

Primary succession trajectories on a barren plain, Mount St. Helens, Washington

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Abstract

Questions: Have predictable relationships between environmental variables and vegetation developed in primary succession following a volcanic eruption? Has the rate of succession changed? Have vegetation trajectories converged or diverged?

Location: The Abraham Plain of Mount St. Helens, Washington, USA (46°12'42"N, 122°08'27"W, elevation 1360 m), was sterilized in 1980 by a blast, scoured by lahars and buried by pumice.

Method: We monitored 400 100 m² contiguous permanent plots annually (1988–2008), and classified each plot from every year into ten community types (CTs). We characterized the terrain by topography and surface features. Redundancy analysis assessed relationships between vegetation and possible explanatory variables, which included sample location. We used detrended correspondence analysis (DCA) to assess successional rates and trends.

Results: Relationships between species composition and explanatory variables were only significant after 1996, when position and presence of rills became significant. By 2006, explained variation remained low (13%) but significant. Species accumulated slowly, restricted by stress and isolation. Changes in mean DCA position slowed. Composition shifted from pioneer to persistent species and vegetation became more stable with time. Species accumulated for two decades and then stabilized, while cover has continued to increase. Diversity increased and then declined slightly as dominance developed and pioneer species became less common.

Conclusions: We demonstrate weak but increasingly predictable trends in species composition using environmental variables. The rate of succession slowed and trajectories formed a reticulate network of transitions dominated by divergence. Convergence was not evident because vegetation responded distinctively to minor topographic features that allowed alternative stable communities to develop.

Keywords: Community assembly; Convergence; Divergence; Permanent plots; Rate of succession; Redundancy analysis; Restoration; Stochastic assembly; Succession network.

Nomenclature: U.S.D.A. NRCS (2009; Appendix S1).

Introduction

One goal of the study of succession is to assess how vegetation develops in response to explanatory environmental variables. Studies of succession in severe habitats suggest that the control of succession shifts from stochastic events to predictable causes (Baasch et al. 2009), but this shift is poorly understood and rarely documented directly. Several succession trajectories are probable during early primary succession when competitive interactions are weak.

Early in primary succession, landscape factors that influence dispersal may be the only predictors of plant patterns (Prach & Rehoukova 2006). This can produce variable patterns in composition with respect to topography (Felinks & Wiegand 2008). Rarity of seedling establishment and extreme weather events can obscure predictable pattern. Therefore, variability of early primary succession vegetation is expected (Robbins & Matthews 2009) because similar sites that receive different colonists often follow multiple trajectories.

While the response of a species to one environmental factor might be predictable, vegetation patterns are less tractable due to complex, interdependent species responses to environmental factors. Variables that are often related to species patterns include soil properties that favour species differentially, favourable microsites and biotic interactions (del Moral 2009a). The effects of such factors should increase with time because, as dispersal limitations ease, more biomass can produce stronger interactions and relationships between topography, or nurse plants can become more evident (but see Walker et al. 2006).

A successional trajectory describes vegetation change; these were once thought inevitably to be linear, convergent and predictable (Pickett et al.

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2009). Now ecologists recognize that vegetation can diverge or follow intricate temporal braids in response to stochastic processes, contingencies and landscape factors.

The vegetation of most new surfaces on Mount St. Helens has developed markedly since the massive eruption of 1980, but on the east slope vegetation remains sparse. Slow primary succession on this barren plain offers a superb chance to evaluate relationships between environmental factors and vegetation at different stages of development. We ask: has a more predictable relationship between environmental variables and vegetation developed over time; has the rate of succession changed as species accumulate; and have trajectories converged or diverged?

Methods

Study site

Abraham Plain, a barren, nearly level site 4 km east of the cone of Mount St. Helens, is centered at 46°12'42"N, 122°08'27"W, mean elevation 1360 m. It received three catastrophic volcanic impacts in rapid succession on 18.05.1980. The lateral blast removed all soil and melted ice fields to produce massive lahars that scoured the site (Swanson & Major 2005). Pumice then smothered the landscape. Pumice rocks have decomposed to gravel and erosion has carved gullies and rills to create protected microsites. Isolation from surviving vegetation, few animal dispersal vectors and winds that direct seeds away from barren sites all restricted colonization. Establishment was constrained by drought stress and infertility.

Vegetation sampling

Errors using chronosequence approaches can accrue when multiple trajectories remain unrecognized. Using permanent plots mitigates the potential for such errors (Johnson & Miyanishi 2008). In 1988, we established 400 contiguous 10 m × 10 m plots (a 10 × 40 grid). We estimated species cover with this index: 1 = <6 individuals; 2 = 6 to 20 individuals; 3 = >20 individuals or cover of 0.25 m² to 0.5 m²; 4 = cover >0.5 m² to 1 m²; 5 = >1 m² to 2 m²; 6 = >2 m² to 4 m²; 7 = >4 m² to 8 m²; >8 m² recorded directly (Wood & del Moral 1988). R. del Moral determined cover from the vertical projection of the canopy of each species annually between 1988 and 2008.

Explanatory variables

We estimated percentage cover of topographic (smooth, rill and gully) and surface (rock, pumice and sand) features in each plot. Rills are narrow, with gentle slopes, and have not exposed the original surface. Gullies are more than 1-m wide with steep slopes and have reached the original surface. Categories were as follows: For smooth, 0 = <20% cover; 1 = 21–50% cover; 2 = 51–90% cover; 3 = >90% cover. For rills, 0 = none; 1 = 1–5% cover; 2 = 6–10% cover; 3 = >10% cover. For gully, 0 = none; 1 = 1–10%; 2 = 11–20% cover; 3 = >20% cover. For rocks, 0 = none; 1 = 1–2% cover; 2 = 3–5% cover; 3 = >5% cover. For pumice, 0 = <80% cover; 1 = 81–90% cover; 2 = 91–97% cover; 3 = >97% cover. For sand, 0 = 0–3% cover; 1 = 4–6% cover; 2 = 7–10% cover; 3 = >10% cover. Position was defined by *x* (north–south) and *y* (east–west) grid coordinates.

