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Pattern and process in primary succession in high elevation habitats on Mount St. Helens

Wood, David Mahlon, Ph.D.

University of Washington, 1987

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Pattern and Process in Primary Succession in High Elevation Habitats on Mount St. Helens

by

DAVID M. WOOD

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

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Approved by Roger del Moral
(Chairperson of Supervisory Committee)

Peter Kareiva

Lawrence C Bliss

J. A. Ammirati

Program Authorized
to Offer Degree Department of Botany

Date 12 June, 1987

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Abstract

PATTERN AND PROCESS IN PRIMARY SUCCESSION IN HIGH ELEVATION HABITATS ON MOUNT ST. HELENS

by David M. Wood

Chairperson of the Supervisory Committee:
Professor Roger del Moral, Department of Botany

The mechanistic basis of primary succession remains poorly known. The facilitation model, thought to describe primary succession, stresses the environmental modifications caused by early colonists as important in promoting the establishment of species intolerant of unmodified site conditions. This model has rarely been tested experimentally. I evaluate the facilitation model in subalpine mudflows created by the 1980 eruption of Mount St. Helens in Chapters 1 and 2. In Chapter 3, I discuss the colonization of pyroclastic flows. Chapter 4 integrates my findings.

Chapter 1: Plant invasion of subalpine mudflows is limited despite the proximity of recovered vegetation. In sampling across the vegetation-mudflow ecotone, I found that (i) most seedlings occurred within 3 m of a conspecific adult, and (ii) intermediate plant cover promoted seedling establishment (nurse plant effects). Survivorship of planted seeds of 22 species in mudflows varied from 0 to 12% and was positively correlated with seed mass. Invasion of mudflows is limited because stress tolerant species are poor dispersers.

Chapter 2: In a direct test of the facilitation model, I predicted that survivorship of stress intolerant species on mudflows would be increased if I experimentally mimicked the environmental effects of plant colonists. I altered both above- and below-ground factors in a factorial design. Both seedling emergence and survival were significantly greater in treated plots than in controls. Seven of 21 species survived only in treated plots. For these, the facilitation model is supported. For the remainder, facilitation is facultative (11 species) or not required.

Chapter 3: Seed rain density into the pyroclastic zone averaged 350 seeds m^{-2} yr^{-1} over 3 yr, with Epilobium angustifolium and Anaphalis margaritacea the most abundant species. These, plus Lupinus lepidus, were also the most common colonizers (n=32 species). Sixteen of 24 species in the seed rain were colonists. Colonists and the seed rain were floristically similar, with herbaceous species predominating. Mean species richness was only 1 per 100 m^2, but wet sites contained up to 12 species per 100 m^2. As yet, most colonization occurs in habitats of low stress and there is no evidence for direct facilitation.

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INTRODUCTION

Primary succession is the sequence of biological events that results in the colonization of newly created habitats, followed by changes in relative abundances of species. Primary successions in the terrestrial environment may arise, for example, following glacial recession or volcanic activity. These pristine landscapes are of great interest to ecologists in general, and community ecologists in particular, because they provide a *tabula rasa* on which to study the processes involved in assembling individuals and species into communities. A better understanding of the "rules" by which this formation occurs should lead to a better understanding of the forces structuring mature communities.

A tremendous opportunity to study primary succession occurred after the 1980 volcanic eruptions of Mount St. Helens in southwestern Washington. This dissertation investigates the ecological processes by which vascular plants colonize newly created habitats on Mount St. Helens.

The ecological effects of a disturbance such as a volcanic eruption can be effectively characterized by such parameters as type, size, and intensity. The considerable heterogeneity in the landscape affected by the Mount St. Helens eruptions is due mainly to variability in these parameters. Examples of disturbance types on Mount St.

Helens include hot pyroclastic flows, aerial fallout of ash and pumice (tephra), cool mudflows (lahars), and debris flows (Lipman and Mullineaux 1981). Each of these impacts affected an area of different size. Thus, in order to gauge the ecological impact of disturbance, it is useful to distinguish two types of disturbance intensity, which I term point and landscape. Point intensity is the impact at any particular location, and is a function of disturbance type as well as such factors as distance from point of origin (e.g., the crater), local topography, and subsequent erosion. Landscape intensity is point intensity weighted by size of disturbance type. For example, on Mount St. Helens tephra had a relatively minor point intensity (del Moral 1983), but since tephra fell over a large area of the Pacific Northwest, it had a large landscape intensity. Conversely, mudflows and pyroclastic flows had high point intensities but low landscape intensities, since their effects were confined to comparably small regions (Franklin et al. 1985).

Much of the literature on Mount St. Helens has described the relatively rapid rate of ecological recovery in sites of low to moderate point intensity, where some organisms survived (del Moral 1981, 1983, MacMahon 1982, Halpern and Harmon 1983, Franklin et al. 1985, del Moral and Wood 1987). These habitats are not undergoing true primary succession, since the colonization phase has been partly circumvented by survivors. Less attention has been paid to habitats of high point intensity, where there were no survivors; it is here that primary succession must occur. This dissertation addresses the mechanisms of primary succession in two such habitats of high point intensity--mudflows in the subalpine zone (Chapters 1 and 2) and pyroclastic flows in the montane zone (Chapter 3).

Chapter 1 is a paper in press (Wood and del Moral 1987) and Chapter 2 is a manuscript in review. Chapter 1 contains the syntax "we", referring to the coauthors Wood and del Moral. The Abstract for each article (Chapters 1 and 2) has been placed at the end of the chapter, designated as a Chapter Summary. Material referred to in Wood and del Moral 1987 as "available from author" may be found in Appendix I.

The major objectives of this dissertation are twofold.

First, I evaluate the applicability of the facilitation succession model in high elevation mudflow habitats. This model, formally defined by Connell and Slatyer (1977), stresses the importance of the environmental modifications caused by early colonists in promoting the establishment of species otherwise intolerant of unmodified site conditions. In Chapter One I pose these specific questions related to the facilitation hypothesis: i) are seedlings colonizing barren mudflows? If not, where does most natural seedling recruitment occur? ii) can any species grow from planted seed in unaltered mudflows? In Chapter Two I use answers to these questions to pose a specific test of the facilitation model. I reasoned that if environmental conditions on mudflows are experimentally modified in ways that mimic the conditions under which natural seedling recruitment occurs, then species requiring facilitation will establish only under these modified conditions.

The second objective is a description of the process of plant colonization on pyroclastic flows north of the crater, which was the region most profoundly affected by the lateral eruption. Here, before detailed experimental tests of the facilitation model can be conducted, it is necessary to have a description of the species comprising this system, since the region is ecologically quite different than subalpine mudflows. Chapter Three thus poses these particular questions. What species are colonizing this region to the north of the crater? Are they the same as those that will colonize higher elevation habitats? What environmental factors control pattern of colonization? What is the composition of the immigrant seed rain? Answers to these questions will, in addition to providing baseline data for analyzing future changes, permit more detailed and refined questions to be posed concerning colonization in this habitat.

CHAPTER ONE

This Chapter is reprinted in its entirety from the article, "Mechanisms of early primary succession in subalpine habitats on Mount St. Helens", by D.M. Wood and R. del Moral, appearing in Ecology, December, 1987.

INTRODUCTION

Most of our knowledge about primary succession comes from descriptive studies of vegetation development in chronosequences (Cowles 1899, Cooper 1923, 1939, Eggler 1948, 1963, Langenheim 1956, Tagawa 1964, 1984, Viereck 1966, Hendrix 1981, Ohsawa 1984). This approach is invaluable for documenting patterns of vegetation change, but it is difficult to draw mechanistic conclusions about the forces driving succession without experimental studies to complement sampling results (Connell and Slatyer 1977). The 1980 eruption of Mount St. Helens in southwestern Washington state afforded ecologists a unique opportunity to study primary succession by direct observations through time (del Moral & Wood 1986) and by experiments. This paper reports sampling and experimental studies designed to reveal factors governing colonization and the rate and direction of early primary succession of vascular plants in subalpine habitats on the volcano.

The classic model of succession was described by Clements (1916) as "reaction". More recently, in their seminal paper on the mechanistic bases of succession, Connell and Slatyer (1977) suggested that the reaction model (renamed "facilitation") will be most applicable to certain primary successions. This model states that certain species can establish in disturbed areas only if initial site conditions have been ameliorated by earlier colonists. The facilitation model may be less applicable, however, if some species capable of colonizing a devastated site are not represented in the pool of immigrant propagules. Under these conditions the explanation for an observed pattern of sequential invasions rests in differential dispersal abilities as well as abiotic habitat constraints.

In the subalpine zone of Mount St. Helens, distances between seed sources and new substrate are in many cases short and easily quantified. Species richness is low and is comprised almost exclusively of native iteroparous herbaceous species.

The basic observation prompting our investigation is this: in the six years since the 1980 eruptions, invasion of barren surfaces in subalpine habitats has been slight, despite the proximity of seed sources from resprouted vegetation in lightly disturbed sites. What are the reasons for this? Is invasion limited by lack of seed rain, or lack of tolerance of potential colonizers, or other factors? Is the facilitation model applicable to any species in this system?

We approached these questions in two ways. First, we determined where seedlings occur and correlated this pattern with factors such as distance to adults (for dispersal estimates) and existing plant cover (for potential site amelioration by nurse plants). Second, to assess physiological tolerances of species in a standardized design, we planted seed from 22 subalpine species in common gardens located in barren substrates and monitored seedling survivorship over 2 yr. These 22 species represent the great majority of the local subalpine flora and nearly all the biomass in recovered communities, so we were able to explore the population basis of succession for virtually an entire community (cf. Peet and Christensen 1980).

METHODS

The Subalpine System

The 1980 eruptions created a range of disturbance around the volcano, including airfall tephra (ash and pumice), pyroclastic flows, hot airblasts, and lahars (unsorted mud and debris flows) (Lipman and Mullineaux 1981). Since the major force of the eruptions was directed laterally to the north, most vegetation on the southern flank of the volcano was not destroyed. Here in the subalpine zone, which on Mount St. Helens begins at an abnormally low 1400 m, the predominant mode of disturbance was lahars triggered by the rapid melting of glaciers and snowpack (Cummans 1981). Vegetation not in the path of a lahar was protected from high air temperatures by a deep snowpack and received only a few centimeters of tephra deposition. Many plants resprouted through this coarse tephra (del Moral 1983), resulting in sharp ecotones between tephra-impacted vegetation (which at Butte Camp has developed on a 400 yr old lahar) and new lahar surfaces (Fig. 1.1). This residual vegetation now provides a source seed pool for colonization of new substrates. Plants resprouted from rootstocks are found occasionally on new lahars, but these individuals are rare. At lower elevations, their frequency increases substantially (Halpern and Harmon 1983). A more complete account of initial subalpine vegetation recovery may be found in del Moral (1983a) and del Moral and Wood (1986).

The subalpine growing season begins with snowmelt in June and ends by early September. Although yearly precipitation is high, summer months are typically dry, and the summers of 1984 and 1985 were unusually so (Table 1.1). Summer temperatures range from 0 to 35^{o} C with a mean of ca. 12^{o} C (Reynolds and Bliss 1986).

Sampling Design for Survey Plots

Eight permanent 5 x 10 m plots were established across vegetation-lahar borders at 2 study sites, 4 plots each: Butte Camp (BC) on the southwest flank of the volcano at 1500 m and Pine Creek (PC) on the southeast flank at 1450 m. These sites are separated by several km. At BC the lahars are persistent and deep, averaging 0.5 m (range 0.2-2 m; Major 1984), whereas at PC the lahar material eroded during the winter of 1980-81 leaving a bare, scoured surface (del Moral 1983). Plots were located subjectively to represent the range of vegetation and to avoid major erosion channels. Spacing among plots varied from 5 to 50 m within a site. The long axis of each plot extended onto the lahar for approximately 3 m.

Each plot was partitioned into a permanently marked regular grid of 50 0.5 m x 0.5 m subplots to permit investigator access. The distance between subplot centers was 1 m. Near the end of each growing season for 3 yr, beginning in August 1983, we estimated percent cover and counted first-year seedlings of all vascular plant species in each subplot (lichens and mosses are virtually absent in these habitats). We also recorded the position of any uncommon species not occurring in a subplot.

Spatial Pattern Data Analysis

The known distance between all subplots permits us to compute the distribution of seedling-adult distances for each species, which we used to estimate dispersal. Aerial fallout traps (Edwards et al. 1986) located in a variety of barren sites collected only a few species from this habitat, presumably due to distance effects. Thus we were unable to measure dispersal directly. In any case, traps that act as sinks are biased estimators of seed rain in this landscape because much dispersal in areas of sparse vegetation probably occurs by seeds moving over the ground in response to wind or water, rather than through the air. We reasoned, therefore, that a useful indirect estimate of dispersal is to simply record seedling presences. Any factors affecting dispersal and seedling establishment, such as weather, microtopography, nurse plants, and differential seed viability, are thereby incorporated. A potential drawback to this method is that in high density situations, represented in the extreme case by a monoculture, nearest neighbor distances always will be short regardless of actual dispersal. However, in our study plants were widely spaced, often occurring as isolated individuals. Thus the nearest-neighbor technique is a valid, albeit crude, estimator of dispersal in this system.

For each seedling in the 1984 or 1985 sample we recorded the distance to the nearest conspecific adult in a subplot of the previous year, since those adults are the most likely parents of that seedling. Although we cannot ascribe exact parentage, a large sample should result in averaging of nonsystematic errors. In some cases, 1983 seedling data were used if the surrounding plant cover was high in that year, as those plants undoubtedly were reproductive in 1982. Distances were rounded to the nearest integer, from 0-5 m, to facilitate analysis. The 0 class designates that an adult was present in the same 0.25 m^2 quadrat as the seedling. The BC and PC sites are combined for all spatial analyses.

To test for nurse plant effects, we used seedling data from all 3 yr, together with the total cover recorded for that subplot in that year. If nurse plant effects are important, then they should positively affect the growing seedling (although nurse plants may act to trap blowing seeds as well).

Adult plant cover was converted into an octave scale for all statistical analyses. This minimizes sampling error while preserving fine-scale differences at low values. The octave classes were: 0 (0% cover), 1 (1%), 2 (2-4%), 3 (5-9%), 4 (10-18%), 5 (19-35%), 6 (36-72%), 7 (73%+).

We used the nonparametric, two-sample, Kolmogorov-Smirnov goodness-of-fit test for comparing various distributions. This test is effective for our purposes because it can exploit the inherent ordering in the data, unlike the alternative chi-square test (Hollander and Wolfe 1973).

Common Garden Experimental Design

In October 1983 we planted seed from 22 species in 20 x 50 cm plots in barren substrate at Butte Camp and Pine Creek adjacent to residual vegetation. The design was a complete factorial, with Species, Site (BC or PC), Nutrient Addition (0 or 8 g of 18-24-6 NPK slow release fertilizer), and Time as factors. Time was included as a repeated measure (see below). Fertilizer was included as a preliminary test of the hypothesis that nutrient deficiencies prohibit seedling establishment. Depending on seed availability, 3 replicate batches of either 50 or 100 seeds were sown per experimental unit, for a total of 21,600 seeds in 264 plots. Seed was collected from numerous individuals in 1982 and 1983 around the volcano, and thoroughly mixed prior to use. Several seed batches were randomly picked for viability determination. Plots were arranged in 6 parallel rows at each site on apparently homogeneous substrate, with a 10 cm buffer between adjacent plots. Each row contained only one species, with position and nutrient addition within rows randomized. Restricted randomization was used to ensure adequate interspersion of species (Hurlbert 1984), although the analysis assumes complete randomization. Seed was covered only to a depth necessary to prevent removal by wind. Beginning in June 1984, and continuing monthly during the growing season for 2 yr, we recorded the number and position of seedlings alive and dead in each plot. The October planting date mimicked time of natural dispersal and ensured that any stratification requirements were satisfied.

Seed viability tests were conducted by placing seed batches in plastic petri dishes, subjecting them to any germination pre-conditions previously established as optimum for that species, and then germinating them in the laboratory. Emergence of any green tissue was the viability criterion. These tests estimate population viability only for some species, however, as aborted or damaged seeds were not included in the experiment if they could be identified by inspection. Data on viability, mass, and germination pre-conditions may be found in the Appendix.

Experimental Data Analysis

We used a repeated measures analysis of variance to help interpret the results, since the number of seedlings alive in a plot at time t_n is not independent of the number alive at time t_{n-1}. Repeated measures designs require additional assumptions about the form of the covariance matrix over time (Winer 1971, Milliken and Johnson 1984). Huynh and Feldt (1970) and Milliken and Johnson (1984) describe the general conditions for satisfying these assumptions. It is possible to adjust the degrees of freedom for the F-tests involving the repeated measure error term according to the magnitude of departure from the Huynh-Feldt criteria (Huynh and Feldt 1976); these results are furnished in the BMDP statistical package (program P2V; Dixon et al. 1981) and are employed here. An alternative to a univariate repeated measures ANOVA is a multivariate ANOVA, where most assumptions are relaxed, but this method is less powerful (Milliken and Johnson 1984).

Seedling counts were converted to percent of viable seeds sown for each species, and then subjected to an arcsin square-root transformation prior to the ANOVA. A posteriori comparisons used Fisher's LSD statistic. Untransformed data are presented in Figures and Tables. Rank correlations employed Spearman's test with zeros excluded.

RESULTS

Colonization

The boundary between new lahar surfaces and residual vegetation remained distinct over the 3 yr of the study, despite the fact that a seed pool is present within meters (Fig. 1.1). The ragged border at PC results from differential resprouting along a gradient of lahar scouring and deposition. The southern exposure of both sites accentuates drought effects, which accounts for the decline in percent cover at BC in 1984 and 1985.

The number of first-year seedlings declined greatly over the study period, both in numbers and frequency: 10.4 seedlingss per plot and 71% frequency in 1983; 2.7 and 64% in 1984; 1.4 and 49% in 1985. We attribute this primarily to drought (cf. Braatne and Chapin 1986).

Species changes in subplots over 3 yr are shown in Table 1.2. Cover of adults and density of seedlings were computed on a relative basis within each year to allow comparison between years without confounding environmental effects. Absolute frequency for each year is presented for information on colonization rate of seedlings and adults (vegetative spread). A seedling colonizing efficiency ratio is calculated for each species by dividing the 3-yr mean seedling relative density by the 3-yr mean adult relative cover. This identifies species that establish more effectively than predicted from source pool abundance. A ratio greater than or equal to 1.0 indicates that the species colonizes to a greater degree than the median species. Eriogonum, Spraguea, Lomatium, Sitanion, Stipa, and Danthonia are included in this group.

Eriogonum consistently had the highest seedling relative density of any species in the community, at or near 50% in 1984 and 1985. Seedling frequency actually exceeded adult frequency in 1983 and 1984, averaging 32%. Pocket gophers (Thomomys talpoides) consumed several individuals in one plot in 1984, causing the slight decline in adult frequency that year. The decline in adult cover is also drought-related. Spraguea, Sitanion, Stipa and Danthonia were all relatively uncommon in the study plots, though Stipa was more common elsewhere. Together, adults of these 4 species never accounted for more than 7% of vegetative cover, yet they totaled 10.0%, 17.9%, and 19.5% of all seedlings in 1983, 1984, and 1985, respectively. All but Danthonia increased in adult frequency; Spraguea and Sitanion increased by over 100% in 3 yr. None has the capacity for vegetative spread, so this probably represents recruitment of new individuals from seedlings.

