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SEED RAIN DURING EARLY PRIMARY SUCCESSION ON MOUNT ST. HELENS, WASHINGTON

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ABSTRACT

Seed rain into sites undergoing primary succession on Mount St. Helens was measured from 1982 to 1986 and again from 1989 to 1990. Study sites were devastated in 1980 by pyroclastic flows of pumice, searing blasts, and lahars. Most sites were several km or more from seed sources. Seed rain density averaged 34 seeds 0.1 m^{-2} yr^{-1} in mid-elevation barren sites, 1,083 seeds 0.1 m^{-2} yr^{-1} in mid-elevation vegetated sites and 2 seeds 0.1 m^{-2} yr^{-1} at subalpine barren sites. A total of 33 species was collected in traps. The relative abundance distributions of species were generally similar across years and sites. A few, wind-dispersed species accounted for most of the seed rain: *Anaphalis margaritacea*, *Epilobium angustifolium* , *E. watsonii (E. ciliatum)*, *Hieracium albiflorum*, and *Hypochaeris radicata*. Seeds of trees and shrubs were virtually absent. The common species in the seed rain were also the most common species in the vegetation, although their absolute abundance is determined by environmental factors. Many uncommon species occurred in the vegetation that were not recorded in the seed rain. Two taxa common in the vegetation, *Lupinus lepidus* and *Salix* spp., were rare in the seed rain. For *Salix*, this is because seed dispersal occurred before traps were in place for the season. *Lupinus lepidus* is not wind dispersed and seeds are not likely to enter traps. We conclude that the seed rain on Mount St. Helens is apparently sufficient to initiate colonization but is depauperate in species. At present the vegetation generally reflects the incoming seed rain.

KEYWORDS: *Primary succession, Mount St. Helens, Seed rain; Dispersal; Volcano*

One cause of succession is differential species availability at a site after a disturbance (Pickett et al. 1987). For vascular plants this differential availability occurs mostly by vegetative regrowth, seed banks, or seed dispersal. In primary succession colonization results mainly from seed dispersal. On large-scale primary successional landscapes the input or "rain" of seeds from long-distance dispersal is the main source for the establishment of most species, because seed banks and regrowth are absent. A complete interpretation of primary succession in particular, and community assembly in general, must therefore include measurements of the density and species composition of the seed rain along with an assessment of environmental and substrate conditions (Wood and del Moral 1987; del Moral 1993; Chapin et al. 1994; Booth and Larson 1998; Dlugosch and del Moral 1999). For example, the absence of a species from a particular site or seral stage could be due as much to its absence from the seed rain as to its inability to establish. Conversely, high abundance of a colonist may be explained as much by its abundant seed rain as by its environmental tolerance, growth rate, or competitive ability. Hypothesized mechanisms of succession such as facilitation (Connell and Slatyer 1977; Morris and Wood 1989) must also consider differential species availability through the seed rain.

Studies of seed dispersal generally are of two types: studies of individual species with the parent plant and its seed shadow as the focus (reviews in Harper 1977; Willson 1993), or studies of the long-distance seed rain into sites where specific seed sources cannot be identified precisely. Seed rain measurements are most appropriate for studies of community assembly in primary succession, but published studies are few (Ryvarden 1971; Stöcklin and Bäumler 1996; Archibold 1980; Jefferson and Usher 1989; Chapin et al. 1994). This paper describes the density and species composition of the seed rain in several contrasting regions and habitats undergoing primary succession on Mount St. Helens, Washington.

The rate of vegetation recovery and plant species composition at various sites have been described for Mount St. Helens following the catastrophic eruption in 1980 (del Moral 1983; Wood and del Moral 1987; del Moral and Wood 1988; del Moral 1993; del Moral and Bliss 1993; del Moral and Wood 1993a,b; del Moral et al. 1995; del Moral 1998, del Moral 1999), but detailed species seed rain data have not been reported with the exception of Dale (1989) who sampled lower elevation lahar (mudflow) sites not included in this study. We pose these questions: For a given site, what is the density and species composition of the seed rain? How do islands of established, reproducing vegetation affect the local seed rain? Does the species composition of the seed rain reflect the species composition of the colonizing flora? Are there species present in the seed rain but absent as colonists? Are there species present as colonists but absent from the seed rain?