Analyses

We calculated species richness, plot cover index, Simpson's dominance [$D = 1 - \sum p_i^2$] and Shannon diversity ($H' = [-\sum p_i \log p_i]$), where p_i is the proportion of the cover index represented by the i th species, from the cover index of each species (MjM Software Design, Glendon Beach, OR, US). We classified all plots in each year into community types (CTs) with flexible sorting (an effective space-conserving group-linkage method that employs $\beta = -0.25$ to limit chaining) using the Euclidean distance between samples (MjM Software Design). The 6464 samples formed a dendrogram that we divided into 10 CTs, recognized when members shared at least 50% of the information. Large differences in species richness distort dendrograms (Clifford 1976), so divisions occurred at different fusion levels. We used multiple response permutation procedures (MRPP; MjM Software Design) to assess validity of the CTs. MRPP calculates a weighted mean within-group distance and a T -value that describes the distinctiveness of the groups. A (0 to 1.0) by describing group homogeneity compared to a random classification. We formed six habitat types (HTs) from the topographic and surface variables using the same classification approach as for species.

Recognizing that succession has encompassed only early primary succession, we divided the CTs into four stages. For convenience, these are: pioneer, early, mid- and late seral. The categories were based

on the dispersal, growth form and longevity of dominant species (Appendix S1).

After 1990, annual species turnover was low, so linear methods could be applied (Legendre & Anderson 1999). We used redundancy analysis (RDA; Lepš & Šmilauer 2003; CANOCO, DLO-Agricultural Mathematics Group, Wageningen, NL) to explore the relationship between species composition (index values) and explanatory variables in 1990, 1993, 1996, 1999, 2003, 2006 and 2008. Species composition in each of these years was regressed with explanatory variables to create fitted species scores. We applied principal components analysis to these values to produce canonical plot scores. RDA then formed linear equations to predict the position of plots. We assessed variation by comparing the result to a null model (2000 random trials). The regression coefficient of each variable with each RDA axis estimated how well variables predicted plot position, determined by a *t*-value ($df = 400 \text{ samples} - 8 \text{ variables} - 1 = 391$). The surplus species variation suggested the importance of unmeasured variables, sampling error and stochastic effects.

Spatial pattern of CTs was determined by comparing the inter-plot distances of a given CT to the distances between *N* random plots and the nearest plot of that CT. Adjacent plots were 0 distance; larger spacings were calculated by Euclidean distance in grid units. The observed mean between-plot distance was compared by *t*-test to that determined from the hypothesis of random distribution.

We used Statistix 9 (Analytical Software, Tallahassee, FL, US) to conduct statistical analyses. Comparisons of cover index values among species in the CTs and among DCA scores of CTs were made with one-way ANOVA or repeat measures ANOVA, as appropriate, each followed by a Bonferroni test of differences. We used χ^2 association tests to relate community patterns to surface patterns. We used Axum 7 (Mathsoft, Insightful Corporation, Seattle, WA, US) to produce graphs and generate random numbers.

Results

Vegetation

Succession on Abraham Plain has been leisurely. By 2009, vegetation remained sparse (Fig. S1) and percentage cover was one-quarter of that observed on a similar grid on the north side of Mount St. Helens, with three-quarters as many species (del Moral 2009b).

The composition of each of the 10 CTs was distinctive (MRPP: $A = 0.278$; $T = -1772$; $P < 0.0001$; Table 1). Each pair-wise comparison by MRPP showed that CTs differed significantly. Pioneer CTs vanished by 2001 (Fig. 1a); they had lower richness (Fig. 1b) and cover indices (Fig. 1c) than did persistent CTs. H' (Fig. 1d) increased with time and was higher in persistent CTs. Each plot supported a mean of 4.95 ± 1.06 CTs between 1988 and 2008. We characterize CT composition below. The number of plots within which the CT ever occurred is in parentheses.

There were two pioneer community types. CT-A (*Anaphalis-Chamerion-Hypochaeris*; $n = 397$ of 400 plots) had sparse cover of a few pioneer species, each with long-distance wind dispersal, herbaceous life form and short life span (Appendix S1). As cover increased, plots developed into other CTs. CT-B (*Lupinus lepidus*; $n = 11$) established first in seven plots near surviving vegetation and was characterized by *L. lepidus* with sparse *Anaphalis* and *Carex mertensii*. We recognized three early seral CTs that always developed from other CTs and had more species and cover than did pioneer CTs. These included a few species that are more persistent. Plots characterized as CT-C (*Anaphalis*; $n = 107$) usually developed from CT-A plots. CT-D (*Anaphalis-Cistanthe-Agrostis*), $n = 319$) was the main nexus through which pioneer CTs developed. It had lower richness and cover than did persistent CTs. CT-E (*Anaphalis-Chamerion*; $n = 208$) had more *Hypochaeris*, *Luetkea* and *Racomitrium* than did CT-D.