Lomatium is a species that apparently recruits well under average, but not drought, conditions. Adult cover and frequency dropped considerably after 1983, as did seedling frequency. Seedling density stabilized at 4-5% however, suggesting that recruitment may continue in restricted microsites.

There is a significant positive rank correlation (r=0.69, 16 df, p<.01) between mean adult relative cover of a species and its mean seedling relative density, suggesting that seedling recruitment is approximately proportional to community abundance. Common species may account for substantial fractions of natural seedlings even though they may be relatively inefficient colonizers. A good example is _Agrostis_, which has a colonizing efficiency ratio of only 0.29, yet contributes approximately 8% of all seedlings because it is abundant and has a high reproductive output. There is no significant correlation between mean adult relative cover and colonizing efficiency ratio ($r=0.02$).

In addition to seedling colonists, plants also may colonize space by vegetative expansion. Species in this group are _Luetkea_, _Penstemon_, and _Agrostis_. All increased in adult frequency, yet had a seedling colonizing efficiency ratio much less than 1.0. _Agrostis_ is the most frequent and dominant species in the study area, due in part to its ability to resprout and spread via tillering along erosion rills. It also recruits some individuals from seed. _Luetkea_ and _Penstemon_ both have a low spreading growth habit and in some places become mat-forming. As vegetative spread is only a few centimeters per year, however, this type of colonization is relatively unimportant in the present context.

Spatial Pattern

Dispersal. Dispersal distance is limited in the 12 species that are actively recruiting seedlings. Estimated seed dispersal distances for these species are presented in Fig. 1.2. (The other 10 species in the study did not recruit enough seedlings for dispersal to be estimated in this way). The great majority of seedlings occurred within a few m of adults, which is consistent with the biology of most of these species: their seeds lack overt morphological dispersal adaptations, are released from low heights (10-30 cm), and are commonly observed on the ground adjacent to parental plants. Isolated plants exhibited the same nearest-neighbor distributions as did plants with neighbors within a few meters. Note that species identified above as good colonizers (*Lomatium*, *Eriogonum*, *Spraguea*, *Stipa*, and *Sitanion*) are all included in this group that we will term "non-dispersers". *Lomatium*, *Eriogonum*, and *Sitanion*, in particular, had no seedlings recorded farther than 3 m from an adult even though dozens of subplots in the higher distance classes were potentially available for colonization. Seeds of non-disperser species were rarely, if ever, found in traps in barren sites.

Aster, a species with a pappus, is the only actively recruiting species with >10% of its seedlings at >5 m distances. Species captured in traps included *Aster*, *Agoseris*, *Anaphalis*, and *Hieracium albiflorum*. Observations of blowing seeds suggest that *Hieracium gracile* and *Antennaria* should also be included in this group that we will term "dispersers" (all have a pappus). *Achillea* (without pappus), Danthonia, and Trisetum should be added to the non-disperser group, as their growth forms closely mimic those of the above non-dispersing species. Juncus and Luetkea, the species with the lightest seeds (.046 and .052 mg, respectively) probably have a high dispersal variance and are thus intermediate cases. Still, seeds of these species were not found in traps.

Nurse Plant Effects. Most seedlings occurred in subplots with intermediate adult cover, and plots with little or no cover harbored very few seedlings. The distribution of seedlings among cover classes is presented in Fig. 1.3. For a given year all subplots were sorted into cover classes, and seedlings within each class were tallied and expressed as the percent of the total for that year. The yearly values were then averaged. A two-sample, Kolmogorov-Smirnov test of the equality of these distributions is rejected at $p<0.01$. Comparisons within each year are also significant, confirming the generality that seedlings are under-represented in low cover plots and over-represented in intermediate plots.

There are two possibilities to explain the paucity of seedlings in open microsites: 1) environmental conditions are so harsh that most species require site amelioration for establishment; or 2) limited dispersal restricts seed rain. These hypotheses, of course, are not mutually exclusive. The data in Fig. 1.2 suggest that the limited dispersal hypothesis may be important, at least for the good seedling colonizer/non-disperser group. For less prolific colonizers, the facilitation hypothesis is supported.

Several species showed significant departures (using the Kolmogorov-Smirnov test) from the mean seedling distribution: Aster, Penstemon, Lomatium, and Polygonum. The first 3 species exhibit an even greater tendency for seedlings to occur in subplots of high percent cover than the sample mean. We interpret this as additional evidence in support of nurse plant requirements in these species.

Aster is a dispersing species and some seeds were found in fallout traps, yet seedlings were rarely found in plots with <2% cover. Seedling frequency also declined from 21% to 4% over 3 yr, suggesting that the abiotic tolerance of this species is limited in subnormal rainfall years. The additional possibility that airborne seeds merely are trapped by vegetation cannot be discounted. Seedling frequencies of Penstemon and Lomatium also declined drastically over 3 yr; 15% to 3% in Penstemon and 21% to 5% in Lomatium (Table 1.2). These data support the conclusion that nurse plants facilitate seedling recruitment in these species. Penstemon has 4% of its seedlings dispersed at least 5 m from adults (Fig. 1.2), suggesting that it may be able to colonize modest distances, as long as established vegetation is already present.

Polygonum is the only species with a bimodal seedling distribution, with peaks in the low cover plots as well as the high cover plots. This indicates both relatively high abiotic tolerance and moderate dispersal ability, since 5% of its seedlings occur at least 5 m from a parent (Fig. 1.2). Polygonum dies back in mid- to late August, at which time dried shoots with some seeds attached break off and are blown across the landscape.

Experimental Garden

Community Pattern. A total of 1,745 seedlings of 17 species emerged out of an estimated 16,000 viable seeds sown. The vast majority of seedlings emerged in the plots in which they were sown, so overwinter movement of seeds and immigration were negligible. Sixteen species had enough seedlings emerge to include in the ANOVA (Table 1.3). The survivorship curves for these 16 are shown in Fig. 1.4. Most mortality occurred in the first yr (1984), with mortality rate declining substantially in 1985. Survivorship was significantly higher at PC than at BC. Significant treatment interactions were also present. The survivorship curves for PC and BC (Fig. 1.4) diverge before August 1984, indicating that the mortality rate was higher at BC during the period of early seedling growth (the Time x Site interaction). Certain species accounted disproportionately for this initial divergence (the Species x Site and the Time x Species x Site interactions). Although the nutrient treatment does not appear in any lower order interaction ($p=.08$ for the main effect), there is a significant 4-way effect among Time x Species x Site x Nutrients ($p=.035$). Apparently, fertilizer had a differential effect among the various species through time, the magnitude of which depended on the site.

We attribute the higher survivorship at PC primarily to differences in substrate quality, although microclimatic differences between sites may contribute to the magnitude of the effect. At PC, the lahar material buried all vegetation during the summer of 1980, but sheet erosion removed it during the winter of 1980-1981. Thus, the present surface at PC is essentially scoured pre-eruption substrate covered with a thin veneer of fine silt and pumice. The BC lahars are still in place, and are composed of an unsorted mass of volcanic ejecta and surface debris (Major 1984). Soil pits at the two sites revealed the presence of organic matter in the rooting zone at PC, but not at BC. Young seedlings therefore encountered less severe conditions at PC at a time when roots were still in the upper substrate profile. After September, 1984, the mortality rate was similar at both sites, suggesting that substrate characteristics became unimportant after seedlings reached a critical size. The rank order of species survival is highly correlated between sites (for emergence, r=0.87, 15 df, p <0.001; for end of 2nd year r=0.80, p<0.001).

Species pattern. Survivorship among species varied widely: several species tolerated barren surfaces much better than others. The survivorship curves for the 10 species with highest totals are shown in Fig. 1.5. *Sitanion*, *Stipa*, *Spraguea*, *Polygonum*, *Eriogonum*, and *Danthonia* (at PC) had the highest percent survival after 2 yr. *Spraguea* was the only species with significant germination in 1985, although a few individuals from several other species germinated in 1985 as well. These additions are reflected in the small increases in the survivorship curves, and do not affect the results of the ANOVA. The decrease in mortality in 1985 is probably due to more extensive root penetration by 2nd yr seedlings. *Lomatium* and *Lupinus latifolius* exhibited the greatest mortality during 1984; in fact, the latter has apparently died out completely at PC.

Sitanion, *Stipa*, *Danthonia*, and *Lupinus latifolius* (before its local extinction) were the only species with significantly higher survivorship at PC for at least 2 time periods (determined by Fisher's LSD), although 15 of the 17 emerging species had higher totals at PC. No species had significantly higher survivorship at BC. No species exhibited a significant response to nutrients. Seedlings in fertilized plots were, however, usually larger and more vigorous than seedlings in unfertilized plots and some attained reproductive maturity.

Although some seedling deaths may be attributed to insects (cutworms and grasshoppers were observed on *Lupinus latifolius* and *Polygonum*), most mortality was probably due to drought (Braatne and Chapin 1986). Dead or dying seedlings typically had a dried appearance indicative of insufficient water. Other mortality sources related to drought, such as heat loading, could not be distinguished. Intraspecific competition was judged to be unimportant, as spacing among seedlings was generally high and mortality was uncorrelated with nearest neighbor distances.

Five species failed entirely to emerge: *Juncus*, *Hieracium gracile*, *Antennaria*, *Luetkea*, and *Anaphalis*. Percent seed viability in these species averaged 70% (mean for all 22 species was 73%; range from 55-92%), thereby excluding inviability as a cause of nonemergence for any species. In *Achillea* only 2 seedlings emerged. Several other species had extremely low emergence rates: *Penstemon*, *Aster*, and *Hieracium albiflorum*. Whether these low emergence totals reflect mortality of seeds in the substrate or failure of germination is unknown.

Synthesis. There is a significant rank correlation between seed mass and emergence ($r=0.73$, 14 df, $p<0.01$). Species with the heaviest seeds had the highest probability of germination and early growth.

There is a significant rank correlation between the seedling colonizing efficiency ratio of natural recruitment (Table 1.3) and 2nd yr survival in experimental gardens ($r=0.59$, 13 df, $p<0.05$). The garden experiment standardized commonness and rarity, and certain uncommon species (*Spraguea*, *Stipa*, *Sitanion*, and *Danthonia*) did disproportionately well. Thus, species that are effective colonizers in natural vegetation are also potentially effective colonizers of barren substrates.

DISCUSSION

Pattern and Rate of Succession

The explanation for the lack of seedling establishment in barren substrates may now be detailed. Species capable of establishing in open microsites are generally incapable of reaching them, due to limited dispersal (*Sitanion*, *Stipa*, *Spraguea*, *Eriogonum*, *Polygonum*, and *Danthonia*). Species capable of reaching open microsites are generally incapable of growing there (the dispersers, *Aster*, *Agoseris*, *Anaphalis*, *Antennaria*, *Hieracium albiflorum*, and *H. gracile*).

The lack of a syndrome that combines colonizing ability and stress tolerance has been discussed by Grime (1979).

Grime concluded that there are few evolutionary solutions to the problems it poses. Stress-tolerant, high dispersal species are uncommon at high elevations (cf. Weidman 1983) and the slow rate of primary succession observed in this study attests to this. The species identified above as capable of growth in barren substrates are stress tolerators because they possess these traits associated with that strategy: large seeds, long life, slow maximum growth rate, and limited response to nutrient additions (Grime 1979). Most of these taxa are characteristic of dry habitats throughout the Cascade range (Hitchcock and Cronquist 1973). In particular, the genera _Sitanion_, _Stipa_, _Lomatium_, _Eriogonum_, and _Polygonum_ are common in semi-arid environments throughout the western United States.

The role of seed mass in determining seedling vigor has been documented in numerous studies, both within taxa (Willson 1983 and included references) and among taxa (Baker 1972, Salisbury 1942, 1974). Baker (1972) found that large seeds were associated with xeric habitats in California, a result comparable to the findings of this study. In the absence of adaptations for animal dispersal, as is the case with most species in this study, large heavy seeds disperse primarily locally and are ineffective long distance colonizers.

Subalpine plants in the Western Cascades commonly encounter prolonged periods of low precipitation and high temperature precisely at the time of seedling emergence in early summer (Reynolds and Bliss 1986). If soils do not hold sufficient water, or if vapor pressure deficits (VPD) are high, then potentially lethal drought stress may ensue. This combination of events almost certainly occurs in barren substrates. Braatne and Chapin (1986) reported a strong correlation between low soil water potentials and pattern of seedling mortality in Lupinus latifolius and L. lepidus in 1983 and 1984 at Pine Creek. Mortality increased substantially when soil water potentials fell below -0.5 MPa in the rooting zone (10-15 cm).

Low nutrient levels do not appear to limit colonization of new substrates, at least for the species that grew in test gardens. The fertilizer treatment enhanced the vigor of many individuals and had a suggestive effect ($p=0.08$) on community survivorship (Table 1.3 and Fig. 1.4), but did not significantly affect the survivorship pattern of any individual species. Del Moral and Clampitt (1985) similarly concluded that by 1983 most species from the subalpine habitat were able to grow in volcanic substrates under greenhouse conditions; apparently substrate conditions had improved from 1980 to 1983. It is well documented that plants adapted to infertile soils generally exhibit reduced maximum growth rates and exhibit a more limited response to nutrient supplements than do plants adapted to more fertile soils (Parsons 1968, Grime 1979, Chapin 1980, Chapin et al.

1986). This may explain the lack of significant differences in the nutrient addition component of our experiment. However, we cannot be certain that those species that failed to emerge in test gardens were not limited in part by nutrient deficiencies. The majority of species had greater success in the test garden at Pine Creek than at Butte Camp, a result which we attributed to differences in substrate. We therefore suspect that an interaction between low soil water potential, high VPD, low nutrients, and unknown substrate factors--such as mycorrhizae--may together act as growth rate limiters, especially for less stress tolerant species.

The importance of nurse plants in this environment seems clear. Many species, including Aster, Penstemon, Lomatium, Agrostis, and Leutkea, had virtually no success in garden trials, yet had hundreds of seedlings in sample plots. The first 3 species exhibited a significant tendency for seedlings to occur in vegetated microsites over and above the community tendency, which itself was significantly different from random expectation (Fig. 1.3). This result cannot be ascribed simply to greater seed output in resprouted vegetation. If this were true, we would expect more success in test gardens where seeds are concentrated well above natural conditions. Hirose and Tateno (1984) found that soils beneath patches of Polygonum cuspidatum, the major early colonist of volcanic substrates on Mount

Fuji, were higher in water content, bulk density, organic matter, and NO_3-N than were adjacent barren sites. Many studies in desert environments have demonstrated the role of nurse plants in promoting seedling establishment of various species (Muller 1953, Muller and Muller 1956, Niering et al. 1963, Turner et al. 1966, Steenbergh and Lowe 1969, Jordan and Nobel 1979, Vasek and Lund 1980). We recognize that nurse plants may confer competitive or genetic (inbreeding) costs upon seedlings (Smith 1984); however, in harsh environments these costs apparently are outweighed by benefits.

Succession Models and the Role of Dispersal

Species with poor growth in test gardens apparently require site amelioration before seedling establishment on new surfaces is possible. This supports the facilitation model of Connell and Slatyer (1977). Conversely, the model clearly does not apply to those species able to grow in test gardens. Here, limited dispersal and/or low frequency, not abiotic constraints, effectively retard colonization rate. The danger inherent in drawing mechanistic conclusions fromsampling data alone is clear: it may be decades before a species such as Sitanion or Danthonia spreads to all barren sites where it is capable of growing, but its appearance in a study plot after the arrival of other (more fortuitously located) taxa does not indicate much about succession, merely that its dispersal rate is slow. As a consequence, we envision a successional scheme almost exactly opposite of that typically seen in secondary succession in productive habitats (Bazzaz 1983): traditional pioneering species, exemplified by Asteraceae, will be followers in this system, not pioneers. Open space on a barren lahar is a detriment, not a resource, for seedlings of fugitive species. Stress-tolerant species must first colonize and alter site conditions in order for more vagile species to invade.

We suggest that the distinction between source pool (all species in proximity to the disturbed site) and immigrant pool (propagules actually reaching the disturbed site) be clearly drawn in studies of succession. In this study, several important taxa in the source pool did not join the immigrant pool except in very restricted circumstances; for these the direct application of mechanistic succession models is irrelevant.

The primary succession process on Mount St. Helens leads to considerable spatial heterogeneity in recovered vegetation. This patchiness is not necessarily a consequence of species assortment along environmental gradients, but rather of limited dispersal, low frequency of efficient colonizers, and idiosyncratic disturbance. Monospecific vegetation patches initiated from rare, isolated colonizations may develop and persist, as ultimate competitive hierarchies will take decades or centuries to unfold (Whittaker and Levin 1977). Therefore, analytical methods of vegetation research such as gradient analysis should not always be expected to reveal significant correlations between species pattern and environmental variation until extended periods of equilibration have occurred.

CHAPTER SUMMARY

In the six years following the 1980 eruption of Mount St. Helens in Washington State, vascular plant invasion of barren substrates in subalpine habitats has been limited despite the proximity of seed sources from resprouted vegetation.

From 1983 to 1985 we counted first-year seedlings and estimated percent cover of adults in grids of permanent plots located across the ecotone between residual vegetation and barren substrate created in 1980. We found that 1) seedling recruitment declined from 1983 to 1985, apparently in response to drought; 2) most seedlings occurred within 3 m of a conspecific adult; and 3) plots with an intermediate vegetation cover (5-72%) contained a significantly higher fraction of seedlings than did unvegetated plots. Thus, dispersal is limited in many species and nurse plants may play a key role in trapping seeds and promoting seedling establishment.

We sowed 16,000 viable seeds from 22 subalpine species into 264 plots in barren substrates at 2 sites on the volcano. The design was a complete factorial, with Species, Site, and Fertilizer as treatments. Survivorship through 1985 varied from 0 to 12%, with *Sitanion jubatum*, *Stipa occidentalis*, *Polygonum newberryi*, *Eriogonum pyrolifolium*, and *Spraguea umbellata* attaining the highest values. Survivorship was correlated with seed mass, and was higher at the site where the pre-eruption surface was exposed. Fertilizer increased the size of most seedlings but had only a marginal effect on survivorship.

Species with high environmental tolerance generally dispersed short distances, whereas species that dispersed farther generally had low tolerances and apparently require site amelioration prior to establishment. The path of early succession depends upon the spatial position and dispersal abilities of species in the seed pool, and may not reflect environmental gradients.

Table 1.1 Growing season precipitation (mm) at Cougar, Washington (elevation 150 m), approximately 12 km from, and 1400 m below, the study sites. DD=dry days, defined as the number of days without measurable precipitation.

