Jonathan H. Titus[1], **Priscilla J. Titus**[1] and **Roger del Moral,** Department of Botany, Box 355325, University of Washington, Seattle, Washington 98195

Wetland Development in Primary and Secondary Successional Substrates Fourteen Years after the Eruption of Mount St. Helens, Washington, USA

Abstract

The eruption of Mount St. Helens deposited new substrates upon which wetlands are now developing. Furthermore, the blast damaged vegetation in wetlands surrounding the deposition area. This study describes wetlands in the blast zone north of the crater as documented 14 years after the 1980 eruption with 220 100 m^2 plots. Five wetland types were recognized in the field: moist areas, wet areas with shallow standing water, seasonal streams, permanent streams, and ponds or lakes. The variables, elevation, slope and aspect were determined; hot water springs were discriminated from cold water springs by a nominal variable, and substrate was characterized as stable or unstable. Four levels of disturbance intensity were recognized. Spatial variables, i.e., the position of wetlands on the landscape, were also used in analysis of the data.

Using TWINSPAN, we organized the vegetation into 24 wetland plant communities. Based on canonical correspondence analysis, we determined that the measured environmental and spatial variables were unimportant in structuring primary successional vegetation. The lack of a relationship between the wetland types and environmental factors in the primary successional wetland communities suggests that stochastic events, such as seed dispersal, have played a leading role in early primary succession. Vegetation within secondary successional wetlands appears to be more closely related to the wetland types and environmental variables. Thus we conclude that environmental factors were more important in structuring wetland vegetation in areas that were less impacted by the eruption than in those areas where wetlands were newly created.

Introduction

The massive 1980 lateral eruption of Mount St. Helens, Washington, destroyed, altered and created many wetland areas. New wetlands were formed in depressions within the volcanic substrates. The blast damaged vegetation in existing wetlands and blanketed vast areas with air-borne tephra. This study documents the plant communities of the many wetlands found in the blast zone north of the crater. These wetlands range from newly formed wetlands to those that were only slightly altered by the eruption. Thus, a gamut of recovery patterns occur and are analogous to those described by Grishin et al. (1996) in Kamchatka, in that primary succession, secondary succession and simple recovery from damage were documented.

Colonization by vegetation in any newly formed wetland requires successful dispersal and establishment. The chance that a propagule will reach an isolated site is low, and is constrained by distance to a source (del Moral and Wood 1993a), weather (Walton 1990, Titus and del Moral 1998), and seed dispersal ability (Stöcklin and Bäumler 1996). The chance that the propagule will lodge in a favorable microsite is determined by surface features (Tsuyuzaki and Titus 1996), the availability of nutrients and water (Stöcklin and Bäumler 1996), and other physical and biological factors. The joint probability that a propagule arrives in a suitable site at the right time must, for isolated sites, be extremely low (Walton 1990), though it increases through time. Consequently, primary succession in isolated areas can be considered strongly stochastic, i.e., subject to random events (Talling 1951, Margalef 1963, del Moral 1993), and this stochasticity may, in part, determine eventual vegetation patterns over large scales (Collins and Glenn 1990, 1991, Collins et al. 1993). In new, barren areas on Mount St. Helens, wet sites were the first to be colonized (del Moral and Wood 1986). The first immigrants were small-seeded species with high dispersal ability (e.g., *Salix* spp., *Epilobium* spp.) or spore-producing species (e.g., *Equisetum*, mosses) (del Moral and Bliss 1993).

We predict that, in early primary succession, environmental stress coupled with a limited potential colonization pool prevents a significant

---

[1] Present address: Department of Biological Sciences, University of Nevada-Las Vegas, Las Vegas, NV 89154-4004

correlation between species composition and environmental factors (Chesson and Case 1986, Davey and Rothery 1993). Alternatively, site-specific conditions could strongly influence early species composition in a consistent way (Tsuyuzaki 1997). In recovering wetlands, i.e., secondary successional, the long history of competitive rearrangement and opportunity for most available species to colonize implies that environmental conditions will constrain community composition and lead to predictable species assemblages. Thus, we hypothesize that secondary successional wetlands are more highly correlated with environmental factors than are primary successional wetlands. This study assesses the vegetation of early successional wetland communities that have assembled within the blast zone of Mount St. Helens, the relationship between these and more developed wetland communities, and the influence of environmental, spatial and stochastic factors on the vegetation.