STUDY AREA

The Mount St. Helens volcano is in the Cascade Range of southwestern Washington at 46°12'N, 122°11'W. The catastrophic north-directed eruption of May 18, 1980, produced a variety of impacts including: a debris avalanche; pyroclastic flows, or incandescent flows of gas and pumice; and lahars, flows of water-saturated debris ("mudflows") triggered by rapidly melting snow and ice (Lipman and Mullineaux 1981; Decker and Decker 1981). Impacts on the vegetation are categorized into four regions: the blast zone, in which most life was destroyed; the blow down zone, in which adult trees were knocked over but some saplings and understory vegetation survived; the seared zone, in which trees remained standing but had their foliage singed by the hot gases of the blast, and the mudflow (lahar) zone in which most vegetation was destroyed (Figure 1). In addition to these four regions, a large region south of the crater received 5-20 cm of tephra (air fall ash and pumice) and most vegetation survived.

We studied three main areas separated by several km and at different elevations: Pumice Plain, Plains of Abraham (both in the blast zone), and Butte Camp (Figure 1). The Pumice Plain is a 20 km^2 region between the crater and Spirit Lake that received the full force of the north-directed lateral eruption, receiving a debris avalanche and pyroclastic flows. These new deposits now overlie what was formerly a montane forest of *Tsuga heterophylla*, *Pseudotsuga menziesii*, and *Abies amabilis* (Kruckeberg 1987). Elevations range from 1000 to 1200 m. Although much of the Pumice Plain was initially flat to moderately hilly, numerous erosion gullies continue to form and deepen. The Plains of Abraham, also a pumice landscape, is located approximately 3 km NE of the crater at 1350 m elevation. It received searing blasts and deposits of tephra, and is predominantly flat with numerous small gullies (del Moral and Wood 1993b). The pre-eruption vegetation of this high montane region was described by Kruckeberg (1987) as a region high in species richness of forbs and grasses but low in cover with scattered conifers. The Butte Camp region is located on the southwest side of the volcano at 1500 to 1600 m. This area of subalpine vegetation was disturbed by several lahars and also received tephra deposits (del Moral 1983, del Moral and Wood 1986). However, seed rain was only measured at the primary succession lahar sites.

METHODS

Seed Collections

Seeds of vascular plants were collected from both wet pitfall traps and dry fallout traps. Pitfall traps, whose primary purpose was to collect ground-dwelling insects (Edwards 1986), consisted of 10 cm diameter plastic cups filled with ethylene glycol, set flush with the ground surface, and covered by a plywood square elevated 1 cm above the cup with corner nails. Pitfall trap data were collected in 1982, 1983 and 1985. The fallout traps consisted of 33 x 33 cm (0.1 m^2) wooden frames 3 cm high with fine nylon mesh bottoms. Frames were filled with a single layer of used golf balls and set flush with the surface (Edwards 1986, Edwards and Sugg 1993). The golf balls (approximately 3 cm in diameter) were used because they were an easily obtainable uniform sphere that mimicked the size and surface texture of the pumice. We also wanted baseline density estimates of the seed rain for relatively flat, open ground. These baseline values may then be adjusted upwards if desired for sites of seed accumulation, e.g. against boulders or in gullies and other depressions (Dale 1989). Sticky traps (Werner 1975) or wet pitfall traps could yield over-estimates of density for flat ground in this open, windy environment due to seed accumulation (Johnson and West 1988). Thus, only fallout traps were used to estimate seed rain density. Fallout traps were used in all years of the study except 1982, and were the only type of trap used in 1989 and 1990. Data from both pitfall traps and fallout traps were used to estimate relative abundance.