Period	1982	DD	1983	DD	1984	DD	1985	DD
June 11-30	26.2	14	140.0	6	104.6	12	2.0	19
July	18.8	20	172.5	14	0.0	31	16.0	30
August	35.3	22	58.2	25	0.8	30	102.6	23
	----	--	-----	--	-----	--	-----	--
Total	80.3	56	364.6	45	105.4	73	120.6	72

Table 1.2 Species changes over 3 years in permanent plots. Sample size is 400 0.25 m^2 plots per year. CER (Colonizing Efficiency Ratio) is mean relative density of seedlings / mean relative cover of adults, for all 3 year. p=present but not occurring in plots. n.a.=not available, as seedlings were not identified to species in this year.

	Adults					
	Relative Cover			Absolute Frequency		
Taxon	83	84	85	83	84	85
Polygonaceae						
Eriogonum pyrolifolium	17.5	10.7	10.5	31	26	32
Polygonum newberryi	7.5	8.9	10.1	8	7	7
Portulacaceae						
Spraguea umbellata	0.6	0.5	0.7	3	4	6
Roseaceae						
Luetkea pectinata	2.8	4.8	5.4	3	3	4
Apiaceae						
Lomatium martindalei	4.6	3.1	0.8	14	3	5

Table 1.2 (continued).

Fabaceae						
Lupinus latifolius	2.0	3.2	0.5	4	5	3
Lupinus lepidus	13.4	6.8	3.6	44	32	17
Scrophulariaceae						
Penstemon cardwellii	5.5	6.5	8.5	12	13	16
Asteraceae						
Achillea millefolium	1.8	3.5	2.7	1	1	1
Agoseris aurantiaca	p	p	p	0	0	0
Antennaria microphylla	p	p	p	0	0	0
Anaphalis margaritacea	p	p	p	0	0	0
Aster ledophyllus	5.3	8.7	6.1	15	13	13
Hieracium albiflorum	p	p	p	0	0	0
Hieracium gracile	p	p	p	0	0	0
Juncaceae						
Juncus parryi	1.1	1.2	1.4	4	4	5
Cyperaceae						
Carex rossii	4.7	7.2	9.0	28	31	32

Table 1.2 (continued).

Poaceae						
Agrostis diegoensis	26.7	29.3	32.8	34	37	42
Danthonia intermedia	0.7	0.9	0.1	1	2	1
Sitanion jubatum	0.7	1.2	1.7	4	8	10
Stipa occidentalis	2.9	2.3	3.4	11	11	13
Trisetum spicatum	0.1	0.1	0.1	2	1	1

Table 1.2 (continued). Right-hand extension to top page.

	Seedlings						
	Relative Density			Absolute Frequency			
Taxon	83	84	85	83	84	85	CER
Eriogonum	39.0	50.0	49.3	36	28	24	3.57
Polygonum	1.6	1.5	1.6	8	4	2	0.84
Spraguea	1.1	0.7		6	3	1	1.56
Luetkea	0.	0.8	2.2	0	2	2	0.23
Lomatium	24.0	4.3	5.5	21	9	5	3.97

Table 1.2 (continued). Right-hand extension.

Lupinus lep.	1.1	1.5	0.5	5	4	1	0.54
Lupinus lat.	3.5	1.5	1.8	22	5	3	0.29
Penstemon	6.4	4.3	2.7	15	7	3	0.65
Achillea	0.	0.	0.4	0	0	0	0.05
Agoseris	0.	0.	0.	0	0	0	0.0
Antennaria	0.	0.	0.	0	0	0	0.0
Anaphalis	0.	0.	0.	0	0	0	0.0
Aster	4.5	4.4	2.7	21	6	4	0.58
Hieracium alb.	0.	0.	0.	0	0	0	0.0
Hieracium gr.	0.	0.	0.	0	0	0	0.0
Juncus	0.	0.	0.	0	0	0	0.0
Carex	2.4	2.8	4.9	11	6	5	0.48

Table 1.2 (continued). Right-hand extension to bottom page.

Agrostis	7.4	9.8	8.3	n.a.	20	10	0.29
Danthonia	0.4	1.1	0.4	1	2	1	1.12
Sitanion	2.9	4.5	4.0	n.a.	7	5	3.80
Stipa	5.7	11.2	14.4	n.a.	13	11	3.64
Trisetum	0.	0.	0.	0	0	0	0.0

Table 1.3. Repeated measures ANOVA for community common garden experiment (del Moral and Wood 1987). Probabilities with superscript a were computed from (df x 0.665), based upon the Huynh and Feldt (1976) criteria for repeated measures error sum of squares (Dixon et al. 1981).

Source	df	F	Tail Probability
Species	15	25.61	0.000
Site	1	19.35	.000
Nutrients	1	3.11	.080
Species x Site	15	2.62	.002
Species x Nutrients	15	1.53	.106
Site x Nutrients	1	1.69	.196
Species x Site x Nutrients	15	1.47	.127
Error	128		
Time	6	321.83	$.000^a$
Time x Species	90	11.99	$.000^a$
Time x Site	6	3.70	$.006^a$
Time x Nutrients	6	.89	$.470^a$
Time x Species x Site	90	3.31	$.000^a$
Time x Species x Nutrients	90	.82	$.822^a$
Time x Site x Nutrients	6	.90	$.463^a$

Table 1.3 (continued).

	df	F	Tail Probability
Time x Species x Site x Nutrients	90	1.39	.035[a]
Error	768		

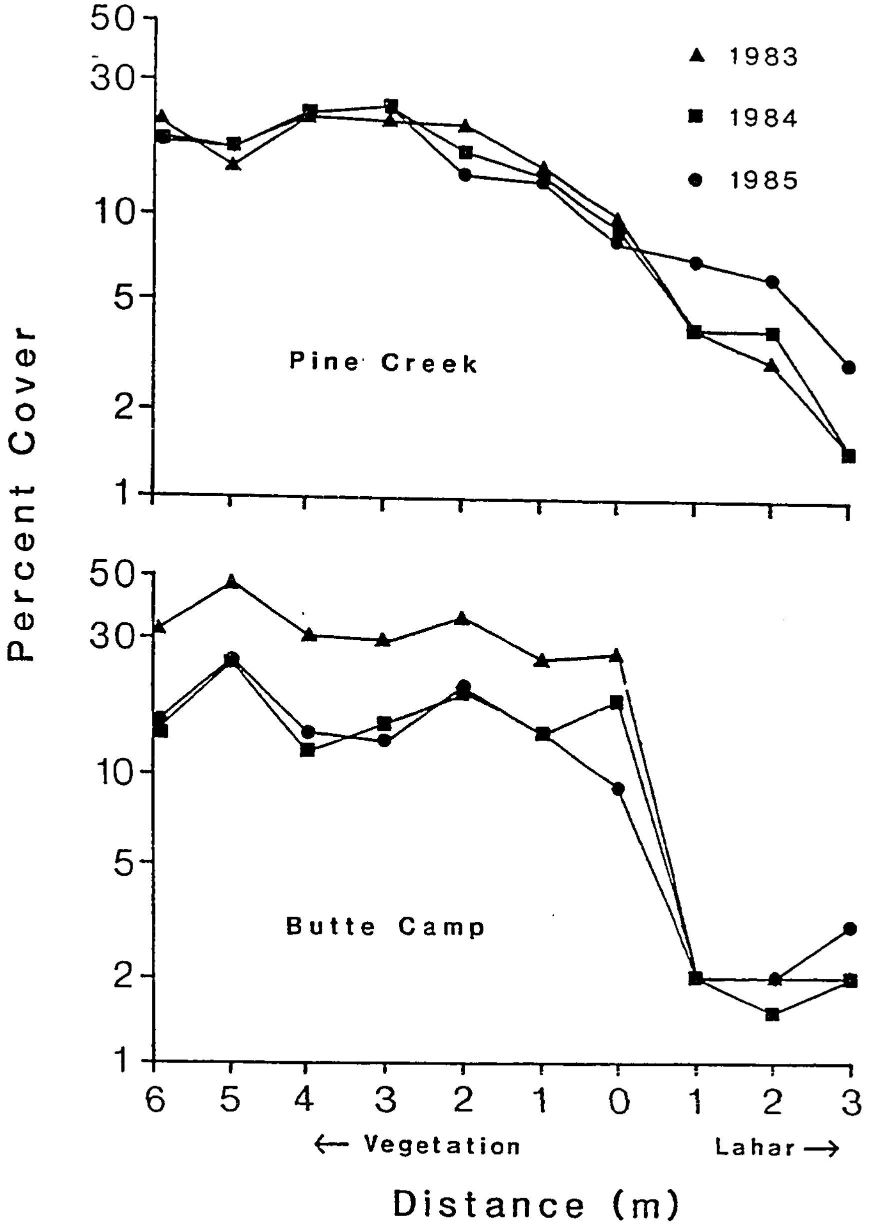


Figure 1.1 Percent cover changes across lahar / vegetation ecotones at Pine Creek and Butte Camp. The cover value at each distance is the mean of 20 0.25 m^2 quadrats per site per year.

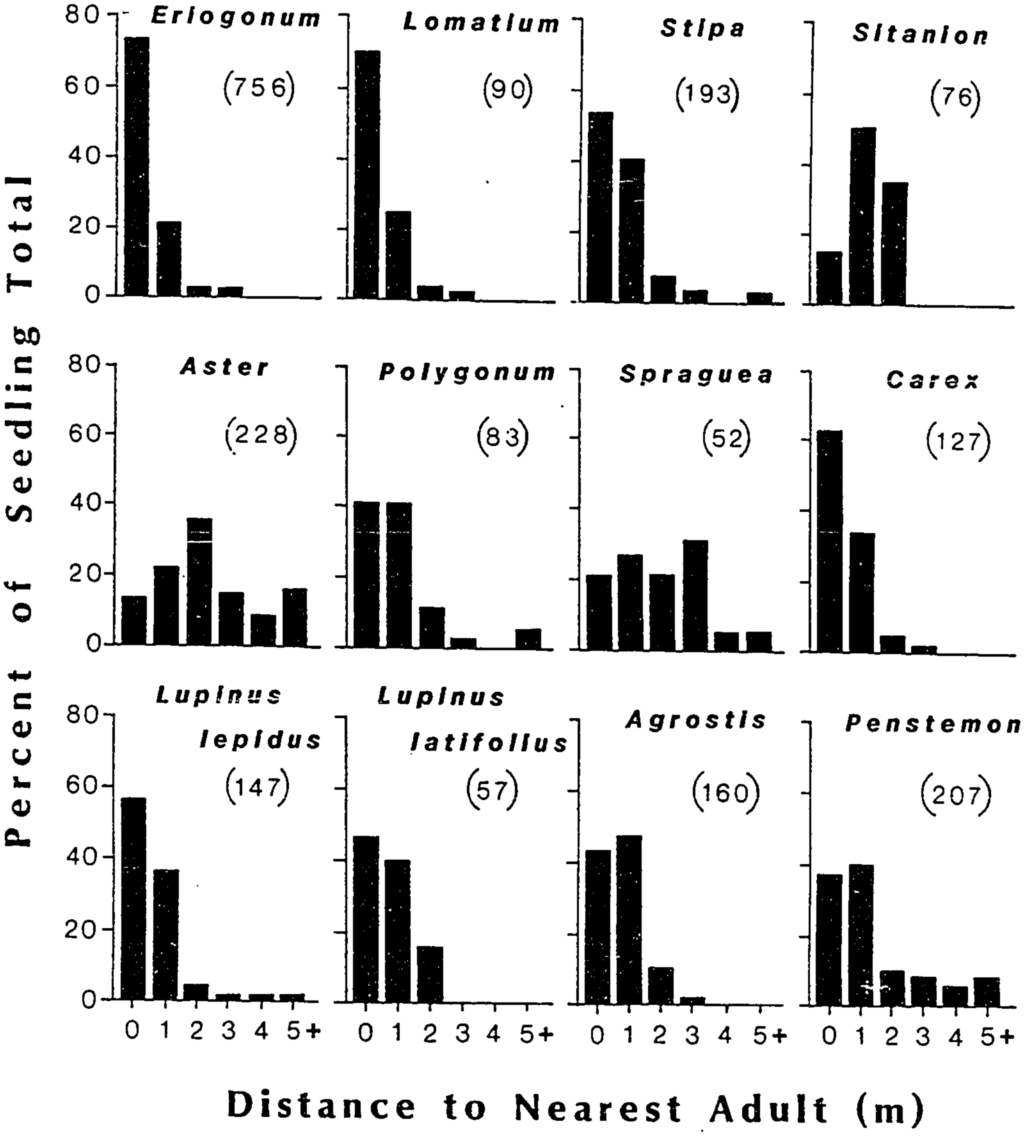


Figure 1.2 Estimated seed dispersal distances from seedling-adult nearest neighbor distributions. Complete species names are in Table 1.2. Number in parentheses is sample size of seedlings.

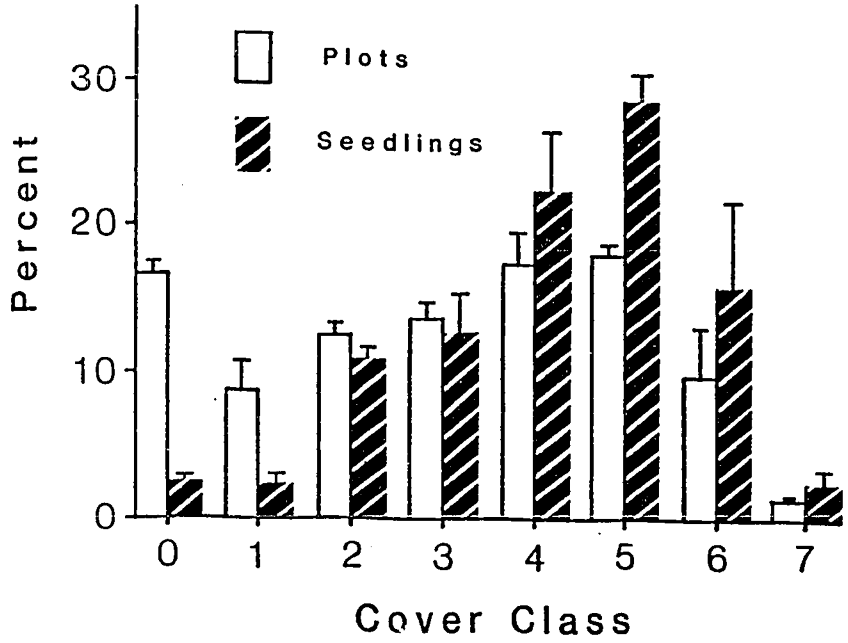
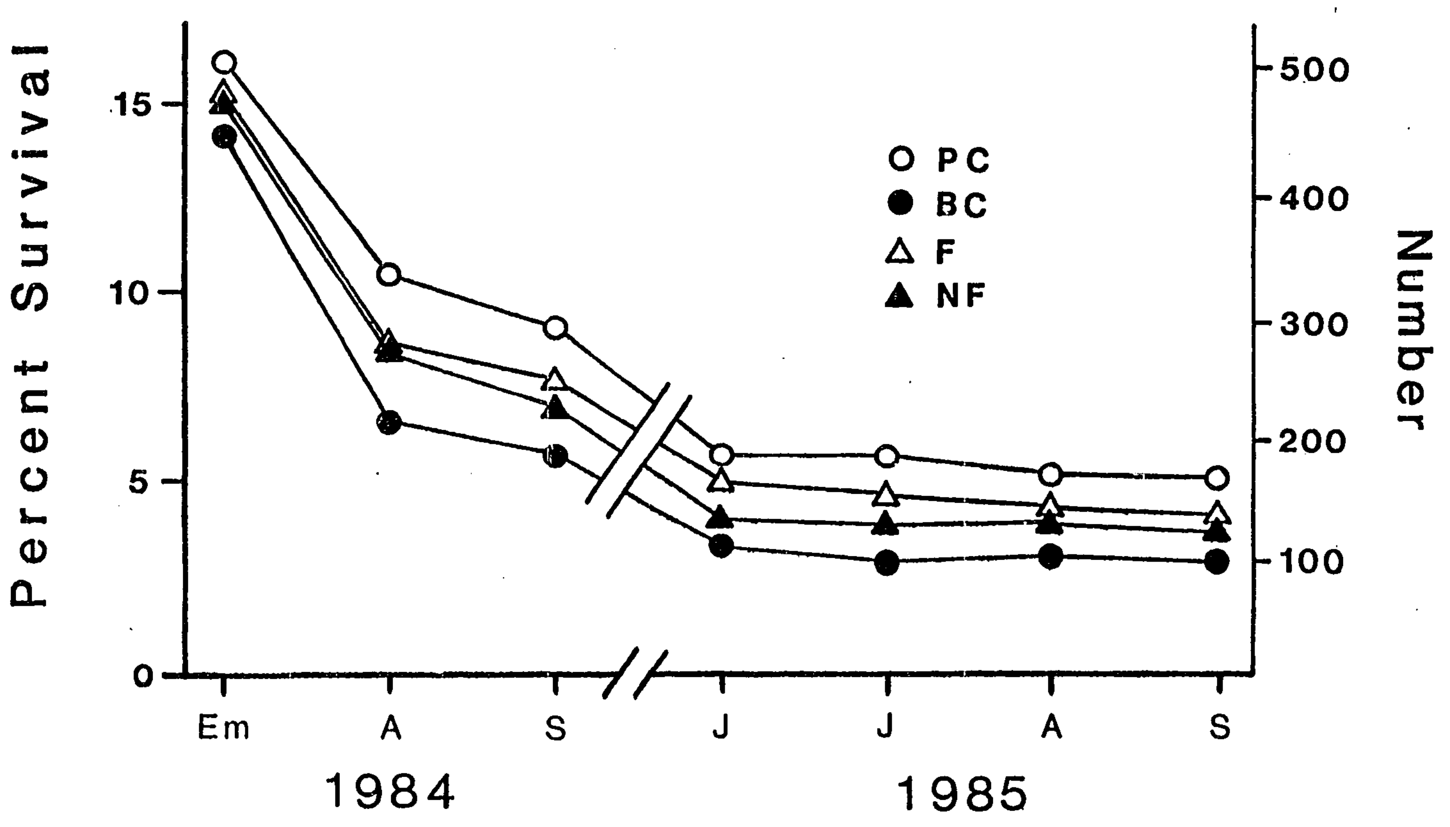


Figure 1.3 Distribution of 0.25 m^2 plots into percent cover classes and percent of first-year seedlings occurring within each cover class. Distributions are 3 year means; error bars are 2 SE. Cover classes are 0 (0% cover), 1 (1%), 2 (2-4%), 3 (5-9%), 4 (10-18%), 5 (19-35%), 6 (36-72%), 7 (73+%).

Figure 1.4 Community survivorship in experimental gardens (del Moral and Wood 1986). Values are total seedlings of 16 species, expressed as percent of the number of viable seeds sown as well as by actual number. PC=Pine Creek, BC=Butte Camp, F=fertilized, NF=not fertilized, Em=emergence, A=August, S=September, J=June, July. There are no significant differences between F and NF.


