The role of refugia and dispersal in primary succession on Mount St. Helens, Washington

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Abstract. An intense lateral blast devastated Mount St. Helens in 1980, but forest understory species survived in some north-slope 'refugia'. We explored the effects of refugia on colonization of barren pumice in 1997 and 1998, 18 yr after the eruption. The seed rain of 23 colonizers came mostly from populations that had previously established in refugia. Parachutists had small, vagile seeds, parasailors had winged seeds, and tumblers were blown along the ground. The latter two groups are heavier and dispersed more slowly, but are more likely to survive. The proportion of the vegetation represented by wind-dispersed species increased with distance from refugia. Parachutist's density declined with time and proximity to refugia. As vegetation adjacent to refugia developed, populations of parasailors and tumblers expanded, foreshadowing their dominance in more remote pumice. Refugia played a critical role in determining the rate and course of succession by providing fertile islands that permitted pioneers and dry meadow species to establish near barren pumice. Species that survived in refugia played a negligible role in colonization. This study showed that when refugia contrast sharply with new substrates, they accelerate recovery by facilitating the invasion of pioneer species.

Keywords: Anemochore; Eruption; Landscape effect; Plant colonization; Pumice; Succession rate; Volcano.

Nomenclature: Taxonomy follows the Integrated Taxonomic Information System (ITIS) (http://www.itis.usda.gov).

Introduction

The course of primary succession is strongly influenced by the proximity of colonizers and their life history characteristics. Catastrophic disturbances may leave remnants isolated by barren terrain. Landscape ecologists emphasize the importance of fragments to sustaining biodiversity (Turner & Corlett 1996) and in the recovery from diverse impacts (Rundgren & Ingolfsson 1999; Poulin et al. 1999), so learning how refugia affect recovery of vegetation informs our understanding of community assembly.

We investigated how refugia influenced succession, because even minor isolation (< 100 m) can affect composition and limit succession rates (del Moral 1999). Colonization requires efficient dispersal and establishment in stressed sites. The eruption provided an ideal site to study successional dynamics. Refugia permitted moist meadow, shrub, and forest understory species to survive. Pioneers and dry meadow species then invaded. By assessing community development relative to distance from refugia, we determined how communities assembled.

Dispersal determines the rate and course of primary succession (Walker & del Moral 2003). Dispersal abilities vary, so isolation from seed sources shapes early community composition and creates steep gradients of richness and cover (Stöcklin & Bäumler 1996). Plants with light wind-borne seeds often dominate early succession (Prach & Pyšek 1999) especially on volcanoes (Grishin et al. 1996). However, such species often establish poorly, while poorly dispersed, large-seeded ones established well (Wood & del Moral 1987). Factors that increase the seed rain of poor dispersers would accelerate succession. Our goals were to clarify how refugia facilitate recolonization after disturbances and to evaluate the roles of dispersal ability and seed size.

Methods

Site description

The directed eruption of Mount St. Helens on 18.05.1980 blasted a wide arc north of the crater and incinerated everything in its path. Pumice buried the sterilized surface and five more eruptions further beset the terrain. A few sites on steep northeast-facing slopes of the crater escaped soil sterilization. Erosion exposed these refugia to allow survivors to resprout.

The study area was near the former timberline (ca. 1350 m), which was suppressed by 600 m (Yamaguchi 1983). Before 1980, habitats formed a forest and meadow complex (del Moral et al. 1995). Sampled refugia were

centered near 46° 14' 20" N, 122° 9' 10" W. Their environment contrasted sharply with that of pumice (see electronic archives). Refugia had reduced insolation compared to pumice. Terrain to the sides of refugia and downhill were on moderate slopes, while uphill terrain and the surrounding pumice matrix were more exposed and less steep. Most precipitation falls as snow from October to May. Summer rain is variable and dry periods common. Refugia soil had four times more organic matter than did pumice. Refugia ($n = 37$) ranged in size from 2 to 10214 m^2 (median = 150 m^2; mean = 691 m^2).