Transitions to persistent CTs involved increasing species richness and cover and greater dominance by longer-lived, often woody, species. We characterized two persistent CTs as mid-seral. Most common species have less effective dispersal than those in pioneer CTs. The richness of CT-F (*Penstemon-Agrostis-Cistanthe*; $n = 338$) peaked when it contained both pioneer and seral species. H' declined as the vegetation matured. CT-G (*Penstemon-Agrostis-Juncus*; $n = 75$) retained *Anaphalis* and developed more of the persistent species (e.g. *Luetkea* and *Racomitrium*) than did CT-F. Three late-seral CTs may represent divergent trajectories towards mature vegetation. CT-H (*Penstemon-Agrostis-Salix*; $n = 266$) also had *Juncus*, *Cistanthe* and *Luetkea*. Common species are long-lived and several are shrubs. CT-H had more species, higher cover and greater diversity than other CTs. It had changed little since 2004. CT-I (*Penstemon-Agrostis-Cistanthe*; $n = 125$) also supported *Juncus* and mosses. Richness, cover and H' were intermediate among persistent CTs. CT-J (*Penstemon-Agrostis-*

Table 1. Structure and mean cover index in 10 community types (CTs). Numbers in parentheses after species are occurrences (plots×years). Values in bold indicate dominant species (high cover index) in that CT. Each structural variable differed significantly among CTs (one-way ANOVA $P < 0.001$; values with same superscript fall within the same group as determined by Bonferroni comparisons). Species cover index means also differed significantly (ANOVA, $P < 0.001$), but patterns were too complex to display grouping patterns. CTs and species were each arranged in order of their DCA scores.

| Structure | CT-A | CT-B | CT-C | CT-D | CT-E | CT-F | CT-G | CT-H | CT-I | CT-J |
|---------------------------------------|--------------------|--------------------|--------------------|---------------------|---------------------|----------------------|---------------------|---------------------|----------------------|---------------------|
| Richness | 3.7 ^a | 3.1 ^a | 5.3 ^b | 9.5 ^d | 8.9 ^c | 10.9 ^c | 12.5 ^f | 12.7 ^f | 11.1 ^c | 9.1 ^{cd} |
| Cover (sum index scores) | 5.2 ^a | 3.8 ^a | 7.0 ^a | 15.9 ^c | 13.6 ^b | 24.2 ^d | 32.1 ^g | 29.8 ^f | 28.1 ^f | 23.8 ^c |
| Dominance | 0.516 ^a | 0.575 ^a | 0.734 ^b | 0.851 ^{cd} | 0.840 ^c | 0.871 ^{def} | 0.890 ^{ef} | 0.890 ^{ef} | 0.877 ^{def} | 0.843 ^{cd} |
| H' | 1.001 ^a | 0.999 ^a | 1.512 ^b | 2.078 ^d | 2.008 ^{cd} | 2.204 ^c | 2.347 ^f | 2.361 ^f | 2.227 ^c | 2.001 ^c |
| Number of plots×years | 1558 | 21 | 108 | 877 | 444 | 1289 | 219 | 1334 | 421 | 495 |
| First year observed | 1988 | 1988 | 1988 | 1990 | 1989 | 1992 | 1996 | 1994 | 1997 | 1997 |
| Last year observed | 2000 | 1991 | 1998 | 2001 | 2000 | 2008 | 2008 | 2008 | 2008 | 2008 |
| <i>Hypochaeris radicata</i> (3011) | 0.444 | 0.000 | 0.491 | 1.197 | 1.380 | 0.497 | 0.365 | 0.412 | 0.214 | 0.040 |
| <i>Anaphalis margaritacea</i> (5784) | 1.557 | 0.810 | 1.713 | 3.304 | 3.459 | 2.370 | 2.717 | 2.147 | 1.337 | 0.802 |
| <i>Chamerion angustifolium</i> (4712) | 0.514 | 0.191 | 0.593 | 1.911 | 1.803 | 1.442 | 0.991 | 1.077 | 0.691 | 0.513 |
| <i>Hieracium albiflorum</i> (3907) | 0.336 | 0.143 | 0.398 | 0.904 | 0.930 | 0.929 | 0.753 | 0.813 | 0.411 | 0.293 |
| <i>Lupinus lepidus</i> (248) | 0.007 | 1.667 | 0.028 | 0.051 | 0.220 | 0.076 | 0.383 | 0.021 | 0.088 | 0.036 |
| <i>Lupinus latifolius</i> (122) | <0.001 | 0.095 | 0.000 | <0.001 | 0.047 | 0.020 | 0.932 | 0.037 | 0.000 | 0.000 |
| <i>Abies</i> sp. (736) | 0.106 | 0.000 | 0.120 | 0.123 | 0.124 | 0.087 | 0.032 | 0.352 | 1.062 | 0.020 |
| <i>Luetkea pectinata</i> (4075) | 0.182 | 0.095 | 0.157 | 0.691 | 0.916 | 1.389 | 2.078 | 2.524 | 1.981 | 1.432 |
| <i>Carex mertensii</i> (2691) | 0.128 | 0.428 | 0.046 | 0.379 | 0.373 | 0.680 | 0.827 | 1.249 | 1.057 | 0.649 |
| <i>Saxifraga ferruginea</i> (1596) | 0.045 | 0.095 | 0.083 | 0.276 | 0.253 | 0.632 | 1.082 | 1.079 | 0.456 | 0.247 |
| <i>Racomitrium canescens</i> (2498) | 0.072 | 0.000 | 0.019 | 0.243 | 0.943 | 0.421 | 2.183 | 1.080 | 1.064 | 0.990 |
| <i>Cistanthe umbellata</i> (4867) | 0.123 | 0.048 | 1.370 | 2.222 | 0.523 | 3.199 | 3.603 | 3.469 | 4.033 | 4.853 |
| <i>Agrostis pallens</i> (5060) | 0.294 | 0.000 | 0.528 | 1.331 | 0.738 | 2.855 | 3.457 | 3.271 | 3.924 | 4.301 |
| <i>Eriogonum pyrolifolium</i> (653) | 0.016 | 0.000 | 0.000 | 0.071 | 0.057 | 0.120 | 0.338 | 0.281 | 0.591 | 0.059 |
| <i>Juncus parryi</i> (4421) | 0.116 | 0.191 | 0.250 | 1.008 | 0.550 | 2.066 | 4.064 | 2.633 | 3.565 | 3.465 |
| <i>Penstemon cardwellii</i> (4489) | 0.195 | 0.000 | 0.278 | 0.520 | 0.484 | 3.165 | 4.489 | 3.591 | 4.197 | 4.216 |
| <i>Salix sitchensis</i> (1858) | 0.037 | 0.000 | 0.000 | 0.140 | 0.188 | 0.216 | 1.237 | 3.144 | 0.271 | 0.073 |
| <i>Carex microptera</i> (1723) | 0.035 | 0.095 | 0.065 | 0.161 | 0.091 | 0.412 | 0.763 | 0.752 | 0.644 | 1.372 |
| <i>Polytrichum juniperinum</i> (1133) | <0.001 | 0.000 | 0.000 | 0.047 | 0.093 | 0.182 | 0.182 | 1.601 | 2.183 | 0.168 |