Traps were set out in June of each year after snowmelt when the roads to the sites became accessible and contents were collected approximately twice a month until November. Fallout traps were collected only once a year in late October, after the fall dispersal period and before sites became inaccessible due to snow. Seeds were stored in alcohol or formalin-acetic acid-alcohol (FAA) and were identified using a reference collection obtained from field specimens and herbarium sheets. Although seed germination was not measured in this study, only those seeds with morphology and coloration similar to viable seeds were counted. Extensive seed germination experience with many species from Mount St. Helens suggests that the appearance of viability under a dissecting microscope is a good predictor of germination—most species had germination rates from 60 to 90% when abnormal-appearing seeds were excluded (Wood and del Moral 1987, Wood unpublished data). Nomenclature follows Hitchcock and Cronquist (1973) with parenthetical updates from Hickman (1993) to correspond to Titus et al. (1998).

Study Sites

From 1982 to 1986 two sites on the Pumice Plain were sampled, Pumice Pond and Spirit Lake. The Pumice Pond site was near the headwaters of the North Fork of the Toutle River on the northwest side of the Pumice Plain about 5 km NNW of the crater. Unfortunately, severe erosion at this site forced it to be abandoned in 1985 (Edwards and Sugg 1993). The Spirit Lake site was near the eastern edge of the Pumice Plain about 2 km south of Spirit Lake and 3 km north of the crater. Traps of both types (pitfall and fallout) were placed at 10 m intervals along 100 m transects, although resultant sample sizes vary because traps occasionally were filled with erosional material or lost (Tables 1 and 3). In 1986 mean percent cover of vegetation on the Pumice Plain in the vicinity of these sites was estimated at 0.09% (Wood and del Moral 1988) and had increased to only 1.4% by 1990 although some small patches exceeded 50% (Wood, unpublished data).

In 1989 and 1990, the number and placement of fallout traps was increased by including a greater variety of habitats within the Pumice Plain. Pumice Plain sites I and II were established in barren areas (defined as having <3% cover) close to the old Spirit Lake site at 1100 m elevation. Each site contained 16 fallout traps arranged in a 4x4 grid with traps separated by 10 m (hereafter referred to as a "16-FT grid"). Due to occasional trap disturbance (e.g. by ravens and elk) resultant sample size again varied (Table 2). The Pumice Ridge site was on an exposed, barren ridge 50 m above the Pumice Plain and contained 5 traps along a 30 m transect. The 16-FT grid Lupine Patch site was in a patch of dense flowering *Lupinus lepidus* (>50% cover) a few hundred m from Pumice Plain I and II. The Willow Spring 16-FT grid was in a relatively open, moderately vegetated site (<20% cover) but was surrounded by a stand of dense, reproductively mature vegetation adjacent to a spring (Wood and del Moral 1988). This vegetation included *Salix* spp. (primarily *S. sitchensis* and *S. commutata*), *Anaphalis margaritacea*, *Epilobium angustifolium*, *E. watsonii (E. ciliatum)*, *Hypochaeris radicata*, and *Lupinus lepidus*.

The Plains of Abraham area contained two sites in barren areas, one 16-FT grid (Abraham I) and one five-trap transect (Abraham II) similar to the Pumice Ridge site described above. Both sites were on nearly level ground and were spaced 200 m apart. In 1989 and 1990, mean percent cover on the Plains of Abraham was estimated at 0.12% and 0.23%, respectively (del Moral and Wood 1993b).

The Butte Camp area contained two sites on lahars (Lahar I and II), both 16-FT grids spaced 200 m apart. Percent cover on the Butte Camp lahars was estimated at 2-3% in 1989 (del Moral 1993).

RESULTS

Density

Seed rain density varied widely over both sites and years (Tables 1 and 2), from a low of 1.2 seeds 0.1 m^{-2} yr^{-1} at Lahar II in Butte Camp in 1989 to a high of 2174 seeds 0.1 m^{-2} yr^{-1} at Willow Spring on the Pumice Plain in 1990 (Table 2). In 1983 and 1984 the Pumice Pond site received more than twice as many seeds as did the Spirit Lake site (Table 1; t-test, log transformation, $p<0.01$ in each year). In both 1989 and 1990, ANOVA revealed a significant difference among the Pumice Plain, Plains of Abraham, and Butte Camp areas as well as significant differences among sites within the Pumice Plain (Table 2; log transformation, $p<0.001$ in each year). In both 1989 and 1990, Willow Spring had a significantly greater seed rain density than all other sites (Table 2; Tukey's HSD multiple comparisons, $p=0.05$). Lupine Patch had the second highest seed rain density in both years, although mean density at this site was not significantly different from Pumice Ridge in 1989 or Abraham II in 1990 (Table 2). Statistical tests were not performed on year-to-year differences within a site due to the lack of clear hypotheses, as variation could be due to unmeasured factors such as differences in wind patterns or growing conditions and seed production in surrounding landscapes.