Vegetation sampling

During 1997 and 1998, we used 1-m^2 quadrats to measure species percent cover in refugia, on transects onto adjacent pumice, and on isolated pumice. Quadrats were arrayed randomly within refugia. Because refugia differed in size, variable numbers of quadrats were required to characterize them. Sampling continued until at least 85% of the species, determined by a relevé, had been recorded. The number of plots sampled per refuge varied from 2 to 35**.** Pumice near each refuge was sampled by transects (20 m long, 1 m wide) that extended from the edge of the refuge upward, along the contour in two directions, and downward onto sites that had accumulated pumice and debris. The edge started where pre-eruption organic soil was buried by at least 15 cm. Five 20 m × 20 m plots that were > 100 m from any refuge were sampled to provide a control. The composition of 20 randomly located 1-m^2 quadrats was described within each plot.

Initially, isolated vegetation should be dominated by vagile species. Then, heavier seeded species that establish more easily should increase. We distinguished three mechanisms of wind dispersal (anemochory) to better study early colonization. The first, plumed anemochores ('parachutists'), had buoyant seeds (Wood & del Moral 1987), and were successful long distance dispersers. The principal parachutists were *Anaphalis margaritacea*, *Hypochaeris radicata*, *Hieracium albiflorum*, *Epilobium angustifolium,* and *Salix* spp. A second type, winged anemochores ('parasailors'), included species whose fruits had papery membranes. *Carex mertensii* and *Cistanthe umbellata* formed this category. Although their seed masses were similar to that of *Hieracium*, the wings present a larger diaspore profile, allowing horizontal movement, but little lift (Augspurger 1986). The third type lacks apparent modification for wind dispersal, yet they are wind-aided ('tumblers'). 'Gravity dispersed' (cf. Tsuyuzaki & del Moral 1995) fails to characterize their mobility adequately. The fruits or infructescences of species such as *Penstemon cardwellii* and *Agrostis* spp. tumble until they are trapped.

We assigned each species to one of six groups based on its dominant habitat occurrence and growth form (Klinka et al. 1989). Pioneers were species that routinely colonize disturbed habitats, regardless of growth forms or dispersal type. Dry meadow species, including two sub-shrubs, commonly occurred in open, exposed sites, while moist meadow species, including three sub-shrubs, were those typical of open forests and meadows. Understory herbs were normally confined to woodland. Shrubs were woody, multi-stemmed plants of moderate height found in forest understories, margins, and meadows. Trees are tall single-stemmed canopy species.

Statistical methods

We compared the species composition of sites using Spearman's rank correlations (r_s) and calculated significance by the *t*-statistic. To limit spatial autocorrelation effects, only quadrats located at 4, 9, 14, and 19 m along each transect were used to estimate the mean % cover. All quadrat data were used for descriptions. Statistical analyses were conducted with Statistix for Windows 1.0 (Anon. 1996). Percent floristic similarity between refugia, the upper transects, and isolated pumice was calculated with relative cover (Kovach 1998).

Results

Vegetation patterns in refugia and pumice

We summarize the cover, habitat status, dispersal mechanisms, seed weight, and vegetative habit of common species in Table 1. Species richness ranged from four to 74 (mean 28.8 ± 2.6), with 122 species encountered (see electronic archive). Mean total plant cover was 85.2% of which 20 species, well distributed among pioneers, meadow species, and shrubs, accounted for 88%. There was a log-linear relationship between refuge size and species richness ($r_s = 0.80$, $P < 0.0001$). Refugia displayed several growth forms: shrubs (28.9%), moist meadow herbs (28.7%), pioneers (23.1%), and dry meadow herbs (17.3%; Table 2), which included both survivors (shrubs and moist meadow species) and recent invaders (all pioneers and most dry meadow species, which do not usually occur beneath canopies). Most species in refugia had non-wind-dispersal mechanisms, especially birds (Table 3).