Cistanthe-Juncus; $n = 145$) also had substantial *Luetkea* and *Racomitrium*. Pioneer species were uncommon and taller woody species (*Abies* spp. and *Salix*) absent. Richness, cover and diversity were all least of the persistent CTs.

Species patterns

Many species increased in cover (Fig. 2; Fig. S2) during the study but cover of pioneer species declined after the mid-1990s. In 2008, 10.93 species/plot were wind-dispersed, while only 0.11 species/plot were animal-dispersed (Appendix S1). Pioneer species have effective long-distance dispersal mechanisms, and while seral species are also wind-

dispersed, their dispersal abilities are more limited (Fuller & del Moral 2003). *Penstemon* and *Agrostis pallens* expanded to occupy all plots, while *Juncus parryi* and *Cistanthe umbellata* occurred in most. *Luetkea* increased steadily, but by 2008 it appeared to be stable. *Salix* increased gradually and sporadically. *Racomitrium* occurred in four plots in 1988, while *Polytrichum* did not occur until 1995. *Carex mertensii* and *C. microptera* were widely distributed, and occasionally abundant; both occur on half the grid. *Saxifraga*, once common, declined in 2008, but this may be associated with dry summer conditions.

Relative cover clearly shows the contrast between pioneer and persistent species (Fig. 3; Fig S3).