When sites were classified by habitat, the variation in density was reduced and a clearer pattern emerged. Mid-elevation barren sites (Pumice Pond, Spirit Lake, Pumice Plain I and II, Pumice Ridge, Abraham I and II) had an overall mean density of 33.6 seeds 0.1 m^{-2} yr^{-1}, ranging from 5.3 at Abraham I in 1990 (Table 2) to 75.5 at Pumice Pond in 1983 (Table 1). High-elevation barren sites (Lahar I and II) had a much lower overall mean density of 1.9 seeds 0.1 m^{-2} yr^{-1} . The highest densities were recorded at mid-elevation vegetated sites (Lupine Patch and Willow Spring) where densities ranged from 94.1 at Lupine Patch in 1989 to 2,174 at Willow Spring in 1990 (Table 2) with an overall mean density of 1,083.

Relative Abundance

The relative abundance of the most common species in the seed rain is presented in Tables 3 and 4. Relative abundance distributions were generally consistent from year to year and from site to site. The most distinctive sites were Lahar I and II, where subalpine species characteristic of that habitat appear. However, no comparison of abundance distributions is significantly different, either among years from 1982 to 1986 (Table 3), between years within a site, or among sites in 1989 and 1990 (Table 4; Wilcoxon Signed Rank Test, all p>0.5). Unfortunately, separate estimates of relative abundance for the Pumice Pond and Spirit Lake sites are not available because sample collections from these sites were combined after counting the total number of seeds in a given trap.

Six species accounted for 85% of the measured seed rain at the two Pumice Plain sites in 1982 and >90% from 1983 to 1986: *Anaphalis margaritacea, Epilobium angustifolium, E. watsonii (E. ciliatum), Hypochaeris radicata, Hieracium albiflorum,* and *Senecio sylvaticus* (Table 3). Six species also accounted for >90% of the measured seed rain at all sites in 1989 and 1990 except for the subalpine sites Lahar I and II (Table 4). These were the same six species listed above except that *Lupinus lepidus* replaced *S. sylvaticus*. The decline of *S. sylvaticus* and the increase of *L. lepidus* were the most noteworthy changes in relative abundance during this study. *S. sylvaticus* decreased from 39% relative abundance in 1983 to zero in 1989 and 1990 at all sites except Lahar I and II (Tables 3 and 4). *L. lepidus* was not recorded from 1982 to 1986 but during the 1989-1990 sampling period it occurred at all sites except Abraham II at least once.

A total of 33 species was collected, including two unidentified grasses (one seed each). Species not listed in Tables 3 or 4, all with three or fewer seeds trapped except as noted, are: *Acer circinatum*, *Achillea millefolium*, *Agoseris grandiflora*, *Agrostis* sp., *Antennaria sp.*, *Carex mertensii*, *Carex rossii*, *Carex* sp., *Cinna latifolia*, *Cirsium vulgare*, *Epilobium luteum*, *Juncus parryi*, *Lactuca muralis*, *Penstemon cardwellii*, *Salix* spp. (12 seeds), *Saxifraga ferruginea*, *Senecio vulgaris*, *Sitanion hystrix (Elymus elymoides)*, *Sonchus asper*, and *Taraxacum officinale*.

As with density, a classification of sites by habitat resulted in a clearer pattern of relative abundance. In both the mid-elevation barren sites and Lupine Patch (which had vegetation mostly <15 cm in height), *Anaphalis margaritacea* and *Epilobium angustifolium* dominated the seed rain. At Willow Spring, which had taller surrounding vegetation (up to 2 m) including a vigorous flowering population of *E. watsonii (E. ciliatum)*, seeds of *E. watsonii* were dominant. Still, densities of *A. margaritacea* and *E. angustifolium* at Willow Spring were similar to the other mid-elevation sites.