Percent Survival
15
10
5
0
Number
500
400
300
200
100
Em
A
S
J
J
A
S
1984
1985
○ PC
● BC
△ F
▲ NF

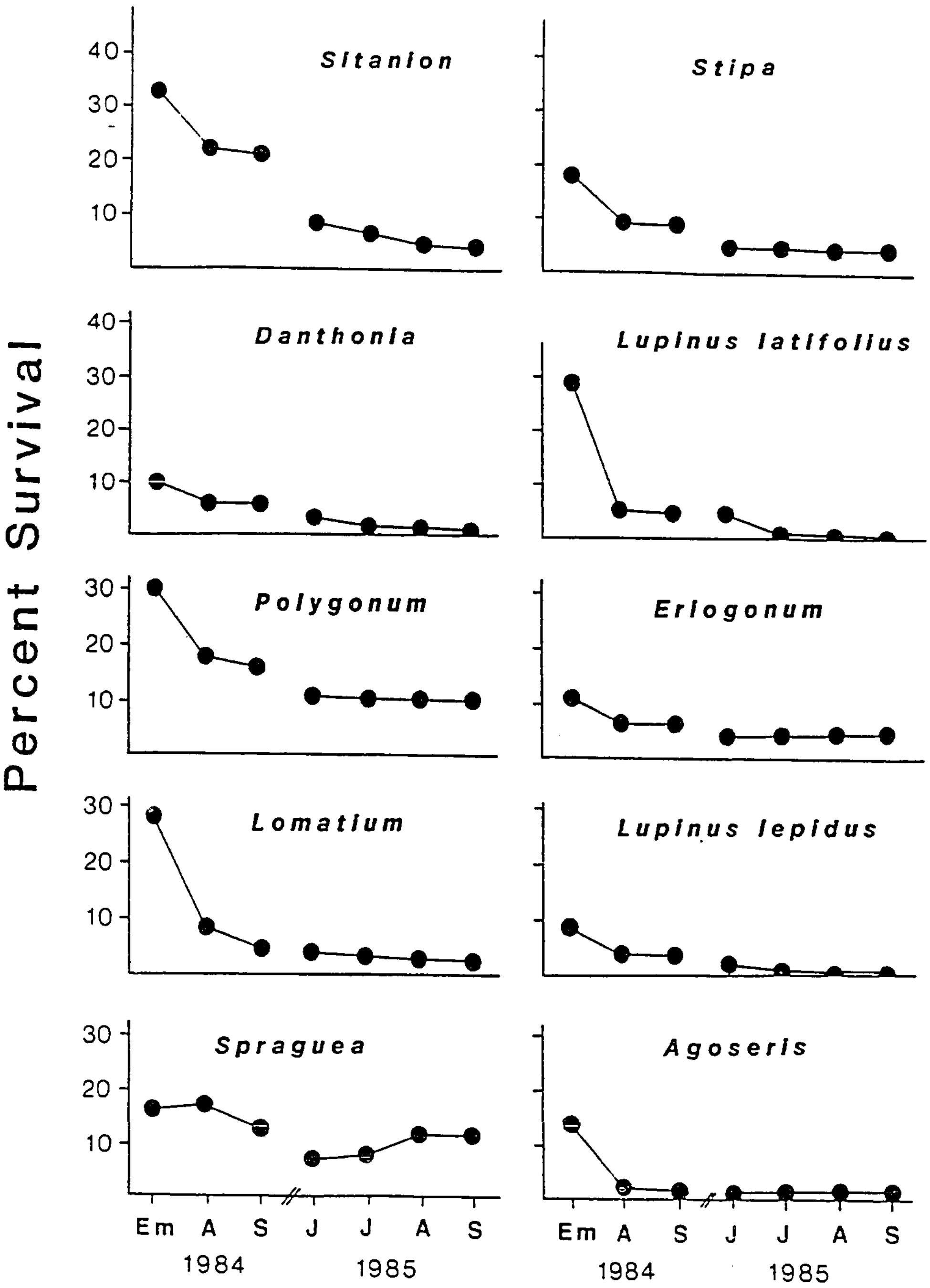


Figure 1.5 Species survivorship in experimental gardens. Values are number of seedlings, expressed as percent of the number of viable seeds sown. Complete species names are in Table 1.2. Open circles=PC, closed circles=BC for those species in which Fisher's LSD (p=0.05) indicates a significant difference. If no difference exists, closed circles=totals for both sites combined. Date abbreviations are as in Figure 1.4.

CHAPTER TWO

INTRODUCTION

It is often assumed that the pattern of sequential species invasions observed in terrestrial primary succession results from progressive amelioration of the physical environment. Early plant colonists modify site characteristics, and this may promote or 'facilitate' the establishment of later species (Clements 1916, Connell and Slatyer 1977). Some evidence from chronosequence sampling studies supports this concept (Crocker and Major 1955, Lawrence et al. 1967, Olson 1958, but see Cooper 1923). However, sampling results alone cannot determine the validity of the facilitation hypothesis. For example, sequential invasions may as well be explained by differential dispersal abilities as by habitat amelioration (Drury and Nisbet 1973). Experimental studies are essential in developing a mechanistic understanding of pattern in primary succession.

The 1980 eruption of Mount St. Helens created a landscape in which to test the facilitation succession model of Connell and Slatyer (1977). In an earlier paper, Wood and del Moral (1987) showed that a majority of species from the subalpine flora on Mount St. Helens did not establish from experimentally planted seed in new, barren subalpine mudflows. They regarded this as support for the facilitation model. However, it remains to be demonstrated that these apparently intolerant species can establish in mudflows if growing conditions are ameliorated in ways that mimic the effects of early plant colonists. This paper describes an explicit test of the facilitation hypothesis in these mudflows.

Natural seedling recruitment in these subalpine communities is concentrated in sites with some plant cover, whereas recruitment on mudflows is rare (Chapter 1). The precise benefits conferred by these "nurse plants" are unclear. Thus, to mimic facilitative effects of early colonists, I grouped the many factors that may benefit seedlings of colonizing species into two types, termed shade and soil factors. Shade factors result from above-ground phytomass, and include lower wind speed, higher humidity, and lower surface temperatures. Soil factors include improved physical properties such as aeration and cation exchange capacity, higher nutrients (especially nitrogen), and biotic amendments such as fungal and bacterial inocula. In the experimental procedure I applied shade and soil amendments to mudflows, sowed viable seeds of subalpine species, and compared seedling survivorship under amended conditions with survivorship in controls. For any species that survives exclusively in experimentally amended plots, the facilitation hypothesis is supported.

METHODS

Study Area. The experiment was conducted at Butte Camp (1600 m elevation) on the southwest flank of Mount St. Helens in Washington state. Numerous small mudflows (lahars) coursed through this site as a result of the eruption of May 18, 1980 (Cummans 1981, Major 1985). These mudflows remain virtually unvegetated, as resprouting of buried plants was confined to erosion rills (del Moral 1983) and seedling colonization was almost nonexistent by 1985 (del Moral and Wood 1986, Wood and del Moral 1987). Climatic data may be found in Reynolds and Bliss (1986).

Experimental Procedure. The experiment was a 2 x 2 factorial (shade and soil), randomized complete block design. Two sites, separated by 400 m distance and 50 m elevation (hereafter referred to as blocks), were chosen to represent barren mudflows. Eight 1 m^2 plots were established per block, with two replicate plots per treatment combination per block. Each plot contained all species used in the experiment. Although replicates within blocks permit testing of factorial hypotheses involving blocks, no a priori hypotheses concerning the two sites were constructed; thus, I regard blocking only in the usual sense of variance reduction.

Treatments were established as follows: in the shade plots, a canopy of mosquito netting (double thickness) was suspended over the plot, which reduced photosynthetically active radiation by 50% as determined by a quantum sensor. Canopies were not erected until after snowmelt, at the time of the first census (see below). In the soil plots, the top 10 cm of substrate was removed and replaced with soil from pocket gopher (*Thomomys talpoides*; Andersen 1981) mounds adjacent to each block in habitats unaffected by mudflows. I used this material because it was a convenient source of pre-eruption soil that was relatively free of root fragments that might resprout, and because gophers mix soil from beneath many species. Ten cm of substrate was removed from all other plots, including controls, and then replaced with gopher mound soil. This ensured that substrate in all plots underwent similar physical disruption.

I used 21 herbaceous subalpine species in the design (listed in Table 3.1). These species comprise most of the subalpine flora, and are the same group as used in Wood and del Moral (1987), except that *Lupinus lepidus* was omitted from the current experiment due to insufficient seed. Seed was sown into plots in October 1985, just before winter snows, which allowed natural stratification. Species position within a plot was randomized, but species were kept separate. All seed was collected from plants on the volcano over several years. Replicate seed batches were determined by weight, with counts estimated from known weights of 100 seeds. Sowing density per species was adjusted to fit expected germination success (Appendix I) wherever possible, but this was sometimes constrained by seed stocks. Estimated sowing densities are given in Table 2.1.

Data Analysis. Plots were censused monthly beginning in June 1986. Unlike the results in Wood and del Moral (1987), however, emergence was not completely synchronized at the beginning of the season; a few seedlings of some species in the amended plots germinated periodically through the season. Thus, data were analyzed in two ways: 1) by tabulating all emerging seedlings in a plot and performing ANOVA on these numbers (square root transformation); and 2) by calculating survivorship, expressing the final (October) census as a fraction of all emergents and performing ANOVA on these fractions (arcsin-square root transformation). A previous experiment in this habitat indicated that most mortality occurred within the first year (Wood and del Moral 1987), hence one year's results are sufficient.

Several species in the amended plots required thinning to preclude density dependent mortality. For these, percent survivorship (2 above) was calculated by first adding the estimated number of seedlings that would have survived had I not thinned; this number was obtained by multiplying the number thinned by the fraction surviving following thinning.

RESULTS

Table 2.1 gives the mean percent seedling emergence for each species in control plots. Because emergence in controls can be regarded as a repetition of a previous experiment conducted in 1984 at Butte Camp (Wood and del Moral 1987), I included 1984 emergence data from control plots at Butte Camp in Table 2.1. For both sets of emergence data, values were corrected for seed viability (unpublished). There is good agreement between the two years (Spearman rank correlation r=0.87, 20 df, p<.001). Of the four species that failed to emerge in controls in 1984, only one (Anaphalis) emerged in controls in 1986, at a rate of only 0.2%. Antennaria, which is rare in these subalpine plant communities, did not emerge even in amended plots in 1986 and is therefore excluded from all analyses.

Species Richness. The number of species emerging was significantly greater in the soil treatment, for which plots contained an average of 16.75 species compared to 13.0 species in controls (Fig. 2.1A and Table 2.2A). Both soil and shade treatment plots retained a significantly greater fraction of emerging species to the end of the season (Fig. 2.1A and Table 2.2B). On average, control plots lost 4.25 species (31% of emergence total), shade plots 1.5 species (10%), and soil plots 1.25 species (8%). There was a highly significant difference between blocks for species retention (p=.009). Reasons for this are uncertain, but include such "demonic intrusions" (Hurlbert 1984) as differential elk trampling, disruption of shade canopies by wind, and date and pattern of snowmelt.

Seedling Density. More than twice as many seedlings emerged in the soil treatment plots as in controls (Fig. 2.1B, Table 2.3A). The shade treatment had no effect on emergence, which is reassuring since canopies were not erected until the first census, by which time most emergence had already occurred. Survivorship was significantly greater only in soil plots, where it averaged 74% compared to 47% in controls (Fig. 2.1B, Table 2.3B).

Species Pattern. Table 2.4 gives the distribution of seedlings of each species among the four treatments for emergence and the final (October) census. In addition to the two species that failed to emerge in controls (Table 2.1), seedlings of five other species emerged in controls but died before October (*Achillea*, *Anaphalis*, *Aster*, *Hieracium albiflorum*, and *Lomatium*). Seedlings of all five species persisted until the end of the season in amended plots.

Nine species had significantly better emergence in gopher mound soil, as determined by ANOVA (Table 2.4). Several *Polygonum* seedlings emerged in August in the soil x shade plots, which explains the significant interaction for this species. Six species had significantly lower mortality rates in soil plots, and three species had lower rates in shade plots. Two additional species that perished in controls, *Anaphalis* and *Hieracium albiflorum*, clearly benefited by amendments but had too few seedlings to permit significance in the ANOVA. *Anaphalis* exhibited a noticeable (but nonsignificant) decline from soil plots to soil x shade plots, which may be indicative of its shade intolerance.

Five species were previously identified as stress tolerators by Wood and del Moral (1987), due to their ability to survive in unamended Butte Camp mudflows: *Eriogonum pyrolifolium*, *Polygonum newberryi*, *Sitanion jubatum*, *Stipa occidentalis*, and *Spraguea umbellata*. *Eriogonum* and *Spraguea* exhibited no response to amendments (Table 2.4), and were two of the three species with at least 20% survival in control plots. The other species with >20% survival in controls, *Lupinus latifolius*, was attacked by larvae of a Nymphalid butterfly and suffered the most severe mortality of any species (99 seedlings survived out of 523 emerged; Table 2.4). Since caterpillars concentrated their attack on the most vigorous seedlings, which were in the amended plots, interpretation of results for *Lupinus* is difficult. The other identified stress tolerators (*Polygonum*, *Sitanion*, and *Stipa*) exhibited some significant response to amendments, but all had moderate emergence and survivorship in controls.

DISCUSSION

The facilitation succession model states that species invasion is possible only following amelioration of environmental conditions. This model is supported for the seven species that survived only in experimentally amended plots: *Achillea millefolium*, *Anaphalis margaritacea*, *Aster ledophyllus*, *Hieracium albiflorum*, *Juncus parryi*, *Lomatium martindalei*, and *Luetkea pectinata*. None of these species survived in control plots in a previous experiment (Wood and del Moral 1987). In 11 other species either emergence or survivorship was enhanced by amendments. For this group, facilitation may be expected to accelerate the rate of invasion, but apparently is not absolutely required. However, since control seedlings were nearly always less vigorous than seedlings in treatment plots, species with low survivorship in controls may not survive future years, rendering facilitation obligate.

Two species, *Eriogonum pyrolifolium* and *Spraguea umbellata*, were unaffected by amendments, had good survivorship in controls both in this experiment and in 1984 (Wood and del Moral 1987), and do not require facilitation (see Chapin 1986 for results detailing the physiological mechanisms of stress tolerance in *Eriogonum*).

Other experimental tests of mechanisms in natural primary succession are rare. Walker et al. (1986) and

Walker and Chapin (1986) found that juveniles of late successional species were present in very early stages of primary succession on river bars in Alaska. They also showed that transplanted seedlings of species from later succession stages survived in the earliest stages. They concluded that facilitation was relatively unimportant, mostly because any benefits conferred by alder, a nitrogen fixer of early stages, were outweighed by competitive inhibition. The difference between these results and those reported in this paper probably is related to the higher productivity of their system. Walker et al. (1986) report a "vegetated silt" present at 7 yr after silt bar formation, and a willow stage at 10 yr; in contrast, mudflows on Mount St. Helens remain virtually unvegetated after 7 yr (del Moral and Wood 1986, Wood and del Moral 1987). I expect the importance of facilitation to increase with increasing intensity of disturbance, as environmental conditions encountered by potential colonists become more severe relative to pre-disturbance conditions.

Both the shade and soil treatments significantly enhanced species richness (Table 2.2B). This suggests that the mechanism of facilitation in primary succession on Mount St. Helens is complex and species-specific. Several studies have demonstrated that total soil nitrogen increases with time in primary succession seres, mostly as a result of biological nitrogen fixation by early colonists (review by

Stevens and Walker 1970; Vasek and Lund 1980, Hirose and Tateno 1984). Such an increase undoubtedly could promote establishment of species intolerant of low nitrogen levels, which may explain why in this experiment more species benefited by the soil treatment than by the shade treatment (Table 2.4). However, shading can affect seedling survival through effects on plant water status, and thus may be an important component of facilitation in dry habitats. For example, Wood and del Moral (1987), Braatne and Chapin (1986), and Chapin (1986) all found that seedling recruitment declined in years with summer drought. Yearly variation in timing and amount of precipitation and temperature (Reynolds and Bliss 1986) add further complexity to the succession process in this environment (del Moral and Wood, MS).

The gopher mound soil used for the soil treatment was shown by Allen et al. (1984) to be relatively rich in spores of endomycorrhizal fungi. Vigor of many herbaceous species is promoted by endomycorrhizal symbiosis (Hayman 1983). Since these fungi release their spores predominantly belowground, Andersen and MacMahon (1985) suggested that gophers can accelerate plant community recovery by dispersing spores along tunnels. Whether mycorrhizae were important in enhancing survivorship for any species in this experiment is unknown, and in any case was confounded with effects of texture, organic matter, and nutrients (especially nitrogen; del Moral and Clampitt 1985). Since gopher burrows are never observed in barren mudflows, gophers are not predicted to affect the rate of early primary succession in these sites. However, the beneficial effect of their excavations on seedling survivorship in this experiment is apparent (cf. del Moral and Clampitt 1985).

The importance of using seeds, rather than seedling transplants, in field experimental tests of succession models is clearly demonstrated. The large number of species (9) that had emergence significantly enhanced by the soil treatment suggests that events occurring during (or soon after) germination may be important determinants of invasion success. For example, several species in this community are capable of germination in the dark at temperatures around 2^{0} C (*Lupinus latifolius*, *Lupinus lepidus*, *Eriogonum pyrolifolium*, *Polygonum newberryi*, *Lomatium martindalei*, *Aster ledophyllus*, *Spraguea umbellata*; Wood, unpublished). These species probably germinate naturally while still under snow, and in this way can begin growth immediately after snowmelt under conditions of high soil moisture. In addition, for species with low endosperm reserves in seeds, probability of quick resource capture following germination will strongly affect survival. Both these aspects of population biology may be missed if seedling transplants are used.

In sum, the facilitation succession model applies to several, but not all, of the species comprising the subalpine flora on Mount St. Helens. To adequately explain the pattern of early primary succession in mudflows, aspects of population biology such as dispersal ability and distance to seed source must also be explicitly considered (Wood and del Moral 1987). Field experiments can distinguish obligate from facultative facilitation.

CHAPTER SUMMARY

An experimental test of the facilitation succession model was conducted on mudflows in the subalpine zone of Mount St. Helens. Previous work demonstrated that many of the species comprising the subalpine flora do not easily establish in these barren substrates. I designed an experiment to test the hypothesis that establishment can be facilitated if growing conditions are ameliorated in ways that mimic the effects of early colonists. I accomplished this mimicry in two ways: 1) by erecting shade canopies; and 2) by replacing mudflow substrate with 10 cm of soil from adjacent pocket gopher mounds. The design was a 2 x 2 factorial in randomized complete blocks. I planted seed from 21 subalpine species into each of 16 plots and monitored seedling emergence and survival.

Significantly more species emerged in the soil plots than in controls (16.75 versus 13.0). Both the shade and soil treatments retained proportionately more species than did controls (shade plots lost 1.5 species, or 10% of emergence total; soil plots lost 1.25, or 8%; control plots lost 4.25, or 31%). More than twice as many seedlings emerged in the soil plots as in controls, where mortality averaged 52% compared to 26% in soil plots. Seven species survived only in experimentally amended plots. The facilitation succession model is supported for these species. For the remainder, facilitation is either facultative (11 species) or not required (2 species).