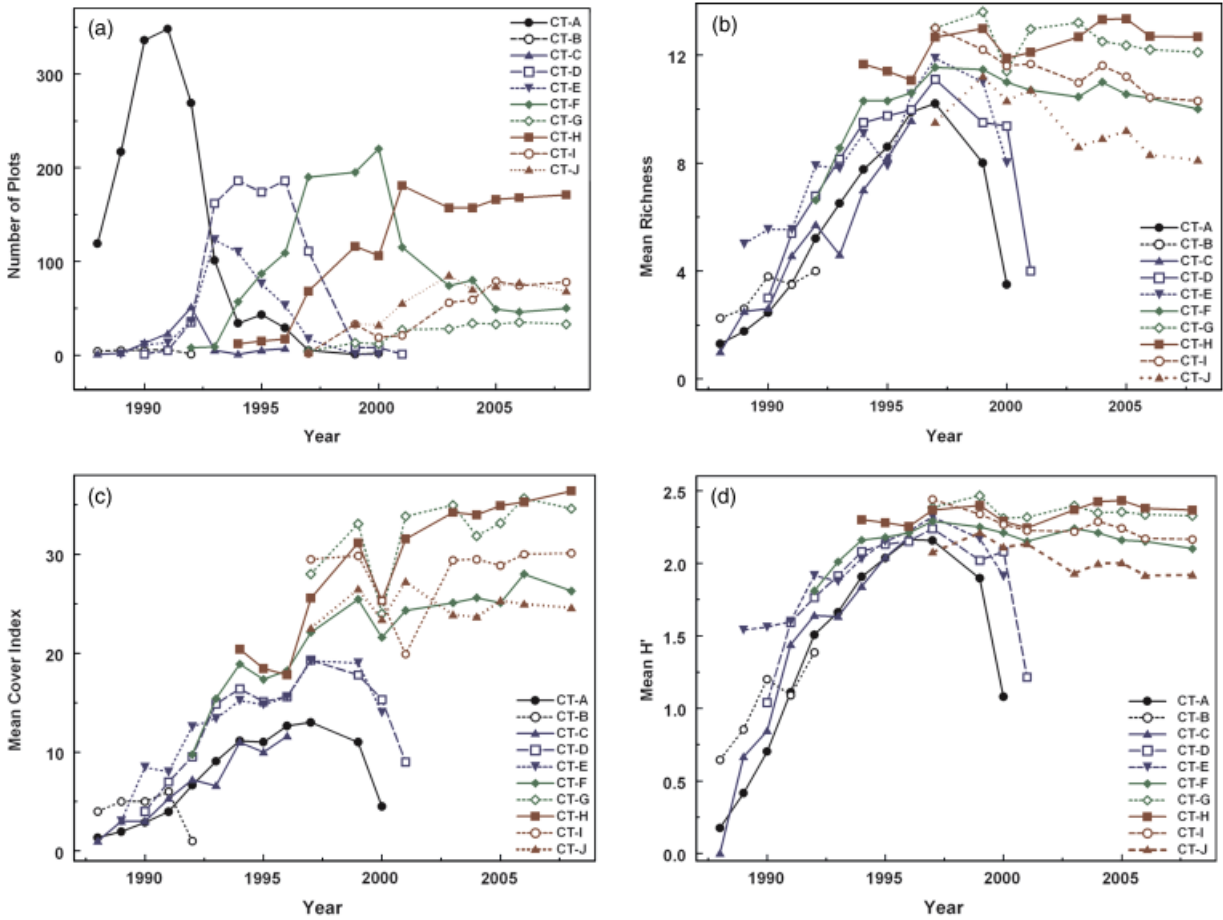


Fig. 1. Structure of CTs from 1988 to 2008. (a) Number of plots. (b) Mean species richness. (c) Mean cover index. (d) Mean diversity index (H').

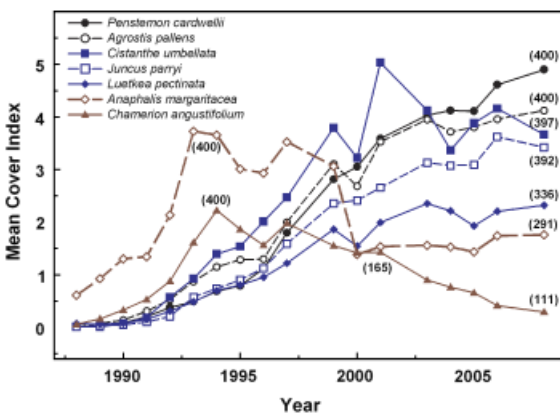


Fig. 2. Changes in mean cover index for abundant species.

Species such as *Penstemon*, *Agrostis*, *Juncus parryi*, *Carex* spp. and *Luetkea* increased across the CTs when listed by their first appearance. These species are long-lived, with strong vegetative growth.

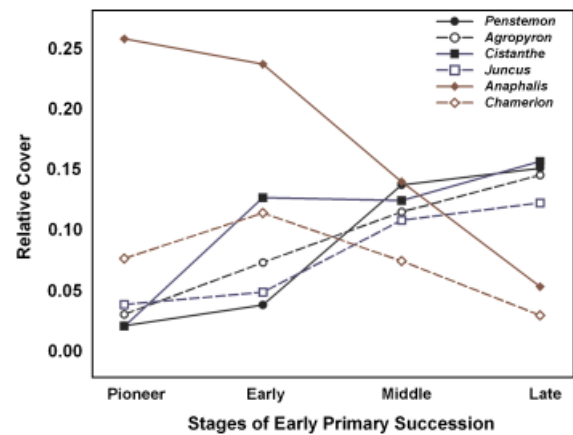


Fig. 3. Changes in relative cover (proportion of total cover in the sample) of common species in the four stages of early primary succession. The first four species are persistent; the last two are pioneer species (defined in Appendix S1).

In contrast, pioneer species soon peaked and then declined.

Habitat relationships

We could use only position, topography and surface conditions as explanatory variables in RDA. Explained variation was low, but increased four-fold from 1990 to 2006 (Table 2). In 1996, we obtained the first significant result when the y-axis (possibly related to distance from survivors) and rill fraction became significant. By 2006, smooth surface also contributed, but topography did not influence the vegetation.

We recognized six habitat types (Table 3). A five persistent CT (Table S1) by six HT χ^2 test was significant ($\chi^2 = 93.5$, $P < 0.0001$; $df = 20$). CT-F (*Penstemon-Agrostis-Cistanthe*) was more common in rills; CT-G (*Penstemon-Agrostis-Juncus*) was more common in gullies; CT-H (*Penstemon-Agrostis-Salix*) tended to avoid smooth plots and was more common in plots with rills or gullies; and CT-J (*Penstemon-Agrostis-Cistanthe-Juncus*) tended to occur in smooth plots, but avoided rills or gullies.

Table 2. Summary of redundancy analysis results using position, topography and surface variables on the grid. The alternate plots sampled in 2007 and 2008 were analysed separately. Percentage variation = how much of species variation is explained by variables; F-values = significance level of Axis 1; trace = percentage variance on Axis 1. *Correlations > 0.5

| Years | Percentage variation | F-value | Trace | Correlated variables* |
|-------|----------------------|---------|-------|-----------------------|
| 1990 | 3.4 | 7.07 | 1.57 | – |
| 1993 | 6.5 | 12.8 | 3.40 | – |
| 1996 | 7.9 | 17.8 | 4.20 | y, rill |
| 1999 | 10.9 | 33.1 | 5.98 | y, rill |
| 2003 | 11.2 | 33.8 | 6.16 | y, rill |
| 2006 | 12.5 | 39.0 | 6.98 | y, rill, flat |
| 2008 | 12.2 | 33.5 | 6.54 | y, rill, flat |

Table 3. Mean value of characteristics of six habitat types (HT). HTs differed significantly for each terrain characteristic ($P < 0.0001$, one-way ANOVA, followed by Bonferroni tests for differences among means. Values with same superscript fall within the same group).