The species recorded in the seed rain at Lahar I and II were distinct from all other sites (Table 4), as expected given the higher elevation, different surrounding flora, and greater physical exposure of these subalpine sites. Although sampled densities were very low (Table 2), making interpretation speculative, *A. margaritacea* and *E. watsonii* were conspicuously absent from the seed rain although *E. angustifolium* was present. Species characteristic of the surrounding subalpine flora that were recorded at Lahar I and II, but were rarely trapped elsewhere, included *Spraguea umbellata (Calyptridium umbellatum); Polygonum newberryi*, *Aster ledophyllus*, *Lomatium martindalei*, *Juncus parryi*, and *Hieracium gracile* (Table 4). *Eriogonum pyrolifolium,* a dominant species in many subalpine sites on Mount St. Helens (del Moral and Wood 1986, Chapin and Bliss 1989, del Moral 1993), was not recorded in the seed rain.

DISCUSSION

Seed rain is a critical factor in determining species composition and abundance in early primary succession on Mount St. Helens. All species in the seed rain with >1% relative abundance at any site are present in the vegetation, and the most common species in the seed rain were also the most common species in the vegetation during the study period (Wood and del Moral 1988, del Moral 1993, del Moral and Wood 1993a; see also Stöcklin and Bäumler 1996). No species with consistent, relatively abundant seed rain appeared to be excluded from establishing at least some individuals on Mount St. Helens due to a lack of ecological tolerance. However, the absolute abundance in the vegetation on Mount St. Helens is determined by a host of other factors in addition to seed rain density including safe-sites for germination (Wood and Morris 1990; del

Moral and Wood 1993b; Titus and del Moral 1998) and facilitation (Morris and Wood 1989; del Moral and Wood 1993a). Most of the common species in the seed rain have seeds adapted for wind dispersal: a feathery coma in *Epilobium angustifolium* and *E. watsonii*, and pappuses in *Anaphalis margaritacea, Hypochaeris radicata, Hieracium albiflorum*, and *Senecio sylvaticus*.

The consistency in species composition of the seed rain among both years and sites suggests that the vegetation will also be similar from site to site, with the exception of the subalpine lahar sites. This prediction is upheld for sites of similar elevation except where patches of *Lupinus lepidus* have developed (del Moral et al. 1995). The species composition of the seed rain also gives some indication as to seed sources. Seeds of common montane species such as *Anaphalis margaritacea*, *Epilobium angustifolium, E. watsonii (E. ciliatum), Hypochaeris radicata*, *Hieracium albiflorum*, and *Senecio sylvaticus* probably originated in seared and blowdown forest 10-20 km to the west and north of the study areas (Figure 1) where recovery of these species occurred relatively rapidly (Halpern et al. 1990). Westerly prevailing winds likely transported these species up the Toutle River valleys to the Pumice Plains sites (Figure 1). Willson (1993) reports a wide range in maximum dispersal distances of herbaceous species with wind dispersal adaptations, from a few m to >4000 m. The dispersal ability of *Epilobium* in particular is extraordinary—Solbreck and Andersson (1987) estimated the maximum dispersal distance of *E. angustifolium* to be hundreds of km under windy conditions. Seeds of the ruderal species in the seed rain such as *Cirsium arvense*, *C. vulgare*, *Taraxacum officinale*, *Sonchus asper*, *Lactuca muralis*, and *Senecio vulgaris* probably had their origin in low-elevation clear-cut or agricultural fields tens of km to the west. Dale (1989) captured several of these same ruderal species at lower elevation on the debris avalanche along the Toutle River to the west.

The only shrub or tree species trapped besides *Salix* was one seed of *Acer circinatum*, in a sample of >75,000 seeds. Since the montane sites on Mount St. Helens will, in the absence of another eruption, eventually succeed to a coniferous forest, the low abundance of late-successional woody species suggests a strong seed dispersal limitation. Similarly, Chapin et al. (1994) detected no spruce seeds and negligible alder seeds in the pioneer stage of primary succession at Glacier Bay at dispersal distances comparable to those of this study (approximately 10 km from seed sources for spruce and 3 km from alder sources). Although not detectable in the seed rain, conifer and shrub seedlings such as *Pseudotsuga menziesii, Abies amabilis, Tsuga heterophylla*, *Pinus contorta*, *Alnus sinuata (A. viridis), Rubus* spp., and *Vaccinium* spp. do occur in low numbers at most of the sites sampled here (see also del Moral et al. 1995). These individuals are either establishing from extremely low seed source inputs and/or our seed trap design did not adequately sample their mode of dispersal (see below).