Table 2.1 Species emergence rates in mudflow control plots in the current experiment (1986) and in 1984 (Wood and del Moral 1987). n=estimated number of seeds sown per plot in 1986. Emergence values are corrected for seed viability, and are means of 4 replicate plots in 1986 and 3 replicates in 1984.

Species	n	Percent Emergence 1986	Percent Emergence 1984
APIACEAE			
Lomatium martindalei	130	7.7	35.9
ASTERACEAE			
Achillea millefolium	400	0.4	0.1
Agoseris aurantiaca	110	3.0	10.2
Anaphalis margaritacea	1000	0.2	0.0
Antennaria microphylla	800	0.0	0.0
Aster ledophyllus	400	0.3	0.9
Hieracium albiflorum	75	0.5	3.5
Hieracium gracile	100	2.1	0.6
CYPERACEAE			
Carex rossii	75	2.4	0.6
FABACEAE			
Lupinus latifolius	65	48.0	21.8

Table 2.1 (continued).

JUNCACEAE			
Juncus parryi	800	0.0	0.0
POACEAE			
Agrostis diegoensis	600	1.3	1.6
Danthonia intermedia	400	12.5	7.1
Sitanion jubatum	150	11.3	21.4
Stipa occidentalis	350	20.7	19.3
Trisetum spicatum	500	0.6	8.3
POLYGONACEAE			
Eriogonum pyrolifolium	90	27.8	13.9
Polygonum newberryi	75	15.3	23.2
PORTULACACEAE			
Spraguea umbellata	75	48.9	32.2
ROSEACEAE			
Luetkea pectinata	500	0.0	0.0
SCROPHULARIACEAE			
Penstemon cardwellii	800	1.4	1.5

Table 2.2 ANOVA of species richness. A) square root number of species emerging; B) arcsin-square root percent decrease from emergence to final census.

A)

Source	df	F	p
Block	1	6.24	.030
Shade	1	0.74	.407
Soil	1	13.43	.004
Shade x Soil	1	0.03	.872
Error	11		

B)

Source	df	F	p
Block	1	9.99	.009
Shade	1	8.05	.016
Soil	1	11.49	.006
Shade x Soil	1	1.81	.205
Error	11		

Table 2.3 ANOVA of seedling density. A) square root number of seedlings emerging; B) arcsin-square root percent decrease from emergence to final census.

A)

Source	df	F	p
Block	1	0.08	.782
Shade	1	0.53	.480
Soil	1	19.71	.001
Shade x Soil	1	0.01	.927
Error	11		

B)

Source	df	F	p
Block	1	0.17	.685
Shade	1	2.08	.178
Soil	1	19.13	.001
Shade x Soil	1	2.68	.130
Error	11		

Table 2.4 Distribution of seedlings of individual species among experimental treatments. Treatment Effect is the results of an ANOVA. EM=emergence, FC=final census, n=number of seedlings.

			Percent of Seedling Total				Treatment
Species		n	Control	Shade	Soil	S x S	Effect (p)
Achillea millefolium	EM	51	12	27	33	27	none
	FC	28	0	29	25	46	Shade .048
Agoseris aurantiaca	EM	33	27	6	39	27	none
	FC	12	8	8	59	25	Soil .040
Agrostis diegoensis	EM	180	12	12	40	37	Soil .010
	FC	138	9	5	44	41	Soil .013
Anaphalis margaritacea	EM	32	8	1	19	4	none
	FC	22	0	5	86	9	none
Aster ledophyllus	EM	27	11	7	59	22	none
	FC	18	0	6	61	33	Soil .010
Carex rossii	EM	64	11	5	28	56	Soil <.001
	FC	61	8	3	30	59	none
Danthonia intermedia	EM	999	17	11	33	39	Soil .004
	FC	732	12	13	35	40	none
Eriogonum pyrolifolium	EM	333	21	23	34	21	none
	FC	312	20	23	34	22	none
Hieracium albiflorum	EM	5	20	60	0	20	none
	FC	1	0	0	0	100	none

Table 2.4 (continued).

Hieracium gracile	EM	85	7	32	29	32	none	
	FC	45	9	22	27	42	Shade	.049
Juncus parryi	EM	33	0	3	18	79	Soil	.002
	FC	24	0	0	25	75	none	
Lomatium martindalei	EM	389	5	15	34	45	Soil	.033
	FC	142	0	10	30	60	Shade, Soil .020, .003	
Luetkea pectinata	EM	3	0	66	0	33	none	
	FC	3	0	66	0	33	none	
Lupinus latifolius	EM	523	22	26	23	28	none	
	FC	99	24	31	18	27	none	
Penstemon cardwellii	EM	735	5	15	34	45	Soil	<.001
	FC	570	2	14	37	47	none	
Polygonum newberryi	EM	308	11	26	33	30	Sh x So	.003
	FC	206	9	28	31	32	none	
Sitanion jubatum	EM	373	9	14	38	39	Soil	<.001
	FC	300	8	14	37	41	none	
Spraguea umbellata	EM	316	28	18	29	25	none	
	FC	256	24	21	30	25	none	
Stipa occidentalis	EM	871	25	21	27	27	none	
	FC	584	13	24	35	29	Soil	.026
Trisetum spicatum	EM	133	3	21	46	30	Soil	.015
	FC	103	1	16	53	30	Soil	.003

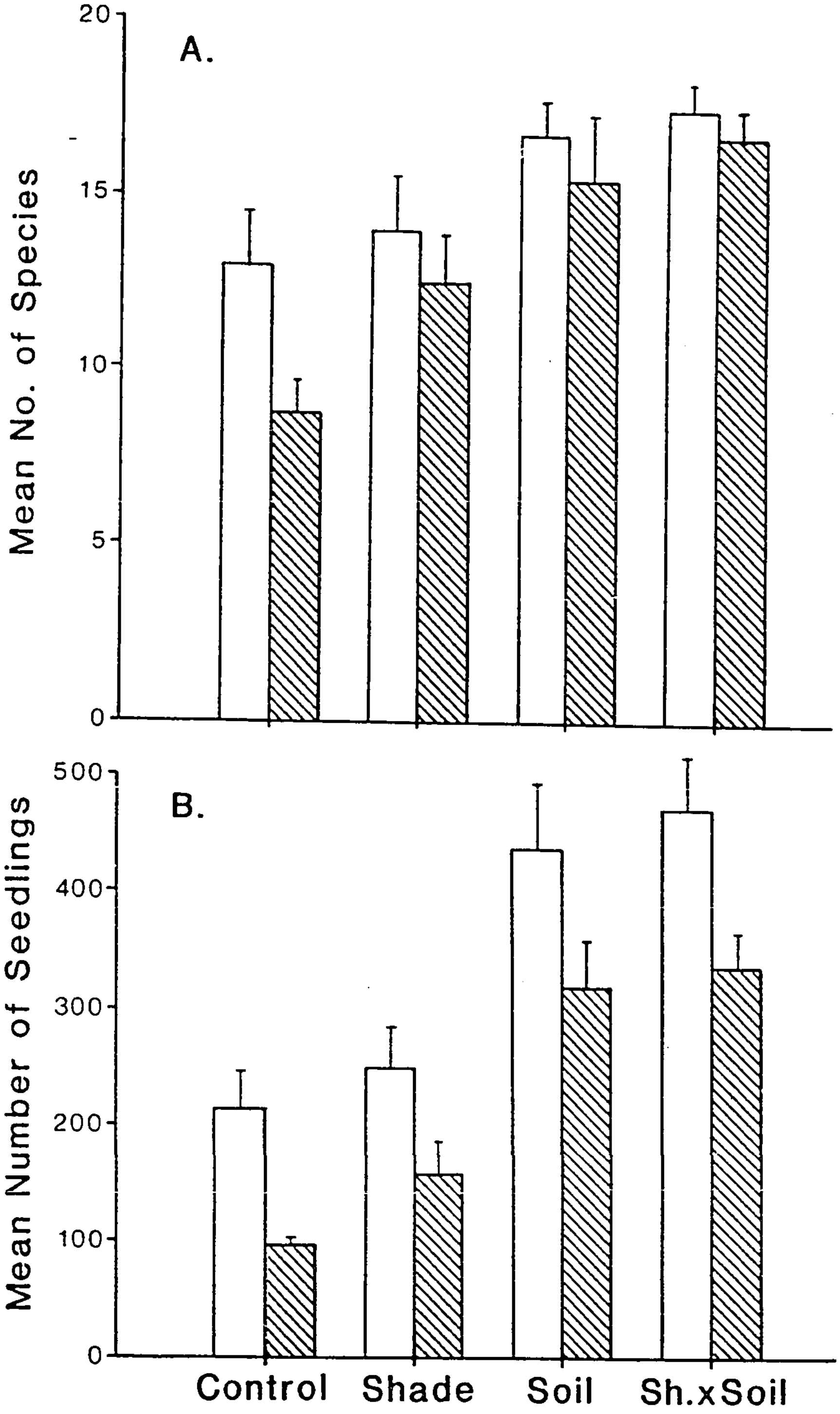


Figure 2.1 Treatment means and standard errors of experimental results for emergence (hatched bars) and the final census (solid bars). Each bar is the mean of four replicate plots. A) species richness; B) seedling density.

CHAPTER THREE

INTRODUCTION

The most striking geological feature of the devastated region immediately north of the crater is the extensive layer of pumice that was emplaced by several pyroclastic flows discharged during the 1980 eruptions (Lipman and Mullineaux 1981). These pumiceous deposits (hereafter collectively referred to as the "Pumice Plains") covered approximately 20 km^2 at 1000-1150 m elevation between the crater and the south and east shores of Spirit Lake (Fig. 3.1), and ranged in thickness from 10 to 200 m (Lipman and Mullineaux 1981). Subsequently, erosion from rainfall, melting snow, and several mudflows (most notably in spring 1982) carved extensive channels in the pumice. The old surface has been exposed occasionally by these erosive events, permitting a few surviving individuals to resprout, but the surface was essentially barren as of 1980. The Pumice Plains landscape in 1986 is thus best described as a dissected plain, with extensive areas of thick pumice interrupted by a network of often deep, sometimes broad, intermittently wet gullies.

Plants have begun to colonize the Pumice Plains in local areas. As most species must disperse many kilometers to reach this site, colonizing species will be those with exceptional dispersal capabilities that also can tolerate the poor growing conditions inherent in this undeveloped substrate.

The purpose of this chapter is twofold: (i) to document immigration (seed rain) onto the Pumice Plains, and (ii) to describe the developing pattern of colonization. I specifically address these questions: First, what life history strategies are represented in the seed rain and among colonizing species? Are they similar? Second, does the species composition of the seed rain mirror that of colonizing plants? Third, is the seed rain uniformly distributed over the Pumice Plains? If so, are colonizing species also distributed uniformly over the landscape? If not, is there a pattern to colonization that might be explained by aspects of topography or life history?

METHODS

Seed Rain

Seeds of vascular plants were collected from traps of 2 types: (i) aerial fallout traps (AFTs), and (ii) pitfall traps (Edwards et al. 1986).

The AFTs consisted of 0.1 m^2 wooden frames with nylon mesh bottoms for drainage, filled with a single layer of golf balls, and set flush with the surface. This arrangement effectively mimicked the size and texture of the natural pumice surface. Because there was no sticky layer to prevent seeds from escaping, the data can be used to estimate seed rain density onto the Pumice Plains where, in the absence of topographic features such as depressions or boulders, strong winds undoubtedly rearrange pattern of initial seed deposition. Traps that act as sinks would therefore yield upwardly biased density estimates for a typical section of the landscape. Ten traps were set out at 10 m intervals at each of two sites on the Pumice Plains, one near the headwaters of the North Fork of the Toutle River (the "Pumice Pond" site), and the other near the eastern edge of the Pumice Plains approximately 2 km south of Spirit Lake (the "Spirit Lake" site; Figure 3.1). Severe erosion at the Pumice Pond site forced the abandonment of five traps by 1984.

Pitfall traps consisted of plastic cups 10 cm in diameter filled with ethylene glycol and set flush with the surface. These were covered by a square of plywood elevated 1 cm above the cup to keep out rain. Pitfall traps were also set out in 10 m intervals, usually along transects 100 m long. Transects were placed at the Pumice Pond and Spirit Lake sites, and in addition were placed at various locations between these two sites (the actual number and placement varied yearly). Pitfall traps acted as sinks and only collected seeds that passed beneath the covering plywood, i.e. those blown horizontally across the pumice. These data therefore were not used to estimate density, but were used to estimate species composition and relative abundance.

Both trap types were collected approximately bimonthly, and the contents stored in alcohol. Seeds from all traps were counted and identified to species by comparison with herbarium material and with seeds obtained from field collections. In some cases only generic identity could be established. I attempted to include only viable seeds by not counting those seeds which were not fully formed and which yielded to a slight pressure from forceps. Many seeds were excluded by these criteria. Viability tests on samples were impossible, as seeds from pitfalls were collected in ethylene glycol, and all samples were stored in alcohol. However, many seeds germinated in these liquids before perishing, and field-collected seeds passing the above criteria always had high viability. Thus my counts probably approximate the true level of viability.

Colonizing Species

In order to describe the spatial distribution of colonizing species on the Pumice Plains, I censused species in grids of contiguous quadrats. This method is an effective compromise between the far more time-consuming technique of complete mapping (the data from which yields a true spatial point pattern; Diggle 1983), and a layout of quadrats unconnected in space from which spatial analysis is difficult.

Two grids were established, one ("Willow Spring") covering an area 400 x 400 m and containing 1600 10 x 10 m plots; the other ("Lupine Patch") covering an area 350 x 250 m with 875 plots. Each grid was subjectively located to sample a heterogeneous, representative section of the Pumice Plains where colonists were present. Colonization densities in other areas of the Pumice Plains were often much lower. Permanent stakes were fixed every 50 m throughout each grid. Temporary stakes were placed every 10 m around the border of a 50 m x 50 m section to be censused. This arrangement allowed me to locate accurately all plots within a section without marking every corner.

Plants were censused in late August and September, 1986, by walking the midline of a plot and recording all plants within 5 m of the midline. Heterogeneous plots were searched more thoroughly. Abundance of a species within a plot was scored as follows: Class 0, barren; Class 1, 0-5 individuals (or clones); Class 2, 5-20 individuals; Class 3, 20+ individuals; Class 4, 0.5% cover; Class 5, 1% cover; Class 6, 2-4% cover; Class 7, 5-9% cover, Class 8, at least 10% cover.

RESULTS

Seed Rain

A total of 24 species in 8 families was collected over a four year period from 1982 to 1985, including three taxa as yet unidentified (Table 3.1). This total may be conservative, since several genera (e.g., *Carex*, *Juncus*, *Salix*) contain species indistinguishable by seed characters alone.

In an attempt to reduce the complexity of the data, for each year I computed separate species frequency distributions from the two data sets (pitfalls and AFTs) and then tested the equivalence of these distributions with a two-sample Kolmogorov-Smirnov test. Comparisons within years were always non-significant (p always >0.05), permitting pitfall and AFT data to be pooled within a given year. Relative abundance estimates calculated from these pooled data are given in Table 3.1.

Seven species accounted for at least 95% of the total seed rain in all years (Table 3.1). All have large appendages on seeds to aid dispersal; a feathery coma in the two *Epilobium* (Onagraceae) species, and pappuses in the five Asteraceae species. The highest relative abundance over the four years from 1982 to 1985 was achieved by *Epilobium* angustifolium, which averaged 39% and comprised 74% of the total in 1985. This species is also one of the most abundant species in adjacent secondary successional habitats, such as the blowdown and standing dead forests (Franklin et al. 1985, and pers. obs.).

Seed rain density varied considerably over the period from 1983 to 1985, depending on year and sample location, but the several values were always within an order of magnitude (ranging from 130 to 755 seeds m^{-2} yr^{-1}; Table 3.2). Values for 1983 are highest, which probably reflects the favorable growing conditions and consequent high plant production in that year (Reynolds and Bliss 1986; W. Pfitsch, pers. comm.). Seed rain density was significantly lower in 1984 than either 1983 or 1985, a decline which may be due to summer drought (Reynolds and Bliss 1986).

The Pumice Pond site received more than twice as many seeds as did the Spirit Lake site in the two years for which a comparison is available (Table 3.2). This difference is probably due to the fact that Pumice Pond is several kilometers closer to the outlet of the main immigration corridor for windblown seeds, the North Fork of the Toutle River (Fig. 3.1).

Yearly densities of the seven most abundant species are given in Table 3.3. Senecio sylvaticus exhibited the highest total of any species in any year in 1983, with approximately 330 seeds m^{-2} deposited at Pumice Pond. The highest total at Spirit Lake was achieved by *Epilobium angustifolium* in 1985, with approximately 124 seeds m^{-2}. Within a year, density at Pumice Pond was generally higher than at Spirit Lake for reasons discussed above. The densities of *Anaphalis* and *Senecio* declined significantly from 1983 to 1985, while *Epilobium angustifolium* increased. The remaining five species in Table 3.3 exhibited no apparent pattern.

Colonizing Species

Of the 1600 plots in the Willow Spring grid, 45.6% were barren of vascular plants, and 35.5% of 875 plots in the Lupine Patch grid were similarly barren. Species richness averaged 1.03 per 100 m^2 plot at WS, and 1.82 at LP.

Table 3.4 gives the frequency and importance value (IV), computed as (relative frequency + relative cover), of all species recorded in 1986. At each site the species with highest IVs are, in descending order, *Anaphalis margaritacea*, *Lupinus lepidus*, and *Epilobium angustifolium*. An IV much greater than frequency indicates that the species is abundant where found; an IV approximately equal to frequency indicates the species is not abundant. For example, *Anaphalis* and *E. angustifolium* sometimes occur at high densities at Willow Spring but not at Lupine Patch, and their IVs are twice that of their frequencies at the former site. Lupinus lepidus occurs at high densities at both sites.

Importance values are plotted against species sequence in Fig. 3.2. The distribution at both sites exhibits an approximately linear (or geometric) slope on a semi-log scale; however, the Lupine Patch site is apparently tending towards a lognormal distribution, as it has more species with IVs close to 10 than does Willow Spring. The mean IV for Lupine Patch is also greater: 7.67, versus 6.19 for Willow Spring (median IVs are 1.65 and 1.05, respectively).

Community composition of the two sites is similar (Spearman rank correlation of IVs=0.773, p<.001). The 16 ha Willow Spring has 32 species (including 2 unknowns), whereas the 8.75 ha Lupine Patch has 26 species (including 1 unknown). No other species was found in a search of a much wider range of the Pumice Plains.

Species richness was significantly clumped at both sites, as determined by variance/mean ratios and by chi-square tests of observed frequencies with Poisson expectation (both p<.001; Diggle 1983). Figures 3.3a and 3.4a depict this clumped pattern. High richness occurred primarily in sites of high soil moisture, due mostly to the presence of streams or underground seepages, and secondarily to such topographic features as depressions and gully slopes where high densities of seeds may accumulate.