| Terrain | HT-1 (n = 128) | HT-2 (n = 28) | HT-3 (n = 37) | HT-4 (n = 64) | HT-5 (n = 61) | HT-6 (n = 82) | F-value |
|---------|-------------------|--------------------|-------------------|--------------------|-------------------|-------------------|---------|
| Smooth | 3.00 ^a | 2.86 ^a | 2.89 ^a | 1.92 ^{bc} | 1.98 ^b | 1.80 ^c | 191.1 |
| Gully | 0.05 ^b | 0.36 ^b | 0.30 ^b | 2.03 ^a | 0.26 ^b | 2.22 ^a | 208.5 |
| Rill | 0.15 ^d | 0.29 ^{cd} | 0.57 ^c | 0.61 ^c | 2.38 ^a | 1.17 ^b | 114.1 |
| Rock | 0.00 ^d | 1.00 ^{bc} | 1.32 ^b | 0.80 ^c | 0.62 ^c | 2.16 ^a | 146.6 |
| Sand | 0.00 ^b | 0.00 ^b | 0.19 ^b | 0.02 ^b | 0.10 ^b | 0.90 ^a | 30.6 |
| Pumice | 3.00 ^a | 3.00 ^a | 2.00 ^c | 2.61 ^b | 2.57 ^b | 1.28 ^d | 147.0 |

The spatial pattern displayed by the CTs reflected some environmental sorting (Fig. 4). Nearest neighbour distances, compared to the random model, suggested that CT-F formed scattered clusters (mean observed distance = 1.42, mean random distance = 2.24; $t = 2.25$; $P = 0.03$). Some plots of CT-G were confined to the eastern edge, while others were in the southwest corner, but overall it was not clustered (observed = 1.90, random = 2.43; $t = 1.90$; $P = 0.06$). CT-H was clustered (observed = 0.15, random = 0.58; $t = 4.83$; $P < 0.0001$) as was CT-I (observed = 0.52, random = 1.45; $t = 4.48$; $P < 0.0001$), concentrated on the east half of the grid. CT-J was clustered (observed = 1.19, random = 2.64; $t = 3.83$; $P = 0.002$) and concentrated on the eastern part of the grid.

Trajectories

We explored vegetation trajectories in several ways. In 1988, richness, the mean cover index (Fig. 5), H' and dominance (Fig. S4) were least. Richness increased until 1999, after which time it varied around 11 species per plot. The cover index continued to increase, while H' and dominance stabilized by the mid-1990s.

Succession began with colonization by highly vagile pioneers such as *Anaphalis*, *Chamerion*, *Hieracium* and *Hypochaeris*. Plots changed into other CTs at variable rates. While we found transitions among all CTs, some trajectories were more typical than were others (Fig. 6). The most likely trajec-

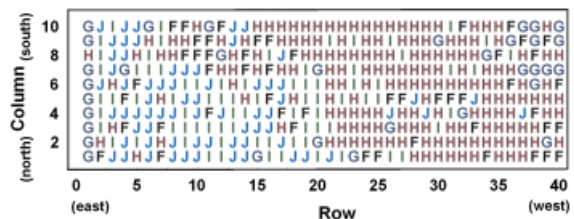


Fig. 4. Distribution of CTs on the grid in 2008.

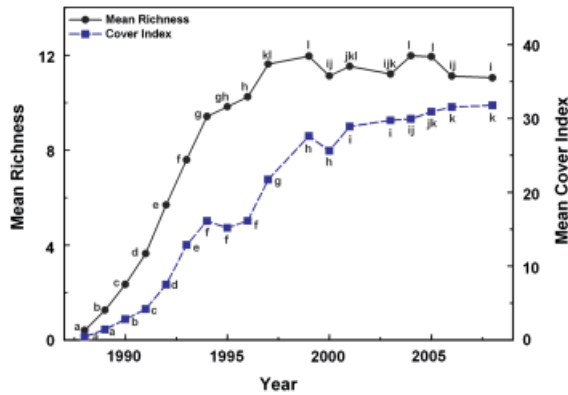


Fig. 5. Annual changes of mean species richness and mean cover index. Differences ($P < 0.05$) among measures determined by a repeat measures ANOVA, followed by the Bonferroni test. Values with the same associated letter fall within the same group of values.

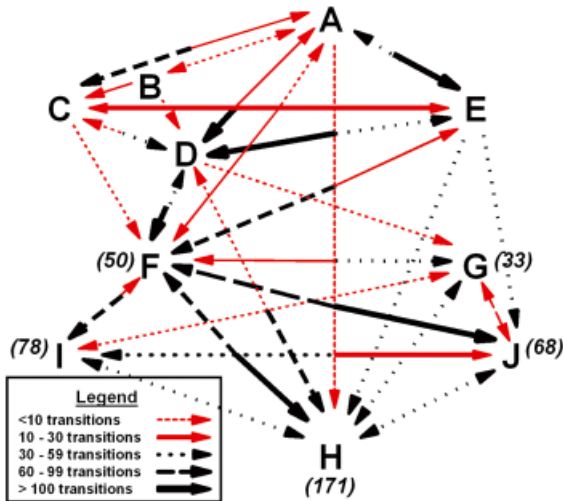


Fig. 6. Trajectories showing the number of transitions between CTs. Numbers in parentheses after persistent CTs are the number of plots in 2008. Many arrows transition near the mid-point to differentiate between transitions to and from a given CT.

jectories proceeded from pioneer plots dominated by *Anaphalis* to early seral types that had accumulated *Cistanthe*, *Agrostis* and *Luetkea*. These developed further into mid-seral communities when *Penstemon* became dominant and *Juncus* became widespread, or they developed directly into late seral communities dominated by *Penstemon* and *Agrostis*. In 2008, some mid-seral CTs persisted, but most plots were in a late-seral community that had changed little since 2005. For each annual interval 1988 to 2008, a plot could persist in a CT, progress to a more developed one, or regress to an earlier stage. There were 301 retrogressions and 1014 progressions. The