Seed traps were designed to estimate the seed rain onto relatively flat, open ground. True densities may exceed our estimates in microsites where seeds accumulate, such as in depressions or wet sites, or about rocks (Dale 1989; Titus and del Moral 1998). Higher densities also may occur in vegetated sites where short-distance dispersal supplements the long-distance seed rain. For example, at Willow Spring and Lupine Patch, seeds produced on or near the site probably equaled or even exceeded the number of seeds arriving by long-distance dispersal. Also, variation among traps was highest at Willow Spring, with standard errors of 29% and 30% of the density means for 1989 and 1990, respectively (Table 2). This suggests that established vegetation islands augment the long-distance seed rain in a patchy manner, in contrast to barren sites which receive a more predictable, albeit low input.

The sharp decline in the seed rain of *Senecio sylvaticus* (Tables 3 and 4) may be explained by its life history—a biennial, it exploits forest clear-cut for only one or two generations before being outcompeted by more aggressive seral species (West and Chilcote, 1968; Halpern et al. 1997). The 1980 eruption of Mount St. Helens apparently created brief but favorable growing conditions for *S. sylvaticus* in surrounding forests that resulted in a pulse of seed rain in 1982 and 1983.

The overall mean density of 33.6 seeds 0.1 m^{-2} yr^{-1} for mid-elevation barren sites on Mount St. Helens is similar to that found by Ryvarden (1971; calculations from Rabinowitz and Rapp 1980), who reported 34.2 to 65.3 seeds 0.1 m^{-2} yr^{-1} for primary succession at the base of a retreating glacier in Norway, and to that of Stöcklin and Bäumler (1996) who found 12.5 seeds 0.1 m^{-2} yr^{-1} for newly exposed terrain in glacial forelands in Switzerland. Archibold (1980) reported 240.0 to 380.0 seeds 0.1 m^{-2} yr^{-1} in strip-mine wastes in Saskatchewan, but this higher figure may be due to the closer proximity of seed sources. The very low mean density of 2 seeds 0.1 m^{-2} yr^{-1} for the subalpine lahar sites was probably because seeds of well-dispersed species such as *Anaphalis margaritacea* and *E. watsonii* did not reach that elevation, and because seeds of species in the surrounding vegetation have poor adaptations for dispersal (Wood and del Moral 1987).

Many species that occur in the vegetation on Mount St. Helens were not recorded in the seed rain. Most of these species are uncommon or rare. This suggests that either their seed rain is below our detection limits or that their mode or timing of dispersal is such that they eluded capture. Although we think that low species richness in the seed rain is more likely, our traps were designed to capture wind-dispersed seed and thus may have missed capturing seeds of species with other dispersal modes. One possible dispersal mode that may be important on Mount St. Helens is that of secondary wind dispersal across hard snow surfaces. Matlack (1989) showed that seeds of *Betula lenta* were dispersed greater distances by secondary dispersal than by primary dispersal to the ground. Because Mount St. Helens receives abundant winter snow and freeze-thaw cycles are common, hard surfaces conducive to secondary dispersal by wind probably occur. Water dispersal (hydrochory) is another unmeasured variable. In addition to permanent streams, numerous small temporary streams commonly develop during spring snowmelt and fall rains, and sheet flow occurs during particularly heavy rains. Seeds can be transported along these watercourses (Stöcklin and Bäumler 1996). Either secondary dispersal or water dispersal may be responsible for the spread of non-wind dispersed species such as *Lupinus lepidus* and the occurrence of the late successional woody species listed above. Animal dispersal (zoochory) is another unmeasured vector. We consider animals to be less important than either wind or water, but we cannot rule out their effect. Plant taxa with fleshy fruits are rare on Mount St. Helens (e.g. *Vaccinium*, *Rubus*; del Moral 1993) suggesting that frugivory as a means of seed dispersal is also rare. However, birds and large mammals such as elk and coyotes travel long distances to the study sites and may disperse seeds by defecation or transportation in their feathers or hair. The potential importance of a rare colonization event that results in local seed production and population spread should not be underestimated.