The spatial distribution of selected species is shown in Fig. 3.3b-f and Fig. 3.4b-c. Three groups of species are evident. First, species such as *Salix commutata* (Fig. 3.3b) and *Cirsium arvense* (Fig. 3.4b) occur almost exclusively near streams and may be classified as "strongly hydrophilic" in this environment. Other species included in this group are: *Cinna latifolia*, *Cirsium vulgare*, *Equisetum* spp., *Epilobium luteum*, *E. watsonii*, *Juncus* spp., *Petasites frigidus*, *Saxifraga ferruginea*, *Senecio sylvaticus*, and *Sonchus arvensis*.

The second group contains *Anaphalis margaritacea* and *Epilobium angustifolium* (Fig. 3.3c-d), species that may be classified as "facultatively hydrophilic". These two species attain their greatest cover in wet sites, but also colonize upland pumice to a significant degree. It is no accident that these rhizomatous species are among the most common colonizers on the Pumice Plains, as they can attain high cover in favorable sites through clonal growth but also can establish in upland pumice where growing conditions are more severe.

The third group is less well defined, and is comprised of species that exhibit no obvious affinity for wet sites. These species are either distributed randomly or are clumped in drier sites. Included here are those species that cannot attain high cover by clonal growth and thus do not exploit wet sites as fully as do species of the first two groups.

This group is exemplified by Lupinus lepidus (Fig. 3.4c), Carex mertensii (Fig. 3.3e), and Hypochaeris radicata (Fig. 3.3f).

Lupine is unique among the colonists on the Pumice Plains in that tremendous population increases have occurred without seed immigration from outside sources. A few (possibly <20), widely scattered individuals somehow survived the eruption and became reproductive as early as 1981 (R. Sugg, pers. comm.). Because lupine seeds are heavy and without adaptations for long-distance dispersal, and have never been recorded in seed traps, all of the thousands of lupines now growing on the Pumice Plains are presumably descended from these few founder individuals. In contrast, virtually all new individuals of other species must arise from long-distance seed dispersal. The highly clumped spatial distribution of lupine (which is not clonal) arises from local or "neighborhood" recruitment about parental plants. This phenomenon frequently results in locally dense populations comprised of hundreds of individuals.

Carex mertensii, Hypochaeris radicata (Fig. 3.4e,f), Hieracium albiflorum, Penstemon serrulatus, and Pseudotsuga menziesii are all distributed essentially at random, and occur almost exclusively as isolated individuals. This random pattern is most pronounced at Willow Spring, because Lupine Patch contains a greater concentration of wet areas that promote more uneven abundance distributions. With the exception of Penstemon, which is a mat-forming species, none of these species in the third group are clonal.

DISCUSSION

Seed Rain

Approximately 370 seeds m^{-2} yr^{-1} fall onto the Pumice Plains, a value obtained by averaging over years and sites. This figure is comparable to that obtained by Ryvarden (1971; calculations from Rabinowitz and Rapp 1980), who reported densities between 342 to 653 seeds m^{-2} 2 mo^{-1} at the base of a retreating glacier in Norway. The only other estimate I could find of seed rain into a barren, somewhat remote site is that of Archibold (1980), who reported a density of 2400 to 3800 seeds m^{-2} yr^{-1} onto stripmine wastes in Saskatchewan. In this case, however, seed sources were presumably much closer than for the Pumice Plains. Density estimates for seed rain in undisturbed vegetation range from 166 m^{-2} yr^{-1} in an oak-pine forest understory (Wagner 1965) to nearly 20,000 seeds m^{-2} yr^{-1} in a tall-grass prairie (Rabinowitz and Rapp 1980). This wide range probably is due to the degree of canopy closure as well as to plants with widely different reproductive potentials.

All species collected are primarily wind dispersed. The most numerous family is the Asteraceae, represented by

11 species, eight of which probably are not native to the western U.S.: *Cirsium arvense*, *Cirsium vulgare*, *Hypochaeris radicata*, *Senecio sylvaticus*, *S. vulgaris*, *Sonchus arvensis*, *Sonchus asper*, and *Taraxacum officinale* (Hitchcock and Cronquist 1973). The remaining three Asteraceae, *Anaphalis margaritacea*, *Agoseris aurantiaca*, and *Hieracium albiflorum*, are widely distributed throughout the Cascade range in Washington (Hitchcock and Cronquist 1973).

Woody species, especially trees, are poorly represented in the Pumice Plains seed rain. Only two of the 21 identified species are woody, the shrubby willow, *Salix commutata*, and vine maple, *Acer circinatum*. Together these two account for less than 1% of the seed rain (*Acer* is represented by just two seeds). In addition, many *Salix* seeds may come from a local source, as a vigorous population of resprouted willow has developed in one location on the Pumice Plains and probably contributes to the measured seed rain, especially at the Spirit Lake site. Archibold (1980) also found that >99% of the seed rain into stripmine wastes was either forbs (97%) or grasses (3%).

Woody species characteristic of early montane succession in the Mount St. Helens region such as alder (*Alnus rubra* and *A. sinuata*), Douglas fir (*Pseudotsuga menziesii*), silver fir (*Abies amabilis*), and noble fir (*Abies procera*) were not recorded in seed traps. However, a few seedlings of Douglas fir and noble fir are present on the Pumice Plains, suggesting that frequency of establishment of these species may be limited by seed availability. Only a few seeds (<<1% of the total) were recorded from the grass species that are a major component of the subalpine flora at higher elevations on the volcano (del Moral 1983).

Seeds of most species must travel many kilometers to reach the Pumice Plains. All species aside from willow (see above) are not represented by populations of sufficient size on the Pumice Plains to account for more than a tiny fraction of the seed rain (e.g., individual or clone density at the Spirit Lake site was approximately 1 per 100 m^2 in 1986, and many of these were not reproductive). The likely immigration corridor for most species is up the canyon of the North Fork of the Toutle River (Fig. 3.1). This river valley originates at the southwest portion of Spirit Lake and extends westward down through clearcuts to low elevation agricultural fields, the apparent source of many of these species. Following the prevailing westerly winds in this region, seeds are carried up the valley of the Toutle and are deposited onto the Pumice Plains. This hypothesized immigration pathway accounts for the fact that the Pumice Pond site, lying closer to the headwaters of the Toutle River valley, receives over twice as many seeds as does the Spirit Lake site several kilometers distant.

Density of several species changed significantly over the collection period. *Senecio sylvaticus* exhibited the most drastic decline of any species. This probably is related to its life history; it is a biennial that (in this region) exploits clearcuts in montane forests for only one generation before being outcompeted, presumably, by more aggressive successional species (West and Chilcote 1968). Apparently, the eruption created good, albeit brief growing conditions for *Senecio* in surrounding forests, which resulted in a pulse of high seed immigration in 1982 and 1983 (and possibly earlier). *Anaphalis* also declined, which may be due to similar circumstances, but since this species is a clonal perennial the explanation is less satisfactory. However, neither did *Anaphalis* decline as drastically as did *Senecio*. The increase of *Epilobium angustifolium* is directly attributable to the substantial population growth of this clonal species in surrounding habitats (Franklin et al. 1985, and pers. obs.).

Colonizing Species

A landscape essentially devoid of plants in 1980 is beginning to be filled with plants, although at an average density of only 1 to 2 species per 100 m^2. Colonizers on the Pumice Plains in 1986 consisted primarily of wind dispersed, herbaceous species. Conspicuously rare were woody species, especially trees, and species employing animal dispersal.

Floristically, the 32 identified species are an odd mix of two general types: a native montane element and a lowland weedy element. The montane group is typified by *Anaphalis margaritacea*, *Carex mertensii*, *Epilobium angustifolium*, *E. watsonii*, *Lupinus lepidus*, *Salix commutata*, and *Spraguea umbellata*. All are common and widespread in the western Cascades (Hitchcock and Cronquist 1973). The lowland group is typified by *Cirsium arvense*, *Cirsium vulgare*, *Hypochaeris radicata*, *Senecio sylvaticus*, and *Sonchus arvensis*. These latter species (all Asteraceae) are typically found in low elevation disturbed sites, have exceptional wind dispersal capabilities, combine exceptional dispersal capabilities with a broad tolerance range, and are all introduced. I know of no analog for this particular floristic assemblage, although many areas of North America have had their floras and plant communities profoundly affected by introduced species (cf. Mooney and Drake 1986).

Moisture is the most significant factor promoting local species richness on the Pumice Plains. Up to 12 species can occur per 100 m^2 in sites with streams or seeps, compared to an overall average of 1.03 or 1.83 per 100 m^2 for Willow Spring and Lupine Patch, respectively. High richness results from the "strongly hydrophilic" group of species that occurs almost exclusively and with high fidelity in wet sites: *Cinna latifolia*, *Cirsium arvense*, *C. vulgare*, Equisetum sp., Epilobium luteum, E. watsonii, Juncus sp., Petasites frigidus, Salix commutata, and Senecio sylvaticus.

Moisture promotes richness for two principal reasons. First, and most importantly, high soil moisture reduces drought stress as a significant cause of mortality. This may be especially important for seedlings, because ground temperatures on the Pumice Plains in summer can exceed 50° C (value recorded at the meteorological station in Willow Spring; Reynolds and Bliss 1986 and pers. comm.). Thus species otherwise susceptible to drought or heat stress may encounter favorable conditions for germination and growth only in wet sites. Second, high richness may simply be due to a greater concentration of seeds in sites of high moisture. Streambeds or gullies may be sinks that trap wind-blown seeds, thereby concentrating rare species and raising the probability of a species occurrence. Very likely there is an interaction between these two scenarios; mere entrapment of seeds is insufficient to promote establishment without concomitant favorable growing conditions, and favorable conditions are found primarily in wet sites.

The analysis of importance value distributions has not yet produced useful generalities (Whittaker 1975). This is due partly to the rather wide range of empirical distributions obtained for different taxa, life forms, and habitats, and partly to the immature stage of development of theoretical community ecology, which results in a lack of well-defined hypotheses about expected forms of IV distributions. Still, when interpreted cautiously, such distributions are a useful way of graphically describing species abundances, and provide a baseline from which to analyze future changes (cf. Bazzaz 1975).

Disregarding the several extremely rare species with low importance values, the IV curve for Willow Spring exhibits a good fit to a linear slope, or geometric distribution, which according to Whittaker (1975) is expected for a severe environment with low richness. Although Whittaker suggested that a geometric distribution was the outcome of competition for shared, limiting resources (the "niche pre-emption hypothesis", defined for communities at equilibrium), on the Pumice Plains commonness and rarity are determined primarily by the differing degrees of habitat tolerance among species. There is no reason to suspect that competition is an organizing force in this landscape, since cover is so low and the environment can clearly support a much higher standing crop. Anaphalis, Epilobium, and Lupinus are abundant not because they are good competitors, but because they are effective colonizers.

The importance value curve for Lupine Patch is apparently tending towards a lognormal distribution. Mean richness and cover are greater in this grid, and consequently more species have attained intermediate IVs. This causes the slight hump in the curve around IV=10, which I expect will become more pronounced as colonization and growth continue. As is the case for Willow Spring, however, there is no evidence for competitive control.

The spatial distribution of Lupinus lepidus is strikingly different from any other species (Fig. 3.4c). Lupine attains its highest cover and density where richness is low, i.e. primarily on upland pumice away from wet areas. This pattern fits well with its habitat preference elsewhere in the Cascades and at higher elevations on Mount St. Helens, where it typically occurs at middle to high elevations on exposed south-facing slopes of low cover, often on loose soils. The only other species on the Pumice Plains with similar habitat preferences are uncommon (Penstemon serrulatus and Spraguea umbellata). These three species are among the few higher elevation taxa to successfully colonize the Pumice Plains.

SUMMARY and CONCLUSIONS

It appears that the species composition of the vascular plants colonizing the Pumice Plains in 1986 directly reflects the species composition of the immigrant seed rain. Of the 24 species recorded in the seed rain, 16 are present on the Pumice Plains. The missing 8 species are extremely rare in the seed rain, representing <<1% of the total. The most abundant species in the seed rain, Epilobium angustifolium and Anaphalis margaritacea, are among the most abundant on the landscape. In general, then, both floristic composition and relative abundance of immigrant seeds approximates that of colonizing plants. The glaring exception to this generality is Lupinus lepidus, which was not found in the seed rain but which is quite abundant on the Pumice Plains as a result of on-site seed production and recruitment from a few surviving plants.

Herbaceous taxa dominate both the colonizer assemblage and the seed rain. However, scattered individuals of Douglas fir and noble fir are present on the Pumice Plains. Since these species were not found in the seed rain, presumably because immigration levels were so low, it is hypothesized that establishment of these (and presumably other) woody taxa is limited by seed dispersal. Although the qualitative relationship between seed immigration density and colonizer abundance is clear, there is no quantitative relationship between the two. This is because colonizer abundance is determined, given some minimum level of immigration, by physiological tolerances for germination and growth that vary among species in ways that only weakly depend on immigration density.

Inspection of spatial pattern maps shows clearly that high species richness on the Pumice Plains is locally concentrated in sites of high soil moisture. Species that posess exceptional wind-dispersal capabilities presumably must "pay" for this capability by sacrificing some aspect of life history, such as seed mass and consequent seedling vigor. Thus it is logical that seedling establishment will be enhanced in sites where abiotic stresses are reduced.

What of the future course of plant succession on the Pumice Plains? I will venture to make a few predictions.

1) There will be a steady but slow rate of increase in species richness, since habitat isolation effectively prevents establishment of species with less-than-exceptional dispersal capabilities. Most species possessing such capabilities are already present. When plant communities develop and structural complexity increases, animal-dispersed plants will become more common. There is presently little reason for animals, particularly birds, to visit the area, and in fact few birds do (D. Manuwal pers. comm., and pers. obs.).

2) Woody taxa, especially trees, will continue to be rare for many years. As compared to herbaceous taxa, trees have a long juvenile period and thus most population growth in the near future must occur from long-distance seed immigration. When tree seedlings now present on the Pumice Plains attain reproductive maturity, then rate of population growth will increase markedly. The timing of this switch among species from outside or "donor-control" to "local control" of population dynamics will be an important aspect

of succession in this landscape. For example, Lupinus lepidus has always exhibited local control and populations are increasing rapidly; Anaphalis margaritacea and Salix commutata are just beginning the switch; and Carex mertensii (and all other species) still retain donor control.

3) Populations of Lupinus lepidus will continue to increase in size and areal extent, since lupine is not restricted to wet sites. Consequently, the pattern of spatial distribution for lupine will become less clumped as populations expand from the several high density patches into areas now essentially barren.

4) Since Lupinus lepidus is actively fixing nitrogen on the Pumice Plains (plants are heavily nodulated), with time this species will act to facilitate the invasion of other colonizers by increasing soil organic matter and nitrogen. This is not yet occurring to any significant degree, as lupine's spatial distribution does not match that of any other species. Also, present population densities may be so high that competitive inhibition outweighs any positive effects of habitat modification. Yet, since nitrogen levels in pumice are low (del Moral and Clampitt 1983, B. Nuhn, pers. comm.), facilitation (Connell and Slatyer 1977) may become important in these sites.

Table 3.1 Relative abundance of species in the seed rain, all sites combined. PF=Pitfall trap, AFT=Aerial Fallout trap.

Species	Relative Abundance (Percent of Yearly Total) 1982	1983	1984	1985
Anaphalis margaritacea	16	36	21	10
Cirsium arvense	13	4	2	2
Epilobium angustifolium	26	8	48	74
Epilobium watsonii	0.5	5	10	3
Hieracium albiflorum	3	1.5	3	1
Hypochaeris radicata	3	2	3	5
Senecio sylvaticus	36	39	7	1
Other[1]	2	4	6	4
Sample Size (# of seeds)	569	1095	296	2056
Trap Type and Number	38 PF	20 AFT	14 AFT	35 PF, 10 AFT

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[1] Other species: _Acer circinatum_, _Agoseris aurantiaca_, _Carex_ spp. (mostly _C. mertensii_), _Cirsium vulgare_, grasses (including _Agrostis_, _Cinna_, _Sitanion_), _Juncus_ spp., _Salix_ spp. (including _S. commutata_), _Saxifraga ferruginea_, _Senecio vulgaris_, _Sonchus arvensis_, _Sonchus asper_, _Taraxacum oficinale_, and 3 unidentified taxa. Not all species are present in all years.

Table 3.2 Mean seed rain density (seeds 0.1 m^{-2} yr^{-1}) estimated from Aerial Fallout traps. Numbers in parentheses are standard error and sample size of 0.1 m^2 traps. Only those values with superscript are not significantly different at the 0.05 level.

Site	1983	1984	1985
Pumice Pond	75.5 (9.5, 10)	38.4 (9.6, 5)	--
Spirit Lake	34.9^1 (5.0, 10)	13.0 (2.9, 9)	25.0^1 (3.0, 10)

Table 3.3 Means and standard errors of seed rain density (seeds 0.1 m^{-2} yr^{-1}) for the 7 species of highest abundance listed in Table 3.1. Values estimated from Aerial Fallout traps; see Table 3.1 for sample sizes. PP=Pumice Pond, SL=Spirit Lake sites.