Vegetative cover on pumice distant from refugia was 4.24% 18 yr after the eruption (Table 1). Richness ranged from nine to 17 species per plot (25 total

Table 1. Species with more than 1% cover in the 37 refugia and all species found in pumice (> 100 m from any refuge). N = number of 37 refugia occupied; AC = absolute cover; RC = relative cover; Habitat status: P = pioneer of barren sites; MD = dry meadow species; MM = moist meadow species; FS = forest shrubs and sub-shrubs; T = trees. Dispersal types: wind (Parachute, Parasail, Tumbler); Other (explosive, miniscule, or gravity); Bird; Spore = moss and fern spores. Seed Weight: H = heavy, M = medium, L = Light. Clonal: Y = yes, N = no. There were no common understorey herbs.

Species	N	Refugia AC (%)	Refugia RC (%)	Isolated pumice AC (%)	Isolated pumice RC (%)	Habitat status	Dispersal type	Seed weight	Clonal (Y/N)
Vaccinium membranaceum	32	7.72	9.36	0	0	FS	Bird	H	N
Lupinus latifolius	25	7.10	8.61	0	0	MM	Other	H	N
Anaphalis margaritacea	35	6.79	8.23	0.91	21.5	P	Parachute	L	Y
Agrostis pallens	36	5.42	6.57	0.53	12.5	MD	Tumbler	M	Y
Luzula parviflora	19	5.32	6.45	0.01	0.24	MM	Other	M	Y
Luetkea pectinata	19	5.02	6.30	0.03	0.07	MM	Other	L	Y
Rubus spectabilis	18	4.29	5.20	0.01	0.24	FS	Bɪʀᴅ	H	N
Penstemon cardwellii	30	4.10	4.97	0.96	22.8	MD	Tumbler	H	Y
Epilobium angustifolium	31	3.67	4.45	0.12	2.83	P	Parachute	L	Y
Sorbus sitchensis	21	3.48	4.22	0	0	FS	Bird	H	N
Rubus lasiococcus	18	3.44	4.17	0	0	FS	Bird	H	Y
Alnus viridis	12	2.16	2.62	0	0	P	Parasail	L	N
Ribes laxiflorum	15	2.03	2.46	0	0	FS	Bird	H	N
Carex spectabilis	22	2.03	2.46	0.02	0.47	MM	Other	M	Y
Carex mertensii	24	2.02	2.45	0.39	9.08	P	Parasail	M	Y
Hypochaeris radicata	24	1.98	2.40	0.17	4.01	P	Parachute	L	Y
Racomitrium canescens	30	1.90	2.39	0.06	1.42	MD	Spore	L	Y
Sambucus racemosa	18	1.70	2.01	0	0	FS	Bird	H	N
Aruncus dioicus	16	1.54	1.87	0	0	MM	Other	M	Y
Polytrichum juniperinum	24	1.28	1.55	0.03	0.59	MD	Spore	L	Y
Hieracium albiflorum	34	0.79	0.96	0.11	2.48	P	Parachute	L	N
Salix spp.	18	0.73	0.88	0.05	1.06	P	Parachute	L	Y
Lupinus lepidus	14	0.71	0.86	0.02	0.47	P	Other	H	N
Juncus parryi	27	0.40	0.48	0.15	3.42	P	Other	M	Y
Carex microptera	19	0.27	0.33	0.02	0.47	MD	Other	M	Y
Saxifraga ferruginea	20	0.20	0.24	0.06	1.30	P	Other	M	Y
Agrostis scabra	14	0.18	0.22	0.51	11.91	P	Tumbler	M	N
Juncus mertensianus	15	0.12	0.15	0.01	0.024	MM	Other	M	Y
Arnica latifolia	7	0.04	0.05	0.01	0.24	MM	Parachute	L	Y
Vahlodea atropurpurea	4	0.03	0.04	0.02	0.47	MM	Other	M	N
Epilobium anagallidifolium	13	0.03	0.04	0.02	0.47	MM	Parachute	L	N
Amelanchier alnifolia	3	0.01	0.01	0.01	0.14	FS	Bird	H	Y
Cistanthe umbellata	0	0	0	0.06	1.42	P	Parasail	L	N
Total absolute cover		82.50	93.2	4.24	100				

species). Ten species accounted for 93% of the cover. *Penstemon cardwellii* and *Anaphalis margaritacea* were most abundant, while the graminoids *Agrostis pallens*, *A. scabra*, and *Carex mertensii* provided 33% of cover. Pioneers and dry meadow species, most of which were wind-dispersed, dominated isolated pumice (Table 2). The three wind-dispersed types were all abundant. All wind-dispersed groups had higher relative cover than they did in the refugia (Table 3).