Whereas relative abundance of a species in the seed rain is a good indicator of its relative abundance in the vegetation, the reverse is not necessarily true. A few species are common in the vegetation but uncommon in the seed rain. These include *Lupinus lepidus*, *Salix* spp., and *Eriogonum pyrolifolium*. Lupine is the species with the greatest disparity between its estimated seed rain density and its abundance. Lupine survived the eruption in a variety of high elevation sites around the volcano (del Moral 1983, 1993; del Moral and Wood 1986) and was present on the Pumice Plain as early as 1981 (C. Crisafulli, personal communication), possibly establishing from seeds or root fragments washed down from high-elevation survivors. Now lupine occurs across the Pumice Plain and other sites on Mount St. Helens (Morris and Wood 1989; Bishop and Schemske 1998; Titus et al. 1998). In spite of this early record of population growth, seeds of *L. lepidus* were not captured in the seed rain until 1989, presumably because of its limited seed shadow. Lupine seeds have no obvious dispersal adaptations except for ballistic dispersal when legumes dehisce, but this type of dispersal probably only achieves a few m (Willson 1993). Thus the rapid increase of *L. lepidus* on the Pumice Plain was due to vigorous seedling recruitment in close proximity to early colonists, not to long distance dispersal (Wood and del Moral, 1988, Morris and Wood, 1989). The low abundance of *Salix* spp. in the samples is probably due to a flaw in the sampling design. *Salix* began reproducing as early as 1985 at Willow Spring (Wood, personal observation) but each year due to impassible roads our traps were put out too late to catch dispersing willow seeds. The high abundance of *Salix* around Willow Spring would undoubtedly have contributed greatly to the seed rain at this site and would have resulted in lower relative abundances of other species such as *E. watsonii*. *Eriogonum pyrolifolium*, a dominant subalpine species, has relatively heavy, round seeds with no obvious dispersal adaptations (Wood and del Moral 1987) and thus its seed shadow apparently did not extend to the seed traps.

The vast majority of incoming seeds in the seed rain fail to establish. Vegetation remained generally sparse by 1990 in spite of a rain of hundreds of seeds m^{-2} yr^{-1} onto most sites. Previous studies demonstrated that limits to abundance on Mount St. Helens are set by environmental factors. Morris and Wood (1989) and del Moral and Wood (1993a) showed that *Lupinus lepidus* may facilitate the establishment of several species including *Anaphalis margaritacea*, *Epilobium angustifolium*, and *Hypochaeris radicata*. Wood and Morris (1990) showed that manipulation of substrate moisture and microtopographic heterogeneity positively affected the rate of establishment of *A. margaritacea* and *E. angustifolium*. Del Moral and Wood (1993b) showed that most species on the Plains of Abraham established in favorable microsites more often than expected by chance. There is also a tradeoff between seed mass and probability of establishment—heavier seeds have a greater likelihood of establishing on Mount St. Helens due to increased seedling vigor but are less likely to disperse a long distance (Wood and del Moral 1987, Wood and Morris 1990). Titus and del Moral (1998) further demonstrated the importance of microsites in seedling establishment. Thus, the vegetation of early primary succession on Mount St. Helens is composed primarily of well-dispersed species in low abundance. Stochastic events such as chance colonization of species with low long-distance seed rain result in heterogeneous communities with little structure (del Moral et al. 1995). As succession proceeds, community composition will become increasingly uncorrelated with the long-distance seed rain.

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Table 1. Mean ± standard error of seed rain density (seeds 0.1 m^{-2} yr^{-1}) for 1983 to 1986 estimated from fallout traps at mid-elevation barren sites. Number in parentheses is number of traps. In 1983 and 1984, mean values for the Pumice Pond and Spirit Lake sites are significantly different.