Methods

Study Area

The lateral eruption of May 18, 1980, created a wide range of disturbance around Mount St. Helens (46°12' N, 122°11' W). The main force of the eruption was directed northwards, hence this study focuses on wetlands in the blast zone north of the crater, much of which is encompassed by the Pumice Plain and the Margaret Range (Figure 1).

The study area climate is maritime with cool, wet winters and warm, dry summers (del Moral and Bliss 1993). Information collected by the former Spirit Lake Ranger Station indicates that annual precipitation fluctuates greatly about a mean of 237 cm, drought is common during July and August, and mean temperatures range from a -4° C minimum to a 0°C maximum in January and a minimum of 7°C and a maximum of 22°C in August (Spirit Lake Ranger Station [987 m a.s.l.], Pacific Northwest River Basins Commission 1969).

Pumice was deposited over the entire study area in depths ranging from hundreds of meters near the cone to tens of centimeters at the edge of the blast zone. Where significant depositions of pumice accumulated, the resulting pumice soils are immature and extremely nutrient poor and contain very low concentrations of carbon and nitrogen (Nuhn 1987, del Moral and Bliss 1993, Titus unpubl. data).

A wide variety of wetland communities with varying levels of damage from the eruption occur within the study area. The crater, 1750-2000 m a.s.l., has several vegetated seeps in stable areas, but streams in the crater are unstable and support no vegetation. Fumeroles on the lava dome create hydric substrates where the steam condenses; these unstable substrates are infrequently vegetated (one plot only in this study). The Pumice Plain, 1150 to 1300 m a.s.l., covers 20 km^2 north of the cone and was formed by the debris avalanche, pyroclastic pumice flows, tephra deposits and later mudflows (Foxworthy and Hill 1982). Pumice Plain vegetation was described by del Moral et al. (1995) and Titus et al. (1998). Streams that dissect the Pumice Plain are either permanent or seasonal, the latter of which flows only during snowmelt. The stability of streambanks varies widely depending upon the stability of upstream tephra deposits. Many cold water springs and occasional hot water springs occur on the Pumice Plain, primarily near the north shore of Spirit Lake. The largest wetlands also occur near Spirit Lake in this same area.

Spirit Lake, 1300 m a.s.l., located north of the Pumice Plain, reformed on new substrates after the eruption. Due to fears of floods along the Toutle Valley, the lake level was lowered in 1983 via a constructed tunnel. Wetlands then formed on the newly exposed surfaces along the south shore of the lake; the other shores of the lake are very steep.

On steep north-facing slopes located near the Pumice Plain and Spirit Lake, areas that were heavily impacted by the blast were covered by snow and faced away from the eruption. These areas provided refuge for many species and enabled them to survive the eruption as rootstock, particularly late-successional forest understory species (Titus et al. 1998). After the eruption, erosion quickly removed the pumice layer and exposed rootstock was able to resprout. Refugia wetlands include riparian wetlands in the Margaret Range, wetlands along Cedar Creek, Smith Creek and other creeks that flow from Windy Ridge, sporadic wetlands along Green River, and wetlands on the east side of the Pumice Plain (Figure 1).

Further from the cone, some vegetation survived at Meta Lake (1103 m elevation, 18 km north of the crater), Ryan Lake (1080 m elevation, 26 km north of the crater), and St. Charles Lake (1262 m elevation, 17 km north of the crater). These lakes have shoreline wetland vegetation