Expansion from refugia

Total cover decreased away from refugia (Fig. 1). It was most pronounced above refugia. Cover declined gradually along the contours. At 20 m, mean cover remained three times higher than in the reference plots. Spearman's rank correlations were calculated among refugia and primary surfaces 4-5 m, 9-10 m, 14-15 m, 19-20 m, and >100 m from refugia. The analyses showed that primary surfaces on transects were similar (r_s = 0.86 to 0.88). A species that could colonize within 5 m of refugia could also colonize 20 m distant. Adjacent pumice was more similar to isolated pumice (r_s = 0.66 to 0.73) than to refugia (r_s = 0.54 to 0.59). There were 60 species within 20 m of refugia, 49 on barren upper transects, compared to 25 species on isolated pumice. The correlation of refugia vegetation to vegetation on pumice > 100 m distant was low (r_s = 0.44). Isolated pumice and refuge vegetation had low floristic similarity (35.4%). Parachutists initially were the most common species (Fig. 2). In 1989, 62% of cover on a nearby pumice sample was comprised of parachutists (del Moral & Jones 2002). By 1998, the relative cover of parachutists on isolated pumice had declined to 33%, while parasailors and tumblers had increased from 22% relative cover (1989) to 58% by 1998.

Table 2. Mean relative cover of life history categories in relation to refugia. *N* = number of species. p = present in one sample.

Life history category	*N*	Refugia	Distance from refuge (m)				
			1-5	6-10	11-15	16-20	> 100
			Relative % cover				
Pioneers	15	23.1	25.8	28.9	30.3	30.5	59.6
Dry meadow	13	17.3	30.1	32.0	32.5	33.2	37.4
Moist meadow	45	28.7	43.7	38.4	36.8	36.1	2.8
Understory	17	1.4	p	p	0	0	0
Shrubs	16	28.9	0.2	0.6	0.4	0.3	0.2
Trees	7	0.6	0.1	p	0	p	0

The absolute cover of pumice colonizers was highest in refugia and decreased with distance from refugia (Fig. 3). However, in refugia, the recently arrived wind-dispersed colonizers each had significantly lower cover than other-dispersed colonizers ($p < 0.05$; Table 3). With increasing distance, the proportion of species that were wind-dispersed increased relative to others. By 20 m, cover of wind-dispersed species predominated. Nearly all species were wind-dispersed (over 92% of the cover) in isolated pumice and the fraction of each wind-dispersal type increased with distance from refugia (Table 3). Within refugia, the seven parachutists exceeded the cover of the five tumblers and parasailors, though tumblers predominated outside refugia. The proportion of the three wind-dispersal strategies remained similar in all pumice sites. Parachutists varied from 23.4 to 33.0% of wind-dispersed species near refugia to 35.8% in isolated sites. Parasailors, varied from 8.4 to 12.4% relative cover near refugia to 12.2% in isolated sites.

Tumblers varied from 55.6 to 61.6% adjacent to refugia and comprised 52.0% in isolated pumice. Three tumblers had higher cover than did the nine parachutists and parasailors combined in isolated pumice, even though they lack dispersal appendages and have heavier seeds than other anemochores.