	1983		1984		1985	
Species	PP	SL	PP	SL	PP	SL
Anaphalis margaritacea	27.1 (3.7)	10.2 (2.0)	8.6 (2.2)	2.2 (0.6)	--	3.7 (1.0)
Cirsium arvense	1.9 (0.8)	2.0 (0.9)	0.4 (0.2)	0.6 (0.3)	--	0.2 (0.1)
Epilobium angustifolium	6.7 (1.0)	3.0 (0.7)	18.4 (4.8)	6.0 (2.3)	--	12.4 (3.7)
Epilobium watsonii	2.2 (0.6)	3.0 (0.9)	2.2 (0.9)	1.9 (0.5)	--	1.1 (0.4)
Hieracium albiflorum	0.7 (0.3)	0.8 (0.3)	1.4 (0.9)	0.1 (0.1)	--	0.5 (0.2)
Hypochaeris radicata	1.6 (0.4)	0.9 (0.5)	2.0 (0.9)	0.1 (0.1)	--	2.2 (0.4)
Senecio sylvaticus	33.1 (5.6)	10.1 (1.9)	2.6 (0.7)	0.7 (0.3)	--	1.3 (0.3)

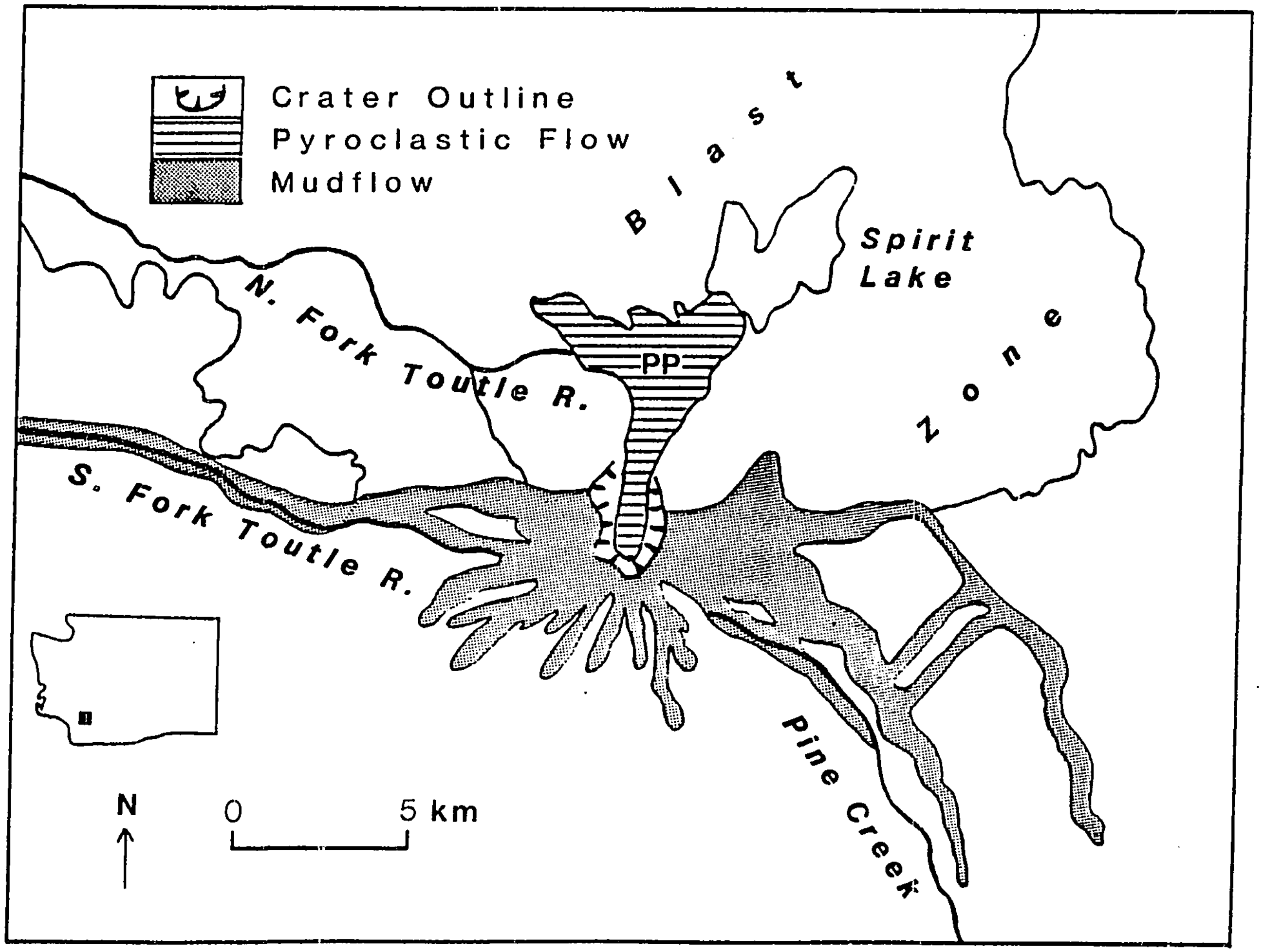
Table 3.4 Species recorded on the Pumice Plains in 1986. F=frequency of occurrence in 1600 plots at Willow Spring, 875 plots at Lupine Patch. IV=Importance Value (relative cover + relative frequency).

	Willow Spring		Lupine Patch	
Species	F	IV	F	IV
Abies procera	0.4	0.6	0.1	0.2
Achillea millefolium	0.1	0.2	0.1	0.1
Agrostis sp.	1.4	2.2	0.3	0.3
Anaphalis margaritacea	33.9	63.1	41.9	44.2
Carex mertensiana	7.9	13.0	11.2	10.0
Cinna latifolia	2.4	4.7	8.3	9.1
Cirsium arvense	0.9	1.5	8.0	7.6
Cirsium vulgare	--	--	0.8	0.5
Equisetum sp.	0.8	0.9	1.5	1.5
Epilobium angustifolium	11.0	20.6	28.1	28.9
Epilobium luteum	0.1	0.1	--	--
Epilobium watsonii	4.2	8.9	13.0	14.6
Hieracium albiflorum	2.2	3.6	3.7	3.3
Hypochaeris radicata	2.4	3.9	8.7	8.0
Iris sp.	--	--	0.1	0.1
Juncus sp.	0.1	0.1	0.9	0.6
Luetkea pectinata	0.1	0.1	--	--

Table 3.4 (continued).

Lupinus latifolius	0.3	0.7	0.1	0.1
Lupinus lepidus	20.3	45.5	26.9	43.3
Luzula sp.	0.1	0.1	--	--
Penstemon serrulatus	2.3	3.8	0.7	0.5
Petasites frigidus	1.3	2.3	2.1	1.8
Phacelia sp.	--	--	0.1	0.1
Polygonum sp.	0.1	0.1	--	--
Pseudotsuga menziesii	1.4	2.2	0.2	0.2
Salix commutata	6.6	14.6	8.8	8.8
Saxifraga ferruginea	0.1	0.1	0.5	0.4
Senecio sylvaticus	1.7	2.7	11.7	11.5
Sonchus arvensis	0.1	0.1	2.7	2.5
Spraguea umbellata	0.2	0.3	--	--
Tsuga heterophylla	0.8	1.2	--	--
Vaccinium spp.	0.1	0.1	--	--
Unknowns	0.5	0.8	1.7	1.2

Figure 3.1 Region around Mount St. Helens affected by the 1980 eruptions. PP=Pumice Plains.


Crater Outline
Pyroclastic Flow
Mudflow
Blast Zone
Spirit Lake
PP
N. Fork Toutle R.
S. Fork Toutle R.
Pine Creek
N
0
5 km

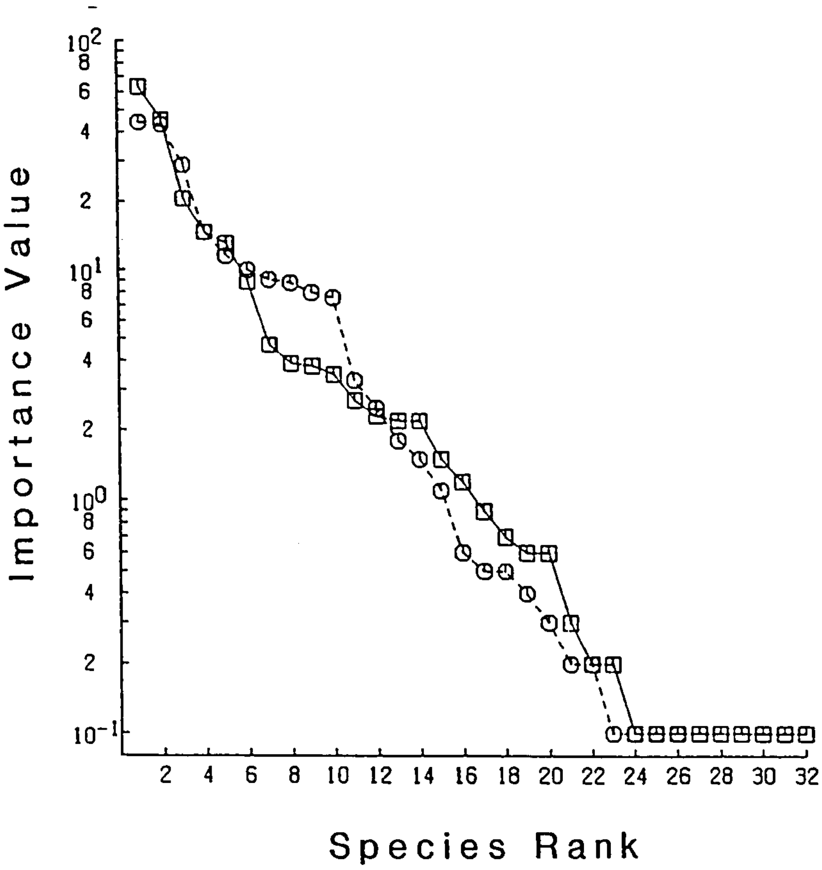


Figure 3.2 Importance value distributions for Willow Spring and Lupine Patch grids.

Figure 3.3 Species richness and abundance of selected species at Willow Spring. Each symbol represents a value for a 10 x 10 m quadrat. a) richness; b) *Salix commutata*; c) *Anaphalis margaritacea*; d) *Epilobium angustifolium*; e) *Carex mertensii*; f) *Hypochaeris radicata*. Codes: blank = 0; + = 1 species or abundance class; ▥ = 2 species or class 2; ░ = 3-4; ▓ = 5-6; █ = 7+ species or abundance class.

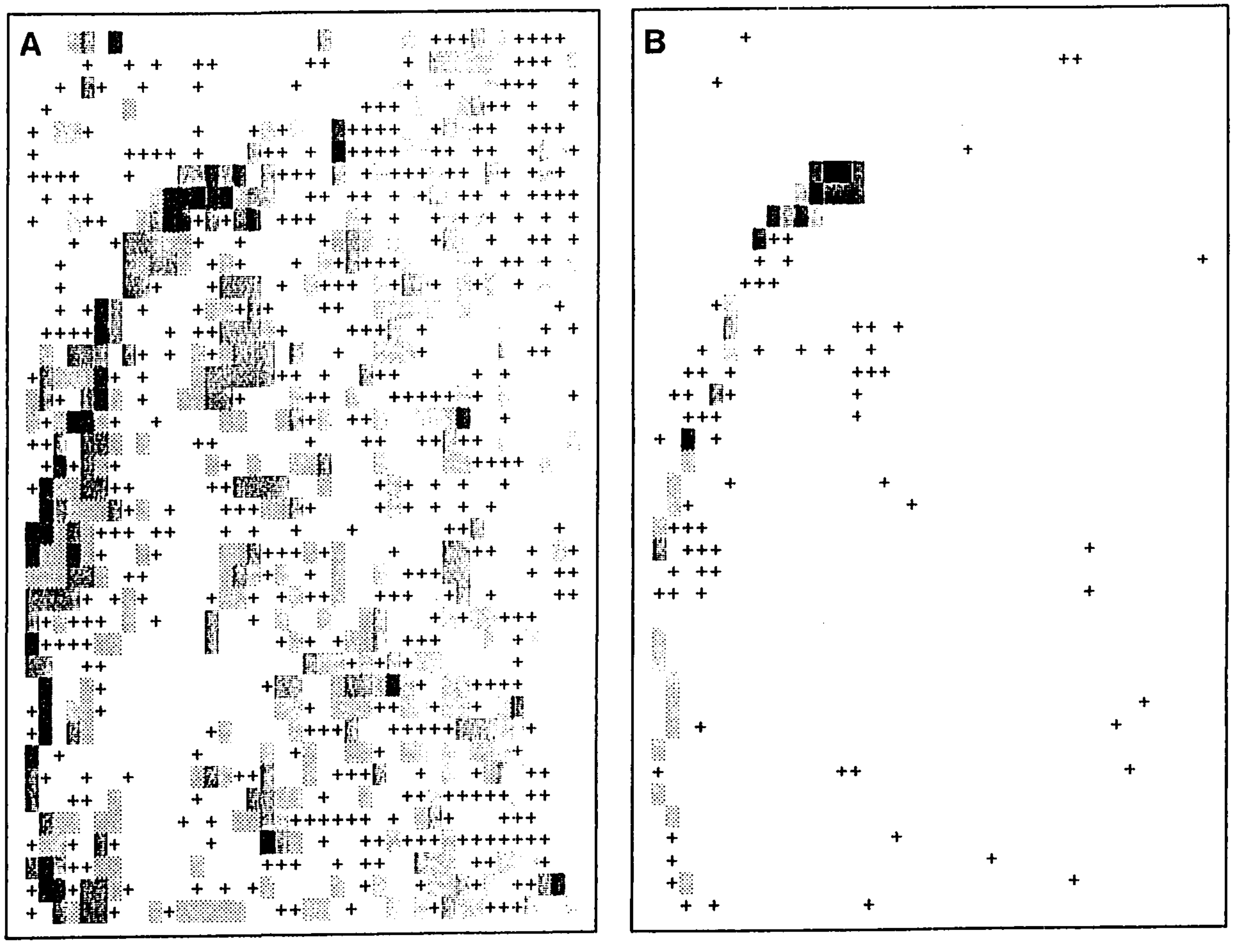
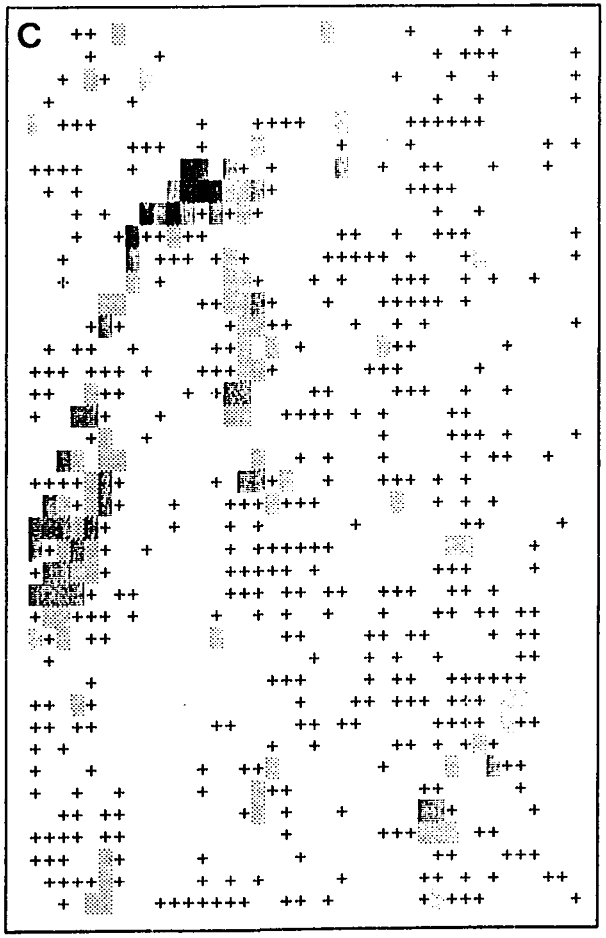

A
B

Figure 3.3 (continued)


C

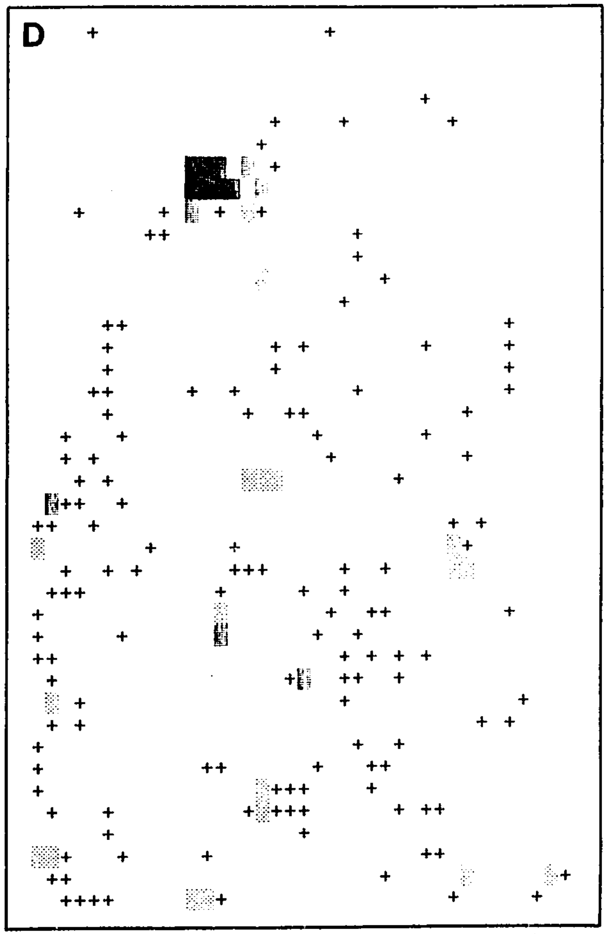
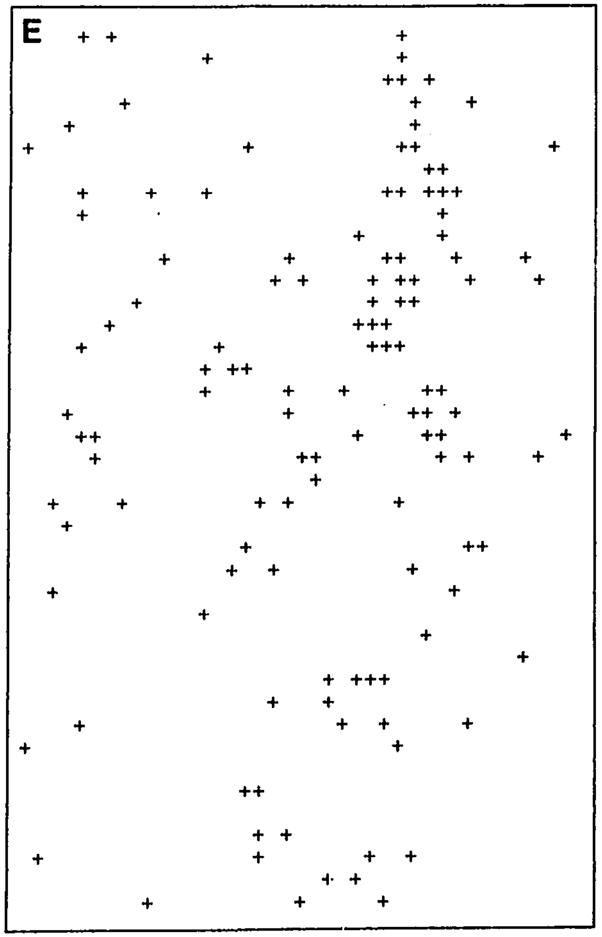

D

Figure 3.3 (continued)


