10	4	1	1
Expected	13.2	2.2	0.7	1.5	1.4
Luetkea pectinata (χ^2 = 108.03 P $\ll$ 0.0001)					
Observed	1	12	9	7	1
Expected	20.9	3.4	1.1	2.4	2.2
Spraguea umbellata (χ^2 = 139.84 P $\ll$ 0.0001)					
Observed	0	21	0	2	1
Expected	16.7	2.7	0.8	1.9	1.8
Carex pachystachya (χ^2 = 90.41 P $\ll$ 0.0001)					
Observed	2	16	4	2	0
Expected	16.7	2.7	0.8	1.9	1.8
Penstemon cardwellii (χ^2 = 214.15 P $\ll$ 0.0001)					
Observed	4	32	0	0	0
Expected	25.1	4.1	1.3	2.9	2.6
All others combined (χ^2 = 255.03 P $\ll$ 0.0001)					
Observed	1	31	21	8	8
Expected	48.1	7.9	2.5	5.5	5.0

cally grow on rill edges or are sheltered by rocks. Virtually every individual of *Epilobium angustifolium* is stunted and on the edge of its physiological tolerance. Edges, undulations, and rocks offer barely sufficient amelioration for seedling establishment. *Hypochaeris radicata* shows a preference for rocks and undulations and avoids edges. *Hieracium albiflorum* is strongly dependent on rocks and undulations. Although it occasionally occurs on smooth substrates, none of those individuals were flowering. *Agrostis diegoensis* avoids smooth surface and drainages and only moderately prefers undulations, but it has a strong preference for rocks.

The other species, including *Abies lasiocarpa, Luetkea pectinata, Spraguea umbellata,* and *Penstemon cardwellii,* all show similar patterns whose details differ. Each avoided smooth substrates and preferred rocks.

DISCUSSION

This study demonstrates the great importance to primary succession of several mechanisms that do not significantly affect secondary succession. Primary succession on the Plains of Abraham has not followed many rules suggested by earlier studies. Physical amelioration and chance (Halpern et al., 1990) have determined much of the early pattern.

Structural development—Annually monitoring species invasions on grids permits a dynamic picture to be assembled. Annual increases in richness, cover, and H' were all significant. Based on conditions observed on less isolated sites on Mount St. Helens, we expect development to continue slowly. Once competition becomes a factor, uncommon species may be excluded. Further colonizations by new species will be slow. As substrate conditions are ameliorated through weathering and the establishment of shrubs and trees, further establishment opportunities should be created. As yet, there is no apparent reason richness should vary among quadrats or why any quadrat should fail to contain any particular species. The pattern of richness for 1992 (Fig. 1c) does not correspond to obvious landscape features. We believe that microscale heterogeneity is the likely reason for these centers of richness.

Cover remains low, but the vegetation may be in the initial phase of accelerated development. A significant (P

< 0.01) linear regression based on 1988–1991 predicted the cover score to reach 5.42 in 1992; that actual value is significantly higher. This suggests that the anticipated exponential increase has commenced, but further observations will be required to distinguish this result from an effect of a single favorable growing season.

H' must, of course, increase from zero since initially most plots were empty or had a single species. As the vegetation develops and richness begins to stabilize, H' should decline, as it has on better developed grids elsewhere (del Moral, unpublished data), reflecting the development of a dominance hierarchy. Competition may further reduce H' by locally eliminating species.

Nature of pioneers—Unlike earlier studies, succession here has not recapitulated phylogeny (cf. Griggs, 1933; Fosberg, 1959; Ball and Glucksman, 1975; Beard, 1976). Lichens, fungi, and cyanobacteria are not apparent, and ferns are sporadic. One unidentifiable moss species now occurs, but it arrived after vascular plants. Flowering plants frequently pioneer pumice substrates (Heath, 1967; Clarkson and Clarkson, 1983; Masuzawa, 1985; Fridriksson, 1987; Tsuyuzaki, 1989) and on the Plains of Abraham they dominate. Dry summers and porous surfaces create an inhospitable habitat for lower organisms. Invaders tend to be stress-tolerant ruderals (sensu Grime, 1977), relative to the available flora (see del Moral, 1983b) capable of reaching isolated sites and establishing at least in the most favorable microsites.