Characteristics of successful colonizers

Eleven of the 25 colonizers of isolated pumice were pioneers that accounted for 60% of cover. Twelve dry meadow species colonized isolated pumice and supplied 40% of the cover while two shrub species supplied a trace. Nine of the 10 most abundant species were wind-dispersed, but only one of the first five wind-dispersed species was a parachutist. *Penstemon cardwellii* provided the most plant cover and had the heaviest seed among colonizers of distant pumice. Fourteen of the 25 colonists had medium-weight or heavy seeds.
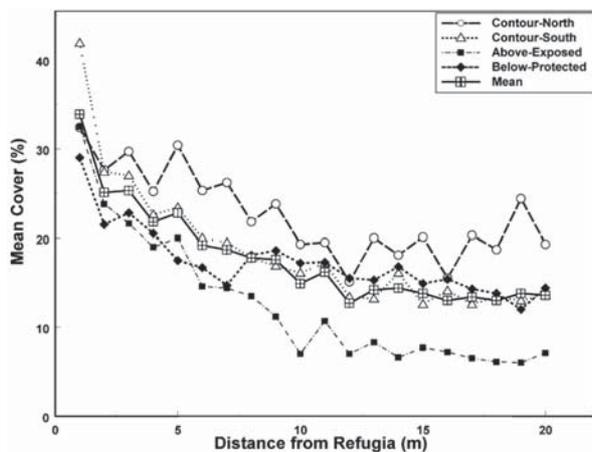
Fig. 1. Vegetation cover near refugia. The cover along each transect is shown, along with the mean of all transects. Uphill transects sampled exposed pumice, while downhill transects sampled sites with accumulated pumice that were protected from wind and extreme exposures. Mean cover in refugia was 85%, while that on pumice over 100 m distant was 4.24%.
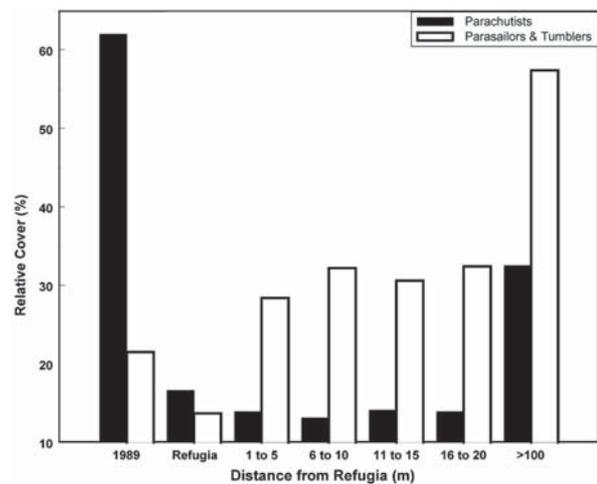
Fig. 2. Changes in relative cover of wind-dispersed species on barren pumice in time and space. The left column is pumice vegetation in 1989 (del Moral & Jones 2002) isolated from large refugia, while all other data are from 1997-1998.

Table 3. Mean relative cover of dispersal categories in relation to refugia.

Dispersal type	Refugia	1-5	Distance from refuge (m) 6-10	11-15	16-20	> 100
			Relative % cover			
Parachute[*]	20.6	15.5	19.9	15.7	23.4	33.1
Parasailor	4.1	5.3	7.0	8.3	6.6	11.2
Tumbler	12.9	26.0	37.7	37.9	48.2	48.1
Other, bird	62.5	53.2	35.4	32.8	21.7	7.6
Absolute cover %	81.78	25.45	13.8	10.29	8.24	4.24

[*] Excludes ferns and mosses

Of the 60 species on transects, the 47 pioneers and meadow herbs comprised over 99% of cover. Most of the common species on barren pumice near refugia were also common on isolated pumice. The difference between the two areas was the predominance of *Lupinus latifolius* (24% relative cover) near refugia and its total absence from the isolated pumice.

Table 2 describes the relative cover of life history categories as a function of distance from refugia. Trees rarely survived the eruption and were negligible on pumice. Shrubs were common in refugia, but they were essentially absent > 1 m from refugia. Colonization of pumice by shrubs was almost entirely by vegetative expansion. Only *Sorbus sitchensis* established seedlings near refugia. Understory species were sparse in refugia and contributed little beyond 5 m. Dry meadow species were abundant in and adjacent to refugia as well as on pumice. Pioneer species also invaded refugia after the eruption. They gradually increased in relative cover away from refugia, from 23% relative cover to 60% in isolated pumice.