Table 4. Number of continuous years (standard deviation) for which each CT persisted. Differences among means are significant (one-way ANOVA, $P < 0.0001$, followed by Bonferroni tests for differences among means. Superscripts indicate membership in same group). Minimum run is one in each case.

| CT | Years | SD | Max |
|----|--------------------|------|-----|
| A | 3.29 ^b | 1.35 | 7 |
| B | 2.00 ^{ab} | 1.15 | 4 |
| C | 1.07 ^a | 0.26 | 2 |
| D | 2.38 ^b | 1.42 | 7 |
| E | 1.81 ^{ab} | 1.17 | 7 |
| F | 3.98 ^c | 2.74 | 10 |
| G | 3.91 ^c | 1.72 | 6 |
| H | 5.58 ^d | 2.56 | 10 |
| I | 4.19 ^{cd} | 1.67 | 8 |
| J | 3.78 ^c | 1.85 | 7 |

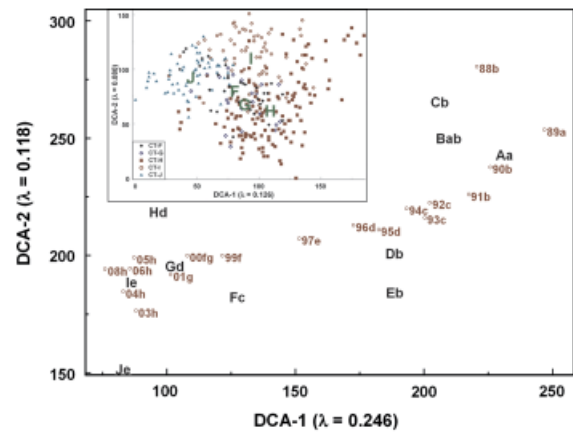


Fig. 7. Detrended correspondence analysis of plots by CT and by year. Differences ($P < 0.05$) among measures determined by ANOVA, followed by the Bonferroni test. For each set, values with the same associated letter fall within the same group of values for DCA-1 (no data for 1998 and 2002; alternate plots were sampled in 2007 and 2008). The inset is a separate DCA of plots in 2008.

five extant CTs persisted significantly longer than did the five vanished CTs (Table 4).

We clarified temporal vegetation changes using DCA (Fig. 7). Total variance (λ) was 1.59 (DCA-1 = 15.5%; DCA-2 = 7.4%). Turnover on DCA-1 was 5.3 half-changes; on DCA-2, it was 3.9. Pioneer species had high values on DCA-1; species with low DCA-1 values appeared later and were persistent. Mean DCA-1 position of the plots changed significantly between years ($r^2 = 0.637$, $P < 0.0001$; Spearman nonparametric correlation, $r = 0.79$, $P < 0.0001$). DCA-1 scores by year changed rapidly through 2001 (ANOVA: $P < 0.0001$) then slowed. DCA-2 changes ceased after 1997, but ANOVA was

significant ($r^2 = 0.206$; $P < 0.0001$; Spearman non-parametric correlation, $r = 0.25$, $P < 0.0001$). The variation in DCA-1 scores within years declined (the linear correlation of years vs. standard deviation was $P < 0.0001$, $t = 5.33$ $r^2 = 0.637$).

The mean DCA position of the 10 CTs did not reveal a single trajectory. CT-C (*Anaphalis*) was more closely associated with pioneer CTs, but was never the first CT on a plot. CT-G (*Penstemon-Agrostis-Cistanthe*) was aligned with late-seral CTs. We also conducted a DCA of 2008 plots (Fig. 7, inset). β -diversity was low, with $\lambda = 0.97$ (DCA-1 = 13.3%; DCA-2 = 8.4%; ca. 1.8 HC along DCA-1). No trajectory was evident from this analysis.

Discussion

There are so few long-term longitudinal studies of early primary succession on stressful sites because, initially, so little happens. The vegetation of the Abraham Plain remains sparse 30 years after the eruption. It has developed by interwoven successional trajectories that include plots that diverge, converge, regress and progress to form a braided succession. Neither habitat factors nor competition appears to have provided strong filtering effects on species composition, although unmeasured soil variables (e.g. moisture and nitrogen content) and factors related to stochastic colonization and establishment (cf. del Moral & Ellis 2004) may explain some of the remaining unexplained variation. The immigration seed density was low (Wood & del Moral 2000); many suitable sites appeared vacant in early years (del Moral & Bliss 1993) and several species occupied similar sites. Chance may govern such patterns. We propose that when environmental variables have only slight effects on species composition, consistent successional trajectories are unlikely to emerge. Below, we discuss questions about predictability, rate and pattern of succession on Abraham Plain that are the focus of this study.

Environment–vegetation connection

Predictable relationships between environmental variables and vegetation had developed by 2008, but they remained low. Priority effects, secondary disturbances, elk grazing and seasonal fluctuations may affect these trajectories in the future, rendering it unlikely that explained variation would become the dominant factor before forests develop.

We did not use soil factors because plants establish at a smaller scale than the plot size and it is impractical to measure such factors as moisture, in even a few plots. Although soils were young and homogeneous, it is likely that inclusion of soil factors (e.g. pH and moisture) would have improved explanatory power; based on similar studies (del Moral 2009a), explained variance might double. Topographic, surface and position factors alone did demonstrate increasing explained variance of species pattern over time, but this trend was less pronounced than in other studies. On the north slope of Mount St. Helens in 1992, only spatial factors explained any variation (15%), but after 10 yr, environmental factors dominated (28%; del Moral & Lacher 2005). Baasch et al. (2009) produced one of the very few primary succession studies to show that relationships between vegetation and explanatory variables increased over time. They too suggested that the impact of stochastic processes declined over time.