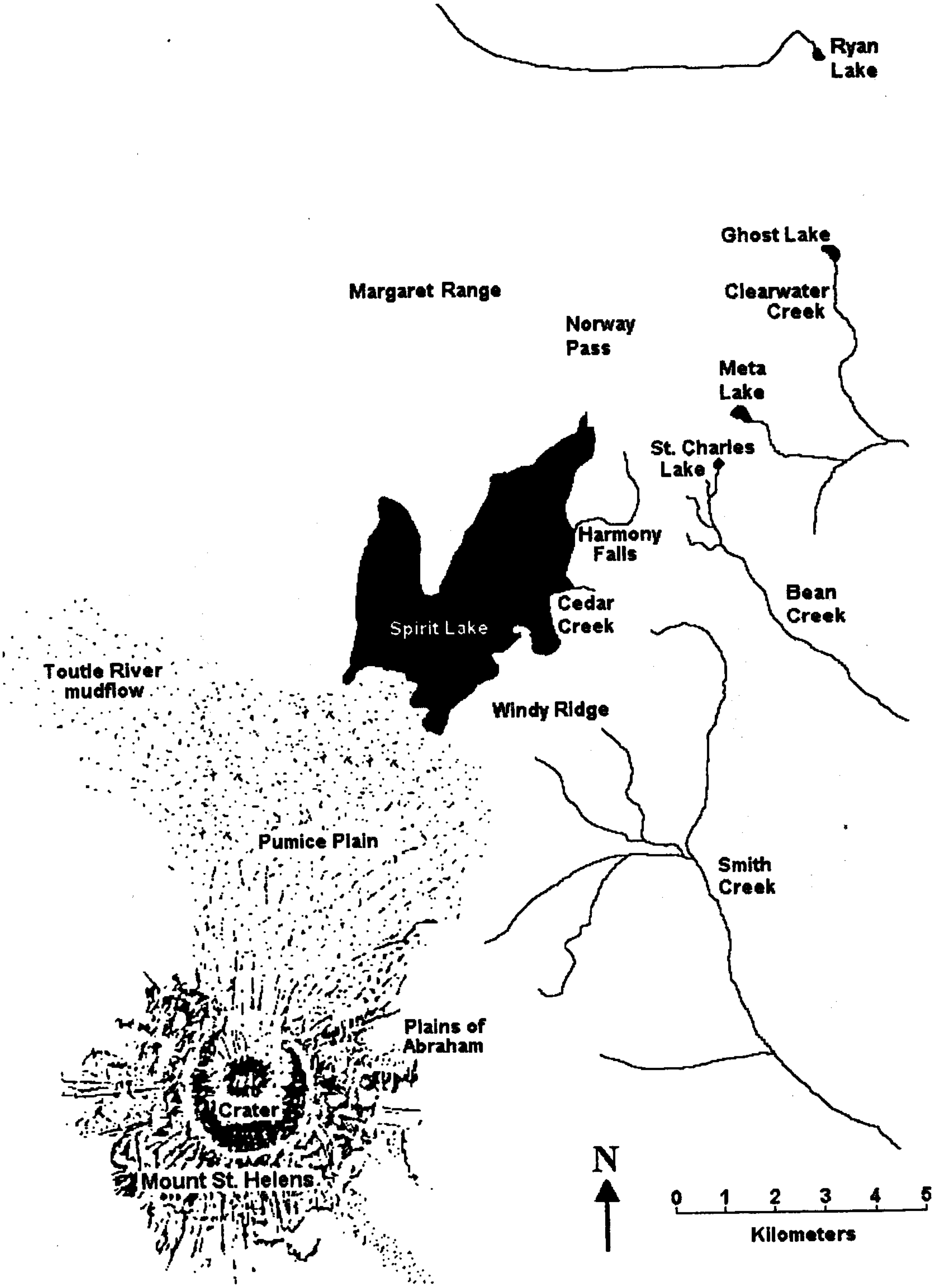

Figure 1. Map of the Mount St. Helens blast zone.

and wetlands occur in low gradient stretches of associated streams (Halpern et al. 1990), but all trees surrounding the lakes were killed during the eruption. In contrast, Ghost Lake (1154 m elevation, 22 km north of the crater) and Clearwater Creek (1349 m elevation, 21 km north of the crater) have both standing dead trees and intact pre-eruption forest on their banks with wetlands that were little altered by the eruption.

Sampling

We sampled wetlands during the summers of 1993 and 1994 by establishing 220 100-m^2 plots. Based on the investigators knowledge of the study area, wetlands were selectively chosen to adequately reflect the range of wetland vegetation, environments, and disturbance intensity described in the previous section. An area was determined to be wetland if the soil was saturated for more than three weeks during the growing season, roughly June to September on Mount St. Helens (del Moral and Bliss 1993). Soil saturation was determined by repeated visits to suspected wetland sites. Wetlands in the blast zone on Mount St. Helens contain large areas of uniform vegetation and zonation is not evident. Circular 100-m^2 plots were selected to sample homogeneous vegetation, except for linear wetlands located along creeks, which were sampled with 5 m x 20 m rectangles. Wetland vascular vegetation data consisted of percent cover of each species. Cover values were estimated by using a 0.25 m^2 PVC frame with strings delineating 25 100 cm^2 squares, thereby allowing for the determination of cover values to the nearest 0.01 m^2 for species with less than 1% cover in a plot. For plants with less than 5% cover, cover values were estimated to the nearest 0.1%. Cover was estimated to the nearest 1% up to 25% cover; and, in 5% increments thereafter. Elevation was determined from contour maps; slope was converted to a 5 state scale (level to steep), and aspect was converted to an exposure scale of 1 = protected, north to 7 = south, exposed, after Whittaker (1960). Nomenclature follows Hitchcock and Cronquist (1976).