Succession rate—Development on the Plains of Abraham is slow. Mean richness in 1989 was significantly lower than that found by Wood and del Moral (1988) on the Pumice Plains in 1986. One difference is that nitrogen fixers (e.g., *Lupinus* ssp.) are rare on the Plains of Abraham. This paucity of nitrogen-fixing plants appears to have slowed early primary succession.

The patterns by which individual species expand their distributions have provided insights into their population dynamics. With the exception of *Anaphalis margaritacea*, species still occur in small, isolated clusters. *Epilobium angustifolium* and *Hypochaeris radicata* are expanding rapidly with clusters that are starting to coalesce. Expansion patterns help determine whether locally produced or immigrant seeds produce population growth.

Physical amelioration and microsites—Harper (1977) described the safe-site concept, which is well exemplified early in primary succession on Mount St. Helens. The presence and development of physical safe-sites is the most important factor governing seeding establishment. No site can initially harbor seedlings. Only as physical amelioration occurs does the landscape develop and differentiate (del Moral and Clampitt, 1985; del Moral and Wood, 1986) to produce more favorable germination sites.

Most invading seeds arrive after being blown across a nearly uniform landscape. About 90% of the terrain lacked discernible physical features that might trap seeds. (Estimates based on Table 7 underestimate smooth surfaces since to be so scored, no other feature could occur. Other microsites are overestimated since a quadrat could be scored in two or more categories.) A favorable microsite traps seeds, accumulates nutrients from fallout, and re-

duces drought stress. As a landscape matures, the probability of seedling success first exceeds zero near rocks. Wood and Morris (1990) found a similar positive effect of rocks on seed germination and seedling establishment. Further, experimentally located rocks harbor significantly more naturally occurring seedlings than do adjacent exposed sites (Wood, unpublished data).

Water erosion has formed rills, which are linear habitats that marginally protect seedlings from wind, collect more snow, have lower solar radiation, and may have rocks to provide additional refuge.

Undulations provide more soil moisture from collected snow and retain more soil fines than do exposed sites (del Moral and Bliss, in press). However, seeds generally settle in these features only when rocks arrest their travel. Species that produce the most seeds (*Anaphalis, Hypochaeris, Juncus,* and *Epilobium*) occur disproportionately in undulations.

Establishment is a low-probability event. Most seedlings are strongly associated with specific microsites, but most apparently favorable microsites are empty. The niches of most invaders overlap strongly, and no safe-site is uniquely suited to a particular species. Which safe-site occupied by which species therefore appears to be stochastic. A given plot could be occupied by any of several species combinations, and not be governed by environmental specificity (cf. Margalef, 1963; Davey and Rothery, in press). The result is a chaotic invasion pattern dictated by idiosyncratic, if not completely random, events as well as the number of available germinable seeds. Tagawa (1992) reported novel communities developing and persisting on Krakatau solely because of dispersal events. We suggest that community composition in general is strongly influenced for many years by seedling establishment chaos.

Facilitation—Physical amelioration plays the role usually reserved for biotic facilitation. Few positive species associations were found and they lack any apparent causal link. In vegetation so sparse, there are few biotic interactions that could produce predictable associations or strong habitat correlations. Rather, pioneers overwhelmingly occur in less stressful microsites that appear to have required 6 to 8 years for sufficient weathering (Ugolini et al., 1992) and nutrient inputs (Edwards, 1986) to occur for seedling establishment. Facilitation by nurse plants is often cited as a succession mechanism (Valiente-Banuet, Vite, and Zavala-Hurtado, 1991), but no facilitation has yet to occur on the Plains of Abraham grid. Seedlings are rarely proximate to established plants. Biologically mediated microsite variation due to mycorrhizae (J. H. Titus, University of Washington, personal communication) or symbiotic nitrogen fixation (see Braatne, 1989; Halvorson, Smith, and Franz, 1991; del Moral, 1993) is unimportant.