Of the 25 species that colonized isolated pumice, 23 had their highest cover near refugia and decreased in cover with distance from refugia. This pattern suggests that population growth on pumice relied on the seed rain from refugia and that the rate of vegetation development depends on distance from refugia. We observed three distribution patterns among colonists of isolated pumice. Species such as *Agrostis pallens*, *Anaphalis margaritacea*, and *Carex* spp. could use the fertile conditions in refugia and tolerate dense vegetation. They achieved their highest cover in refugia and declined gradually with distance from refugia. There were 18 colonists of isolated pumice, representing 81% of plant cover, in this group. Five smaller mesophytic species (notably *Lupinus lepidus* and *Saxifraga ferruginea*) achieved their peak cover values near refugia where vegetation density was reduced, but conditions were better than distant pumice. These species represented 6% of the plant cover on isolated pumice. The third distribution pattern was demonstrated by *Agrostis scabra* and *Cistanthe umbellata*, small drought-tolerant species, that reached their peak cover on isolated pumice under stressful, low-density conditions. They represented 13% of plant cover on isolated pumice.

Table 4. Percent cover of the most common colonists of pumice. Species listed by their abundance 1-5 m from the refugia.

Species	Refugia	1-5	Sites 6-10	11-15	16-20	>100
Lupinus latifolius	7.10	6.94	4.76	3.27	3.24	0.00
Penstemon cardwellii	4.10	3.33	2.88	2.19	2.58	0.96
Agrostis pallens	5.42	3.08	2.10	1.59	1.20	0.53
Anaphalis margaritacea	6.79	1.86	1.03	0.75	0.76	0.91
Luzula parviflora	5.32	1.81	0.90	0.55	0.58	0.01
Luetkea pectinata	5.02	1.47	0.47	1.06	0.52	0.03
Lupinus lepidus	0.71	1.12	0.98	0.89	0.91	0.02
Carex mertensii	2.02	0.97	0.69	0.66	0.51	0.39
Carex spectabilis	2.03	0.96	0.60	0.44	0.42	0.02
Epilobium angustifolium	3.67	0.64	0.57	0.39	0.34	0.12
Juncus parryi	0.40	0.50	0.56	0.49	0.51	0.15
Hypochaeris radicata	1.98	0.49	0.32	0.28	0.19	0.17
Salix spp.	0.73	0.37	0.27	0.50	0.50	0.05
Saxifraga ferruginea	0.20	0.33	0.23	0.35	0.27	0.06
Hieracium albiflorum	0.79	0.24	0.17	0.15	0.09	0.11
Alnus viridis	2.16	0.21	0.34	.04	0.03	0.00
Carex microptera	0.27	0.18	0.18	0.13	0.15	0.02
Total plant cover	48.2	26.5	18.3	15.2	14.0	4.24
Total richness		53	45	44	43	25