Nominal variables were used to characterize the following five wetland types: wetlands with ephemeral water; wetlands with permanent, shallow, standing water; seasonal streams; permanent streams; and pond or lakes. Water depth was not measured because it varies daily and/or seasonally in many of these wetlands. Spring waters were discriminated by touch for two nominal water temperature variables: hot and cold. Substrate was characterized by nominal variables for stable or unstable (unstable sites are subjected to active substrate movement by snow melt in the spring).

Site disturbance intensity was characterized by four disturbance levels as follows: 1 = wetlands surrounded by standing dead trees and with surviving ground vegetation; 2 = wetlands surrounded by fallen dead trees and with some surviving ground vegetation; 3 = wetlands where aboveground vegetation was eliminated, but some belowground plant organs survived; and 4 = newly formed wetlands on primary successional post-eruption substrates. Thus, plots in Disturbance Levels 1 to 3 are secondary successional, whereas those in Disturbance Level 4 are primary successional (i.e., the Pumice Plain). Some plots in Disturbance Level 1 appear to be composed of climax perennial wetland vegetation and are primarily recovering from biomass loss without large changes in species composition.

Data Analysis

Four vegetation analysis techniques were conducted to elucidate vegetation patterns within the blast zone. First, in order to distinguish the wetland plant communities, TWINSPAN cluster analysis was used based on species cover (Hill 1979). For each community, mean species cover, species richness, and diversity (Shannon-Wiener index, base e) was calculated.

Detrended Correspondence Analysis (DCA) was used to obtain indirect ordinations (Hill and Gauch 1980). An indirect ordination yields an ordination diagram that shows the degree of similarity in species composition between plots, or the degree of similarity of species distributions within plots. As species distributions diverge, the distances between points on the species ordination diagram increase. First, three DCAs were conducted: the entire data set, primary successional substrate plots, and secondary successional substrate plots were analyzed. Species cover percentages were log-transformed to improve plot spread in ordination space, and infrequent species were downweighted. Downweighting decreases the influence of a species on the outcome of the ordination. Finally, a fourth DCA was conducted in order to assess the relationship between the four disturbance levels. To do this, each plot was represented by its disturbance level in the DCA.

Spearman rank correlation tests were used to make comparisons between the five wetland types (Zar 1984) and to determine how important the wetland types are in structuring the vegetation in the primary and secondary successional areas. Spearman's test determines the degree of correlation between two wetland types, i.e., if there is a significant result the two wetland types have similar vegetation. To complete this analysis, the cover of each species in the plots that comprise each wetland type were averaged and these average values were ranked and assigned a score based on their ranked position. The outcome was corrected for ties in the ranks, and then tested by Spearman's test.

Relationships between the environmental variables and the plot and species data were explored by Canonical Correspondence Analysis (CCA, ter Braak 1990). CANODRAW and CANOPOST graphics were used, which produce ordination biplot diagrams that show the relationship between plots or species and environmental variables (Smilauer 1993). On the biplots, Axis I represents the direction of the greatest amount of variation and Axis II represents the second greatest amount of variation in the data set. CCA determines the percentage of variability in species composition of the plots that can be explained by the environmental variables.

The entire data set was analyzed by CCA to determine overall patterns, and subsequent analyses were conducted on plots in both primary and secondary successional environments. In order to assess the contribution of each environmental variable in determining vegetation structure, interset correlations and t-values for each variable are examined. Interset correlations are the correlation of each environmental variable with the CCA axes. The t-values of each environmental variable are compared with the Student t-distribution; a variable may contribute significantly to vegetation structure if it greatly exceeds the appropriate critical value (i.e., $t>3$). Thus, environmental variables that contribute significantly to observed patterns were inferred (Jongman et al. 1987, ter Braak 1990). Note that variables that have high correlations with the CCA axes do not necessarily contribute significantly to observed patterns. In addition, in CCA the relationship between the species data and the environmental data can be tested to determine if the relationship is stronger than relationships generated randomly by using the Monte Carlo test (ter Braak 1990). This was tested for the first axes and all the axes combined (called the trace). In all of the CCAs, species cover percentages were log-transformed and infrequent species downweighted. This was done to improve species spread on the ordination diagrams. Finally, a CCA was conducted using wetland type as the only environmental variable. This allowed us to determine the importance of the relationship between wetland types and the wetland plant communities.