The question of communities—This grid contains less habitat variety than sites studied by Wood and del Moral (1988), having only a few shallow runnels and no oases. If habitat differentiation at the scale of these quadrats has occurred, and if dominant species are equilibrated to habitat conditions, then the 12 community types described in 1992 should demonstrate geographic cohesiveness and

annual repeatability. They do neither. The size of groups of contiguous quadrats of the same community type remains small, averaging from 1.11 to 7.62 quadrats. They are widely dispersed (Table 6). Only 47% of the quadrats could be assigned to the same CT in successive years. Likewise, species showed few geographic patterns (Figs. 3–8) and few positive associations. These patterns probably result because the vegetation has yet to become equilibrated, but it may be that the vegetation has equilibrated with fine-grained environmental patterns below the resolution of the grid.

After 13 years, both flora and vegetation remain dominated by wind-dispersed species that invaded from beyond the grid. A few species have barely begun significant seed production. This contrasts with other primary successions on Mount St. Helens (del Moral and Wood, 1988, 1993; del Moral, 1993) and on other volcanoes (Tagawa, 1965; Frenzen, Krasney, and Rigney, 1988) where seral species are pioneers and plant communities have established. As yet, there has been only local turnover, and many species common in undisturbed subalpine meadows of Mount St. Helens are absent or rare (e.g., *Phlox diffusa, Polygonum newberryi, Lomatium martindalei, Achillea millefolium, Eriogonum pyrolifolium,* etc.). Bird- and mammal-dispersed species are absent, and other large-seeded species have limited distributions.

Colonization has been slow and populations remain sparse as a result of isolation, lack of survivors, and stress. As succession continues, recruitment will come increasingly from local plants. We expect that the anarchic pattern will become more ordered with the development of explicable relationships between vegetation and habitat characteristics, but as yet, only microscale patterns are predictable. Therefore, we believe there is no evidence that any true plant community exists on the Plains of Abraham. Plants certainly occur, but they interact little or not at all. Statistical identification of community types that change drastically between years and weak species associations on a scale of 100-m² imply that few functional interactions have yet developed. Chance remains a dominant determinant of this succession.

The future—By 1992, it appeared that the grid would become dominated by *Anaphalis.* However, we predict that *Anaphalis* will decline as taller, shade-generating species increase. Major successional development may occur where tall, woody species establish and grow. Because growth rates are slow, it will be several decades before shrubs and trees have an appreciable impact. Succession remains in an "early assembly" phase typical of stressful environments (Bliss and Peterson, 1992), and it appears that the assembly will continue for many years. Eventually, the site should become fully occupied and regain the considerable species richness described by Kruckeberg (1987). However, it is likely that the vegetation will retain significant differences from that vegetation because the current succession is unfolding in a different context than did earlier successions. Previous eruptions did not devastate such huge areas creating large populations of *Anaphalis* and *Epilobium* and isolated habitats. Alien species capable of altering succession, such as *Hypochaeris,* had not yet reached western North America.

Early succession on the Plains of Abraham is unique

on Mount St. Helens. Plant cover is much lower than at any other studied area. In newly created habitats immediately adjacent to intact vegetation, invasion commenced within 2 years, mean richness is three times higher, and cover is nearly eight times greater than here (del Moral and Bliss, in press). In other devastated expanses, succession has also proceeded more quickly than here. On the Pumice Plains, patches of survivors fuel recovery (del Moral and J. H. Titus, unpublished data) and drought stress is lower because the Plains of Abraham are in a rain shadow.

The Plains of Abraham provide an opportunity to understand how a plant community establishes. Distance limits the colonist pool and initially restricts the number of propagules. Establishment by ruderal species is limited to a small fraction of the landscape. After 13 growing seasons, cover is very sparse, meaningful differentiation on the landscape has not occurred, and few plant interactions have developed.

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