Discussion

Proximity to relict vegetation

Vegetation near intact vegetation develops more quickly than on isolated sites (del Moral 1998) because larger, stress-tolerant seeds can quickly colonize. Large local seed output can swamp seeds invading from long distances (Drake 1992) because rare long-distance dispersal events produce few seedlings. Therefore, proximity to reproductive adults accelerates the rate of succession. Species richness and cover were much higher near refugia than on isolated pumice. However, vegetation on adjacent pumice was more similar to vegetation on isolated pumice than to that of refugia because most surviving refuge species, usually shade tolerant mesophytes, can rarely invade pumice. The important species next to, and distant from, refugia were the same other than *Lupinus latifolius*. This similarity suggests that vegetation of pumice depends on the robust populations in refugia for recruitment. The distribution of 23 of the 25 distant colonizers showed dense concentrations in and near refugia with gradual cover declines with distance, supporting this inference. Differences between isolated and adjacent pumice were due to the filtering effects of distance. This result suggests that the direct refuge effect is spatially limited. Refuge effects do not depend on the expansion of survivors. They occur because meadow and pioneers species invade fertile sites that now lack a dominant stratum.
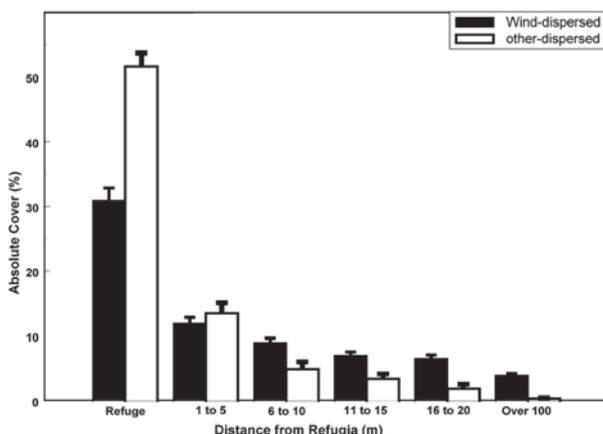
Fig. 3. Distribution pattern of the 14 pioneer and 33 meadow species that colonized primary surfaces. The species were divided into Wind-dispersed (parachutists, parasailors, tumblers) and Other-dispersal types. Error bars are the standard deviations. All but two species had dense populations in or near refugia with decreasing cover as distance from refugia increased.

Differential dispersal

Wind-dispersed species comprised most cover > 100 m from refugia, but wind and other-dispersed species were equally abundant within 20 m. This confirms the hypothesis that less adept dispersers that are more stress-tolerant can spread from refugia to eventually colonize the pumice. Differences between isolated and proximate pumice are due to distance because these pumice habitats were similar in soil texture, fertility, and moisture (see electronic archives).

Composition of vegetation on isolated pumice developed in a way that was consistent with the composition of species on the margins of refugia and their dispersal ability. Wind-dispersed species were dominant throughout the Pumice Plain, and common within refugia. The three categories of wind-dispersed species had developed robust populations in refugia, even though they were previously uncommon in refugia (del Moral & Bliss 1993). These small areas produced most of the seeds that subsequently invaded both near and distant pumice surfaces.

Early population growth in isolated pumice required seeds that crossed long distances. Because dispersal events were infrequent, the rate of early development was restricted (donor control). Population growth comes under local control when early colonists mature and begin to produce seeds. Once plants matured on isolated sites, they produced large amounts of seeds in their immediate vicinity (del Moral & Wood 1988, 1993). Any factor that reduces the time it takes to switch from donor to local control of population growth increases the succession rate. Refugia accelerated this switch by providing a fertile habitat for pioneers to quickly establish locally reproductive populations. Pioneer species were important on primary surfaces, but typical meadow species (e.g. *Penstemon cardwellii*, *Luetkea pectinata*, and *Carex* spp.) were a significant component of isolated pumice. Refugia also provided a local source of seeds for these species. Twenty-three of the 25 successful colonizers of isolated pumice probably first established in refugia. As an important source of propagules, refugia drive the rate and trajectories of primary succession on the Pumice Plain.

Seed size and dispersal

Species with light, wind-borne seeds are the most usual initial colonizers (Poli 1970; Willson et al. 1990; Fort & Richards 1998). In this case, wind-dispersed types shifted from parachutists towards heavier-seeded parasail and tumbler species. This confirmed our hypothesis that as succession unfolds, wind-dispersed species are represented increasingly by those with larger

seeds. On isolated pumice, the heavy-seeded *Penstemon cardwellii* had the highest cover. On adjacent pumice, the leading species, *Lupinus latifolius* and *Penstemon,* had the heaviest seeds of all common colonists. Seedlings from small seeds usually dehydrate in the dry pumice before their roots establish (Braatne & Bliss 1999), while larger-seeded species survive.