Geographic position has been found to play a role in determining which species colonize a site (Primack and Miao 1992; del Moral and Bliss 1993). Borcard et al. (1992) outlined how CCA can separate environmental variation from variation in the species data caused by spatial factors. Spatial positions of the plots were assigned by mapping the location of each plot on a grid of squares with 25 east to west rows, (X), and 16 north to south columns, (Y). Thereby, each plot had a X and Y location and each square represented 0.64 km^2. In order to assess the importance of complex spatial patterns, the matrix of two dimensional coordinates, X and Y, was expanded into a cubic trend surface regression by adding locations represented by X^2, XY, Y^2, X^3, X^2Y, XY^2 and Y^3. These nine spatial variables were analyzed using "forward selection of explanatory variables", a multivariate extension of stepwise regression. Species data were analyzed by the following traits: (a) constrained by the environment after spatial factors are removed, i.e., nonspatial environmental variation, which is the portion of the species variation that can be explained by the environmental variables independent of any spatial structure, (b) constrained by spatial factors after removing environmental effects, i.e., spatial patterns in the species data that are not shared by the environmental data, (c) constrained by spatially structured environmental variables, i.e., spatial structuring in the species data that is shared by the environmental data, and (d) unexplained variation, which includes variation due to unmeasured environmental variables and stochastic factors (Borcard et al. 1992).

Results

Plant Communities

Twenty-four wetland plant communities were distinguished by TWINSPAN analysis (Tables 1 and 2; species composition of each plant community available from the first author upon request).

TABLE 1. Number of plots, successional status (1 = primary, 2 = secondary), mean total percent cover of all species, species richness and diversity (Shannon-Wiener index, base e) of 24 wetland communities from the blast zone of Mount St Helens.

Plant Communities	Sample Size	Succ. Status	% Cover	Species Richness	Species Diversity
1. Aquatic vegetation	11	1,2	69	6.8	0.60
2. *Equisetum fluviatile* wetland	6	2	88	15.8	0.68
3. *Carex interrupta* wet meadow	18	2	111	19.9	1.51
4. *Carex aquatilis-Carex lenticularis* wet meadow	19	2	99	13.7	1.31
5. *Carex canescens* wet meadow	6	2	97	18.2	1.89
6. Disturbed herbaceous streambanks	17	1,2	27	19.9	1.91
6a. Primary successional dist. herb. streambanks	2	1	28	14.5	1.36
6b. Secondary successional dist. herb. streambanks	15	2	27	20.6	1.98
7. *Rubus spectabilis* thickets	1	2	120	26.0	2.22
8. *Alnus sinuata* thickets	5	2	37	22.5	2.02
9. Secondary succ. *Salix sitchensis/Equisetum arvense*	21	2	46	25.3	1.76
10. Primary succ. *Salix sitchensis/Equisetum arvense* A	4	1	63	13.8	0.78
11. Primary succ. *Salix sitchensis/Equisetum arvense* B	11	1	42	15.7	1.18
12. *Salix sitchensis* primary successional wetlands	23	1	39	14.3	1.16
13. *Salix sitchensis/Carex mertensii* wetlands	5	1	51	19.6	1.27
14. Primary successional *Equisetum arvense* wetlands	18	1	47	11.2	0.83
15. *Juncus bufonius* wetlands	7	1	48	10.0	0.94
16. *Juncus articulatus* wetlands	4	1	75	10.3	1.01
17. *Juncus drummondii* wetlands	3	1	14	7.3	1.04
18. *Juncus tenuis* wetlands	1	1	62	9.0	0.63
19. *Juncus ensifolius* wetlands	6	1	69	13.0	1.33
20. *Typha latifolia* wetlands	12	1,2	91	10.5	1.14
20a. *T. latifolia* primary successional wetlands	10	1	87	10.8	1.21
20b. *T. latifolia* secondary successional wetlands	2	2	111	9.0	0.82
21. *Scirpus americanus* wetlands	1	1	46	10.0	1.14
22. *Epilobium watsonii* wetlands	9	1	65	12.0	1.15
23. *Epilobium angustifolium* wetlands	4	1	10	13.0	1.56
24. *Calamagrostis canadensis* wetlands	9	1	6	16.8	1.96

In a few cases, communities occurred in both primary and secondary successional substrates, however, in most cases species composition differed significantly between primary and secondary successional areas. Most widespread species, with the exception of *Salix sitchensis* and *Equisetum arvense*, were confined to either primary or secondary successional substrates. For example, *Juncus* meadows only occurred in primary successional areas, while *Carex* meadows were only in secondary successional areas.