The spatial distribution of CTs suggested some environmental influence. Rills provide havens for pioneers (e.g. *Anaphalis*, *Hieracium* and *Hypochaeris*). Gullies offer protection from wind and accumulate snow, which allowed species such as *Anaphalis* and *Salix* to colonize and persist. *Penstemon* and *Juncus* were common in more exposed sites, where cover and diversity were least. In such sites, species that are less stress tolerant (e.g. *Salix*, *Polytrichum*, *Saxifraga* and *Juncus mertensianus*) were uncommon, while stress-tolerant species such as *Cistanthe*, *Juncus parryi*, *Agrostis pallens* and *Carex microptera* reached their maximum values.

Rates

Habitats with limited fertility or moisture typically have low succession rates (Donnegan & Rebertus 1999; Anderson 2007), and succession on Abraham Plain has been no exception. Mean annual DCA scores were in a single group of values. Between 1988 and 1999, these scores formed seven groups. Surrounding habitats on Mount St. Helens developed more rapidly. On an exposed lahar on the south slope, richness averaged 16 species and the cover index averaged 73 (del Moral 2009b) prior to 2008. In contrast, mean richness on the Abraham Plain in 2008 was 10.8 and the mean cover index was 31.4. The proximity to forest, more fertile soils and abundance of the N-fixing *Lupinus* may all contribute to accelerated primary succession at such sites relative to Abraham Plain.

Trajectories

Succession trajectories have been discussed thoroughly (cf. Lepš & Rejmánek 1991). When the vegetation of initially homogeneous sites develops locally distinctive characteristics, divergence occurs (Bossuyt et al. 2003). Divergent trajectories occur on many surfaces, including landslides, glacier forelands, wet slack dune vegetation, floodplains and mine tailings (Walker & del Moral 2003). Lanta & Lepš (2009) showed experimentally that differential dispersal could promote divergence when there are priority effects. Divergence may be more likely in stressful habitats when different species arrive first and where climatic factors are highly variable (MacDougall et al. 2008). Convergence describes trajectories that become more similar over time. Convergence has been assumed to result when climatic factors dominate, and there is evidence that when dispersal effects are small and competitive effects are strong, convergence to a single community does occur (van Oijen et al. 2005; Anthelme et al. 2007). Convergence is also more likely when there are few alternative stages, as on glacial forelands (Hodkinson et al. 2003; but see Robbins & Mathews 2009).

Here we show directly that early succession under stressful conditions can include trajectories that diverge, converge, regress and progress to form a reticulate succession. Our study joins a growing body of work that demonstrates the frequency of multiple trajectories in early primary succession (e.g. del Moral 2007; Prach & Hobbs 2008; Walker & del Moral 2009). Forecasting trajectories and identifying factors that limit their development is crucial to understanding community assembly mechanisms. On the Abraham Plain, persistent species gradually replaced readily dispersed pioneer species. Subtle habitat variation, annual weather fluctuation and landscape effects combined to produce communities related through a network of development and responsible to topographic variation.

The first colonists were species with excellent dispersal, but isolation allowed for only a meager seed rain; they established pioneer communities that soon developed into other CTs characterized by species with greater persistence (cf. Ejrnaes et al. 2006). Several alternative transitions were possible for most CTs, suggesting that stochastic processes initially dominated transitions. Gradually, persistent species invaded and attained dominance. Minor topographic variation affected composition somewhat, resulting in some successional transitions that are more common than others. Of annual transi-

tions between successional stages, 5.1% were regressions and 17.0% were progressions. DCA revealed no single trend among the CTs. The two mid-seral community types were central to the transition patterns, while the three late-seral CTs occurred in different directions from this centre.

It is unlikely that complete convergence will occur. Even when trees dominate, understorey vegetation is likely to retain variation initiated during early succession and maintained by topographic variation and priority effects. The understorey of forests on the south side of Mount St. Helens demonstrates such variation (del Moral & Ellis 2004). There is no evidence yet for a single target community.

Strong assembly rules are more likely to produce convergent trajectories than weak ones. While strong assembly rules may exist in mature vegetation (see Navas & Violle 2009), they appear weak on Abraham Plain and are more effective for functional types than species. One rule may be that long-lived, wind-dispersed species accumulate at the expense of short-lived pioneers. A second may be that graminoids with rhizomatous growth (e.g. *Agrostis pallens*) and prostrate shrubs (e.g. *Penstemon*) are complementary and can coexist indefinitely. A third may be that fleshy fruit-producing shrubs (e.g. *Rubus* spp., *Vaccinium* spp.) cannot establish under current conditions. Finally, although seeds of conifers and *Populus balsamifera* are common, conditions do not yet favour their development. These rules are weak and exceptions are common. The spontaneously developing vegetation of the Abraham Plain is constrained by isolation from potential colonists as well as a habitat that challenges plant growth.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Fig. S1. Abraham Plain, Sept 1980, pumice deposits over scoured bedrock; looking north towards the study site.

Fig. S2. Abraham Plain, July 2009, looking northwest across the study site.

Fig. S3. Changes in mean cover index for less common species.

Fig. S4. Relative cover (proportion of total cover in the sample) of less common species in the four stages of early primary succession. The first four species are persistent; the last two are pioneer species (defined in Appendix S1).

Fig. S5. Annual changes of mean H' and mean Simpson's dominance index. Differences ($P < 0.05$) among measures determined by a repeat measures ANOVA, followed by the Bonferroni test. Values with same associated letter fall within the same group of values.

Table S1. Structure and species composition of CTs found in 2008.

Appendix S1. Characteristics of species encountered on Abraham Plain grid.

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