Pumice Plain Sites	1983	1984	1985	1986
Pumice Pond	75.5 ± 9.5 (10)	38.4 ± 9.6 (5)	no data	no data
Spirit Lake	34.9 ± 5.0 (10)	13.0 ± 2.9 (9)	25.02± 3.0 (10)	26.9 ± 4.9 (10)

Table 2. Mean ± standard error of seed rain density (seeds 0.1 m^{-2} yr^{-1}) in 1989 and 1990. Number in parentheses is number of traps. Means with the same letter within a year are not significantly different at p=0.05 by Tukey's HSD. MEB = mid-elevation barren; MEV = mid-elevation vegetated; HEB = high-elevation barren.

Butte Camp Sites	Habitat	1989	1990
Lahar I	HEB	1.2^{a} ± 0.7 (15)	no data
Lahar II	HEB	2.8^{a} ± 0.8 (16)	no data
Plains of Abraham Sites			
Abraham I	MEB	11.8^{b} ± 1.7 (16)	5.3^{a} ± 2.8 (16)
Abraham II	MEB	9.0^{b} ± 2.0 (5)	$66.5^{a,b}$ ± 12.3 (4)
Pumice Plain Sites			
Pumice Plain I	MEB	$24.7^{b,d}$ ± 4.1 (15)	50.6^{a} ± 8.2 (16)
Pumice Plain II	MEB	$21.9^{b,d}$ ± 3.3 (15)	50.6^{a} ± 8.2 (16)
Pumice Ridge	MEB	$68.2^{c,d}$ ± 19.4 (5)	9.6^{a} ± 2.3 (5)
Lupine Patch	MEV	94.1^{c} ± 10.8 (16)	355.6^{b} ± 48.6 (16)
Willow Spring	MEV	1709.1 ± 489.7 (16)	2174.4 ± 645.1 (16)

Table 3. Relative abundance of common species in the seed rain for 1982 through 1986. The Pumice Pond and Spirit Lake sites are combined. See text for additional species. Distributions between years are not significantly different by a Wilcoxon Signed Ranks test.

	Relative Abundance (%)				
	1982	1983	1984	1985	1986
Anaphalis margaritacea	16	36	21	10	70
Epilobium angustifolium	26	8	48	74	13
Epilobium watsonii (E. ciliatum)	<1	5	10	3	5
Hypochaeris radicata	3	2	3	5	3
Hieracium albiflorum	3	2	3	1	3
Senecio sylvaticus	36	39	7	1	1
Lupinus lepidus	0	0	0	0	0
Number of pitfall traps	38	32	0	35	0
Number of fallout traps	0	20	14	10	10

Table 4. Relative abundance of common species in the seed rain for 1989 and 1990. See text for additional species. All values are %. Distributions between years within a site or among sites are not significantly different by a Wilcoxon Signed Ranks test.

	Pumice Plains I		Pumice Plains II		Pumice Ridge		Lupine Patch		Willow Spring		Plains of Abraham I	
	‘89	'90	'89	'90	'89	'90	'89	'90	'89	'90	'89	'90
Anaphalis margaritacea	29	24	42	47	40	17	18	22	4	4	6	15
Epilobium angustifolium	26	54	40	39	18	13	6	6	1	4	67	69
Epilobium watsonii	19	5	5	4	12	0	36	30	95	89	9	5
Hypochaeris radicata	14	11	7	3	13	58	8	29	<1	1	11	3
Hieracium albiflorum	2	4	2	3	2	10	1	4	<1	<1	1	1
Lupinus lepidus	<1	0	0	1	13	0	29	8	0	<1	0	1
Senecio sylvaticus	0	0	0	0	0	0	0	0	0	0	0	0
Cirsium arvense	0	<1	0	<1	0	0	0	<1	0	0	0	0
Spraguea umbellata	0	0	0	0	0	0	0	<1	0	0	0	0
Polygonum newberryi	0	0	0	0	0	0	0	0	0	0	0	0
Aster ledophyllus	0	0	0	0	0	0	0	0	0	0	0	0
Lomatium martindalei	0	0	0	0	0	0	0	0	0	0	0	0
Hieracium gracile	0	0	0	0	0	0	0	0	0	0	0	0