In 1989, seed traps contained 77% of the parachutists *Anaphalis margaritacea*, *Epilobium* spp., and *Hypochaeris radicata* (Wood & del Moral 2000). The shift to parasailors/tumblers supports our hypothesis that larger seeds established more frequently on primary surfaces than smaller seeds. On stressful sites, the greater food reserves of large-seeded species enable them to reach stable moisture supplies more often, so these species gradually dominate.

Early establishment of pioneers on the edges of refugia allowed parachutist populations to grow rapidly and develop local control. These robust refugia populations shed copious seeds onto the surroundings. Succession was accelerated near refugia as parachutists increased rapidly. Species composition has changed as less vagile anemochores, parasailors and tumblers, developed dense populations in and near refugia and diffused onto the barrens. Although populations of each group of wind-dispersed species continue to increase, the tumblers are increasing more swiftly. Their more rapid population growth results directly from the higher rate of establishment provided by their larger seeds.

Predicting future development on isolated pumice

Just as the present community on isolated pumice owes much to dynamics on the margins of refugia, future vegetation development can be predicted by analyzing pumice near refugia. Thirty-five species that had yet to invade isolated pumice did occur within 20 m of refugia. These species should continue to expand. Migration rates are related to dispersal mechanisms, seed size, and the number of seeds dispersed. The success of a species can be predicted by examining its population size near refugia and its seed characteristics. The large populations of *Luzula parviflora*, *Luetkea pectinata*, *Lupinus latifolius*, *Carex spectabilis,* and *Juncus parryi* near refugia suggest that they are poised to invade more remote areas. Many of these 'incipient' colonizers are tumblers or parasailors (e.g., *Luzula parviflora*, *Lupinus latifolius*, *Luetkea pectinata*, *Lomatium martindalei*, *Phacelia hastata,* and *Carex* spp.) and may be expected to reach isolated areas more quickly. Any species that can take advantage of frequent high winds on Mount St. Helens for dispersal will colonize isolated areas more quickly.

Community structure on isolated pumice will become more similar to pumice near refugia as new species arrive and as the existing populations expand. Diversity will increase substantially as less common species expand (e.g., *Carex microptera, C. spectabilis, Juncus mertensianus, Luetkea pectinata,* and *Luzula parviflora*) and as new species arrive (e.g. *Achillea millefolium, Carex rossii, Castilleja miniata, Lomatium martindalei,* and *Phacelia hastata*).

After physical substrate amelioration allowed colonization to begin, dispersal, not biotic interactions, appears to have controlled early vegetation development on primary surfaces. Although short-term development on isolated surfaces can be predicted by examining the vegetation near refugia and by extrapolating density and compositional gradients, later development is less predictable because it will depend on complex species interactions. *Salix* spp. are common on the Pumice Plain, but they suffer chronic mortality when rodents strip their bark. Conifers continue to establish, but they grow slowly and perish often. With the nearest seed source several km distant, their rate of population growth has been slow.

While *Lupinus lepidus* improves soil fertility, only species already established near them appear to benefit by achieving larger biomass and greater fecundity (Bishop 2002). New colonists that would accelerate development towards woodlands have yet to establish in sites once dominated by lupines (del Moral 2003). The long-term course of succession may be significantly affected by such complex interactions.

The importance of refugia

Many landscapes have refugia (Pickett & White 1985). Nunataks (Stehlik 2000) and rock outcrops (Danin 1999) can accelerate succession because survivors can colonize barren habitats directly. Refugia may augment diversity in nearby habitats (Labus et al. 1999). However, the role of refugia as hosts for newly colonizing species is less appreciated. In this study, refugia were more fertile than surrounding barrens, yet they lacked species that could invade pumice. Our study shows that these refugia accelerated species assembly by providing fertile stepping-stones. They offered pioneer and dry meadow species a chance to establish populations from which they could expand (Meirelles et al. 1999). Refugia have accentuated differential rates of succession and created a mosaic of communities. Vegetation near refugia is more predictable than that of isolated sites because the denser seed rain has swamped the effects of rare establishment events that characterize distant sites.

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