E

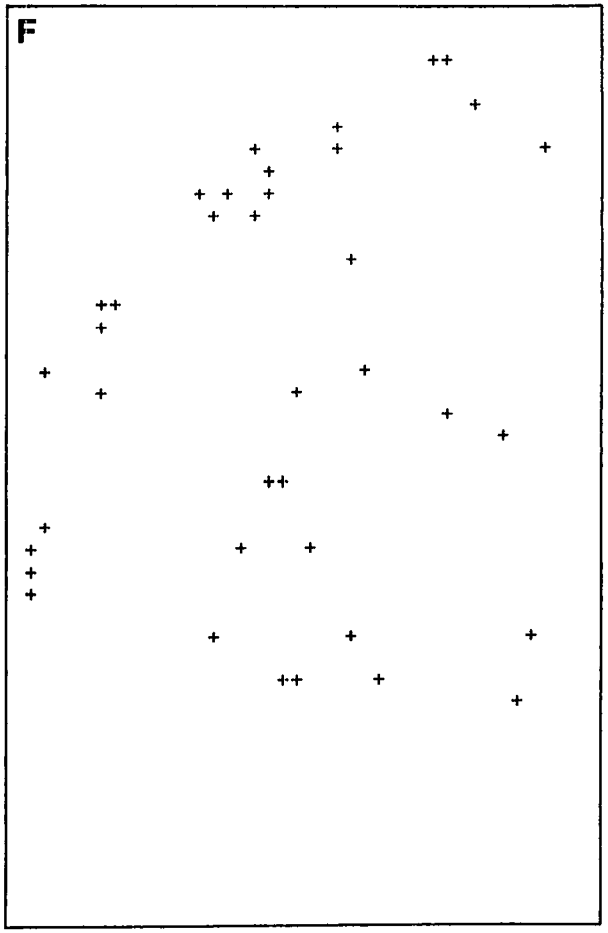
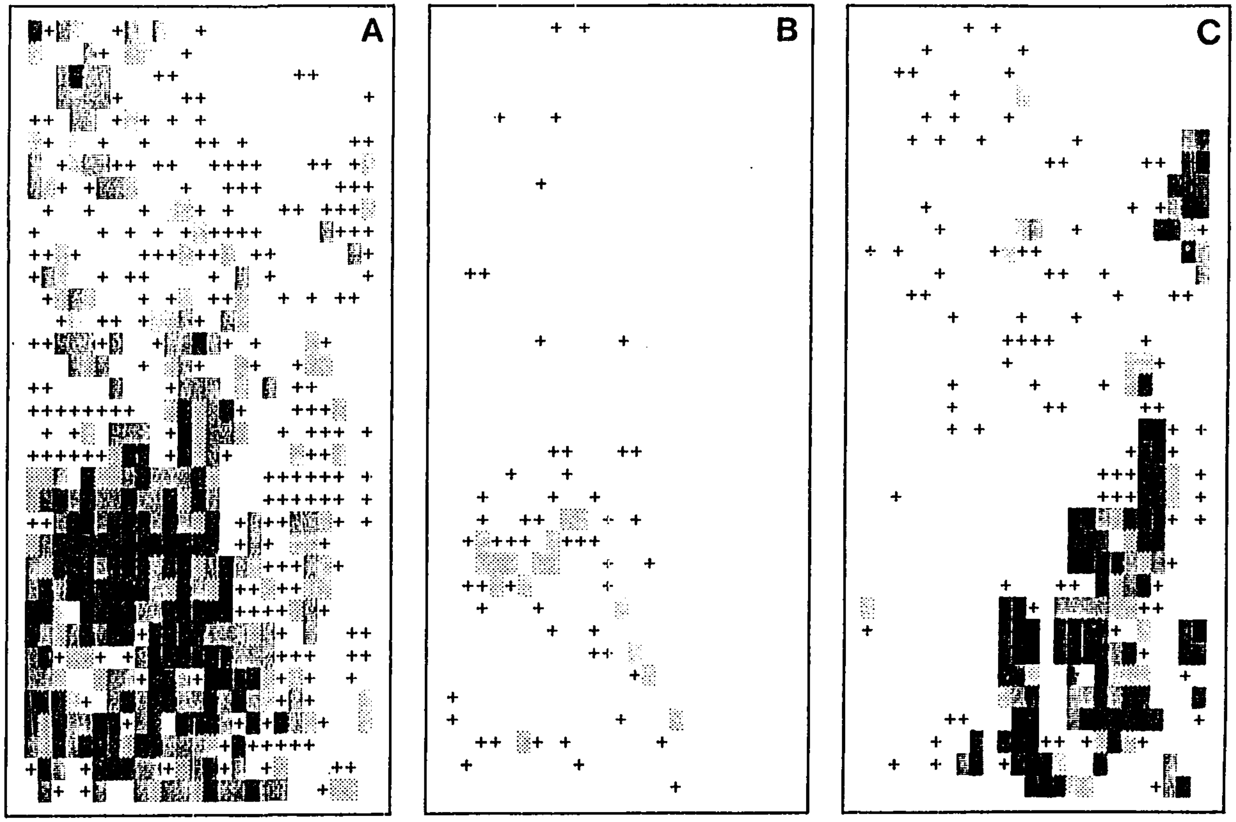

F

Figure 3.4 Species richness and abundance of selected species at Lupine Patch. Each symbol represents a value for a 10 x 10 m quadrat. a) richness; (b) *Cirsium arvense*; c) *Lupinus lepidus*. Codes: blank = 0; + = 1 species or abundance class; ▥ = 2 species or class 2; ▒ = 3-4; ▓ = 5-6; █ = 7+ species or abundance class.


A
B
C

CHAPTER FOUR

INTEGRATION

It is now possible to evaluate the mechanistic basis of early primary succession on Mount St. Helens. The initial establishment of species on barren substrates--high point intensity disturbances--was shown to be related to dispersal properties of individual species, to their tolerance (or lack thereof) for harsh conditions found on these substrates, and, for some species, to the actions of other species that facilitate the invasion of less tolerant species.

The applicability of the facilitation model of succession, as defined by Connell and Slatyer (1977), was shown to be adequate, although subject to several important qualifications related to individual species and habitats.

First, I demonstrated that facilitation is a species property, not a habitat property. It does little good to state without qualification that facilitation is or is not "important" in succession at a particular site. I showed in two separate experiments in two different years that several species of the subalpine flora (Eriogonum pyrolifolium, Spraguea umbellata, and, to lesser degrees, Sitanion jubatum, Stipa occidentalis, and Polygonum newberryi) are capable of growing from seed in new mudflows. These species can be classified as stress tolerant in the sense of Grime (1979), and the facilitation model does not apply to their invasion of barren sites. For a lucid discussion of how E. pyrolifolium and P. newberryii utilize different suites of physiological mechanisms to attain their stress tolerant habit, see Chapin (1986). I concluded that the rate of colonization of the above five stress tolerant species was limited by their poor dispersal abilities, not by habitat severity. Yet for the many other species (e.g, Agoseris aurantiaca, Achillea millefolium, Aster ledophyllus, Juncus parryi, and Agrostis diegoensis) that had poor or no survivorship in mudflows, experimental results were consistent with the predictions of the facilitation model. These species survived on mudflows only when I altered environmental conditions in ways that mimicked the alterations effected by early plant colonists.

Second, not only is facilitation a species property, its importance for any given species can change between habitats. This facultative nature of facilitation was demonstrated by showing that seedling survivorship of species such as Danthonia intermedia, Lupinus latifolius, Sitanion jubatum, and Stipa occidentalis was higher in eroded mudflows at Pine Creek than in uneroded mudflows at Butte Camp. Facultative facilitation is also demonstrated by comparing the Pumice Plains habitat with that of subalpine mudflows. One of the few species common to both environments, Anaphalis margaritacea, was shown to require facilitation in the subalpine (seedlings survived only in treatment plots, and adults are rarely found even in lightly disturbed communities), but on the Pumice Plains at a lower elevation it is the most abundant colonizer and seemingly does not require facilitation. Thus, a species on the edge of its physiological tolerance range (as evidenced by its extremely low frequency of occurrence) may require facilitation, whereas elsewhere in its range, where it is normally abundant, it may not require facilitation.

In the same way that the relative importance of facilitation for any species may be dependent upon habitat, so may stress tolerance (Grime 1979) be dependent upon habitat. For example, research in progress by D. Chapin and the author suggests that for Epilobium angustifolium, a common colonizer on the Pumice Plains which attains its greatest frequency and abundance only in wet sites, infection by vesicular-arbuscular mycorrhizae (VAM) fungi (Hayman 1983) may play a key role in determining pattern of establishment. Individuals of E. angustifolium are frequently very small in stature when growing on dry pumice away from wet sites, and are not infected by VAM fungi. Yet individuals from adjacent clearcuts are heavily infected and are not confined to wet sites. Therefore it is possible that E. angustifolium can tolerate some drought stress provided that VAM infection is present; without infection it is more restricted to wet sites. Here, stress as perceived by a species is conditioned by additional factors.

Third, it is important to distinguish between the true mechanism of facilitation, which results directly from habitat modifications brought about by colonizing plants, from that of habitat modifications that occur as a result of physical events such as erosion and atmospheric deposition of organic material and nutrients. These events are not directly related to the actions of colonizing species, yet they may have effects similar to that of facilitation. i.e. providing "safe sites" (Harper 1977) for species invasions into habitats otherwise unsuitable for seedling establishment. An example of such physical habitat modification may be found on the Pumice Plains, where the rate of plant invasion is greatly accelerated in areas of streams, moist gullies, and seepages. Research in progress by W. Morris, D. Chapin, and the author suggests that germination of *Anaphalis margaritacea* and *Epilobium angustifolium* on the Pumice Plains increases in sites of high soil moisture and large (3-5 cm) diameter pumice, in comparison to drier sites with small (1-2 cm) diameter pumice. Presumably, the larger diameter pumice creates a more favorable microenvironment for germination and early seedling growth through increased shading and resultant higher moisture regime.

Fourth, facilitation may act in a density-dependent manner. Whereas colonizing plants at low to intermediate densities may facilitate the invasion of seedlings by providing ameliorated environmental conditions, high densities of colonists may inhibit invasion by increased competition. Del Moral and Wood (1986) found some evidence for this effect in fully recovered subalpine meadows. Research in progress by W. Morris and the author suggests that this phenomenon may also be occurring in patches of the nitrogen-fixing species Lupinus lepidus on the Pumice Plains. Few seedlings of either Anaphalis margaritacea or Epilobium angustifolium survive in high density (60-100% lupine cover) patches, in comparison to adjacent barren control sites, but many seedlings survive in lower density (30-50% cover) patches.

The importance of facilitation--or physical habitat amelioration--in initiating and accelerating succession in barren areas is perhaps best put into context by comparison with other habitats on the volcano where some organisms did survive the eruption. In many of these areas, including subalpine meadows and forest clearcuts that received only light deposits of airfall tephra, recovery of vegetation has been relatively rapid (del Moral 1983, Franklin et al. 1985, Antos and Zobel 1985) due to the growth of herbaceous species rooted in pre-eruption soil--part of the "biological legacy" of these habitats (Franklin et al. 1985). In stark contrast, both the subalpine lahars and the Pumice Plains remain, in general, sparsely colonized. This comparison suggests that when these barren habitats become colonized to a greater degree, and physical changes accrue, then rate of recovery will greatly accelerate. This hypothesis can be tested, particularly on the Pumice Plains, by continued monitoring of plant establishment in permanently marked grids, where rapid increases in species richness and abundance are expected in those plots already possessing some colonists.

A situation analagous to the above scenario on Mount St. Helens may be found on the semi-arid volcanic Isla Fernandina in the Galapagos Islands, where much tephra was ejected during an eruption in 1968. Hendrix (1981) sampled colonizing plants nine years after this eruption and found that only a few species of composites and grasses had become established in areas of tephra several meters deep, usually in erosion gullies. By contrast, where plants were buried but not killed, resprouting of perennial rhizomatous herbs resulted in nearly complete vegetation cover in just nine years.

The role of seed dispersal has figured prominently throughout this dissertation. This area of plant ecology is greatly in need of more focused research. Other biological disciplines, such as population genetics, have long recognized the importance of gene flow (via pollen or seeds) in both empirical and theoretical studies of population structure. It is now time for plant community ecologists, particularly those working on succession, to explicitly incorporate dispersal into their conceptual framework and field methodology. For example, Marks and Mohler (1985) steam-sterilized plots in a New York old field to remove the seed bank, and monitored succession relative to sterilized-reseeded control plots over two years. They found that invasion of sterilized plots was extremely slow despite the proximity of abundant goldenrod in the surrounding field, and concluded that dispersal rates were limiting seedling establishment. McEvoy and Cox (1987), working in the Oregon Coast range, found that most seeds of the ragwort <u>Senecio jacobaea</u>, a wind-dispersed weed, traveled less than six meters even when the surrounding vegetation was mowed to enhance seed movement. They remarked that, in general, "more is known about what dispersal ought to do than what dispersal can do". On Mount St. Helens I showed that the floristic similarity between colonizing plants on the Pumice Plains and the immigrant seed rain was quite good, but that neither flora contained many individuals or species of the eventual community dominants, trees. Thus I hypothesized that establishment of trees is probably limited by seed availability, since most of the other species in the seed rain do establish somewhere on the Pumice Plains. This hypothesis can now be easily tested experimentally, but the hypothesis itself was constructed only because seed immigration rates were estimated.

Is succession predictable in any of these barren habitats? Two components of predictability should be distinguished: a) the rate of succession, or the time necessary to attain the value of some community or structural parameter such as percent cover; and b) the species composition of particular stages; when stages are linked in temporal sequence then this component is referred to as succession "direction" or "pathway". In subalpine mudflows, the early primary succession process should lead to considerable heterogeneity both within and among successional stages. This patchiness is not necessarily a consequence of species assortment along environmental gradients, but rather of limited dispersal, low frequency of efficient (i.e., stress tolerant) colonizers, rare colonization events, yearly changes in precipitation and temperature (see Reynolds and Bliss 1986), and such geomorphological habitat modifiers as erosion. For example, Danthonia intermedia sometimes occurs in dense swards in Butte Camp meadow communities, but only a few individuals are present at Pine Creek. Yet this species was among the five most successful colonists in test gardens at Pine Creek. Was this species common at Pine Creek before the eruption, where there is some evidence (del Moral and Wood MS) that selective extinctions have occurred? If so, how much time will elapse before it regains its former stature in the plant community? Examples such as this indicate that predictability of succession direction will be difficult.

Del Moral and Wood (MS) used several techniques, including ordination, to analyze species changes as recorded yearly since 1980 in permanent plots representing nearly all subalpine disturbance types, including lahars. Their results showed that there is much variation in species composition both among plots within a given habitat as well as among habitats. They concluded similarly that the ability to predict the direction of succession on Mount St. Helens is, at present, weak. Stochastic events such as the dispersal of a single seed from a tolerant species, or the chance survival of an adult, will influence strongly the early phases, and may have long-term repercussions. Other biological influences such as herbivory may also influence the direction of succession at particular sites. Research in progress by M. Andersen and the author indicates that herbivory by elk (*Cervus canadensis*) on flower and seed heads of *Aster ledophyllus* at Pine Creek greatly lowers *Aster* seedling recruitment at this site, and thus may strongly affect community structure since *Aster* is an important species in the community at Pine Creek.

As for prediction of succession rate, the large number of species that had seedling survivorship significantly enhanced in the facilitation experiment (the "facultative facilitation" group) suggests that rate of succession will also be a function of the degree of early, often chance, colonizations. Rate is therefore only weakly predictable at this early stage, but is expected to increase sharply as early colonists alter the environment.

This dissertation has emphasized the importance of such ecological variables as distance of seed dispersal, location of source seed pools, and position of environmental "safe sites" such as gullies and wet areas in relation to source pools. To incorporate these aspects into conceptual and analytical models of succession requires a spatial approach to modeling succession. Such spatially structured models are presently little used in succession studies (Loucks 1981), partly because of their difficult and computer-intensive algorithms, but as the availability of powerful microcomputers continues, so should their use increase. The best simulation models of forest succession such as FORET and JABOWA (Shugart 1981) follow species development in small plots according to specific and well-defined rules of growth, shade response, and crowding. But because they lack spatial structure, they consequently do not permit inclusion of habitat variability, dispersal rates, or species invasions as influenced by proximity to seed source. As a result, they lose generality, especially when ecosystems other than forests are considered. The data and analysis presented in this dissertation point strongly to the need for succession models that explicitly incorporate spatially arrayed variables.

Interpreting the complexity of the succession process on Mount St. Helens promises to test both theories of succession and the patience of investigators. However, I have shown that by employing a combination of sampling and experimental methodology, it is possible to achieve at least a partial understanding of the mechanisms driving primary succession, and to clarify the meaning of some fundamental ecological concepts. The value of perturbation experiments, whether through seed additions or habitat alterations, was clearly demonstrated. Continued monitoring of permanent plots will eventually support or refute several hypotheses and assertions made in this dissertation. Disturbance is an integral factor in the development of all ecosystems, and uncovering the mechanistic basis of ecosystem response to disturbance is a task of great importance to both theoretical and applied ecology. This dissertation approaches that task and suggests directions for future work.

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APPENDIX A

RESULTS OF SEED VIABILITY TESTS

Species	Growth Characteristics
Achillea millefolium	Erect, multiple stems
Agoseris aurantiaca	Erect, single stem
Agrostis diegoensis	Tillering grass
Anaphalis margaritaceae	Erect, single stem
Antennaria microphylla	Rosette
Aster ledophyllus	Erect, multiple stems
Carex rossii	Bunch graminoid
Danthonia intermedia	Bunchgrass
Eriogonum pyrolifolium	Rosette
Hieracium albiflorum	Tall erect, single stem
Hieracium gracile	Small erect, single stem
Juncus parryi	Bunch graminoid
Lupinus latifolius	Deciduous tall
Lupinus lepidus	Evergreen low
Luetkea pectinata	Low spreading
Lomatium martindalei	Small, several stems
Penstemon cardwellii	Low spreading
Polygonum newberryi	Deciduous tall
Sitanion jubatum	Bunchgrass
Stipa occidentalis	Bunchgrass
Spraguea umbellata	Rosette
Trisetum spicatum	Bunchgrass

[1] Values in parentheses are number of replicate petri dishes and number of seeds in each dish.

[2] If "yes", then seed was not sorted prior to viability tests. If "no", then damaged or aborted seeds were removed prior to tests.

[3] Overall means are computed from means of 5 batches of 10 seeds each; standard deviation in parentheses is based on 4 degrees of freedom.

Appendix A (continued). Right-hand extension to first page.

Percent Viability[1]	Population Viability Estimate?[2]	Germination Preconditions	Seed Mass[3] (mg)
92 (2,60)	Yes	a	0.176 (0.025)
68 (2,50)	No	b	2.10 (0.116)
81 (2,50)	Yes	a	0.140 (0.015)
82 (2,50)	Yes	b	0.042 (0.003)
75 (2,50)	Yes	b	0.075 (0.003)
77 (2,50)	No	b	2.12 (0.228)
55 (2,25)	No	c, d?	0.86 (0.027)
84 (2,50)	Yes	a	1.50 (0.034)
70 (2,25)	No	c	3.13 (0.172)
73 (2,25)	No	a	0.300 (0.025)
72 (2,25)	Yes	a	0.184 (0.022)
55 (2,50)	Yes	b	0.052 (0.003)
77 (2,50)	No	c,d	17.34 (1.014)
65 (2,25)	No	c,d	4.87 (0.251)
60 (2,50)	Yes	a	0.046 (0.020)
90 (2,100)	Yes	c	7.94 (0.281)
68 (2,50)	Yes	b	0.465 (0.024)
72 (2,50)	Yes	c	9.25 (0.136)
87 (2,40)	Yes	a	4.88 (0.188)
76 (2,50)	Yes	a	1.55 (0.069)
60 (2,25)	Yes	c	0.360 (0.038)
68 (2,50)	Yes	a	0.386 (0.053)

[a] None, although possibly time for after-ripening
[b] Cold-moist stratification necessary for highest yield
[c] Cold-moist stratification obligatory, 2-3 months
[d] Scarification may overcome obligate stratification

VITAE

DAVID MAHLON WOOD

Date and Place of Birth: 24 January, 1952
Blue Island, Illinois

EDUCATION	PhD Plant Community Ecology, University of Washington, Seattle, WA, 1987. MA Biology, California State University, Fresno, CA 1982. BA Zoology, University of California, Davis, CA, 1975.
GRANTS	Northwest Science Association, 1983. National Science Foundation Dissertation Improvement Award, 1985.
PUBLICATIONS	Wood, D.M., and R. del Moral. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. Ecology, in press.