In the DCA analyses, aquatic vegetation plots (composed of submerged or floating-leaved vegetation) were removed from the analyses due to high dissimilarity with the other communities. The DCA of the entire data set comprised 203 plots and 204 species. The first two axes of the DCA ordination explain 9.3 and 8.3% of the variance in the species data, respectively. Thus, the axes explain only a small percentage of the variation in the species data. Axis I in this ordination is 4.7 half-changes long, which is indicative of a data set with a wide range of species composition. In the primary successional data set (116 plots [one outlier plot removed] and 104 species), the first two axes account for 14.4 and 9.9% of the variance, respectively (Figure 2). In the secondary successional data set (86 plots and 177 species), these axes account for 11.7 and 9.0% of the variance, respectively (Figure 3).

Disturbance levels separated moderately well in ordination space (Figure 4). Primary succession plots (Disturbance Level 4) and heavily impacted plots (Level 3) were separated from Levels 1 and 2 along Axis I. Levels 1 and 3 are distinct from Levels 2 and 4 along Axis II.

TABLE 2. Descriptions of 24 wetland communities from the blast zone of Mount St Helens.

Plant Community[1]	Occurrence	Common Species[2]	Notes
1. Aquatic vegetation	Occurs in deep water in all the ponds and lakes examined.	*Potomogeton foliosus* *Potomogeton natans* *Ranunculus aquatilis*	Floating leaved and submerged vegetation. The alga *Chara* is common.
2. *Equisetum fluviatile* wetland	Only occurs in deep water at Ryan Lake.	*Carex aquatilis* *Carex brunnescens* *Typha latifolia*	*Equisetum fluviatile* occurs in deep water. Most of the other species occur on the pond shore.
3. *Carex interrupta* wet meadow	Occurs in low disturbance wetland areas by Ghost Lake and along Clearwater Creek.	*Calamagrostis canadensis* *Equisetum arvense* *Juncus ensifolius* *Salix sitchensis* *Viola glabella*	*Salix sitchensis* is often co-dominant. *Eriophorum angustifolium* occurs occasionally.
4. *Carex aquatilis-Carex lenticularis* wet meadow	Most common along the shore of Meta Lake.	*Equisetum arvense* *Juncus effusus* *Ranunculus sceleratus* *Salix sitchensis* *Salix sitchensis* and	*Equisetum arvense* is common.
5. *Carex canescens* wet meadow	Occurs along the shore of St. Charles Lake.	*Alnus sinuata* *Equisetum arvense* *Potomogeton foliosus* *Salix sitchensis* *Sparganium emersum* *Typha latifolia*	*Salix sitchensis* is often co-dominant.
6. Disturbed herbaceous streambanks	Occurs in higher elevation heavily disturbed secondary successional sites, such as along creeks in Pumice Plain refugia and the Margaret Range; also in primary successional sites along creeks on the Pumice Plain.	*Carex spectabilis* *Lupinus latifolius* *Juncus mertensianus* *Mimulus lewesii* *Valeriana sitchensis*	These areas are often species rich with more than 20 species per plot. Recovering habitats of this type are much more diverse than recently initiated habitats. Slopes are steep, especially in secondary successional sites.
7. *Rubus spectabilis* thickets	Occurs only on the banks of Ryan Lake.	*Athyrium filix-femina* *Epilobium angustifolium* *Glyceria elata* *Petasites frigidus*	Diverse secondary successional type; cover is high due to dense multiple vegetation layers. This vegetation is common as forest understory in wet sites throughout the Pacific Northwest (Kunze 1994, Christy & Titus 1997).
8. *Alnus sinuata* thickets	Occurs in moist, heavily disturbed secondary successional areas.	*Aruncus sylvester* *Athyrium filix-femina* *Epilobium watsonii* *Salix sitchensis* *Saxifraga arguta*	Understory is diverse with usually more than 20 species in a plot. *Alnus sinuata* thickets are common on primary successional substrates on the Pumice Plain, but only in upland areas.
9. Secondary Successional *Salix sitchensis/Equisetum arvense* wetlands	Found in heavily impacted sites along creeks in Harmony Basin and the Margaret Range, and along the Green River and Bean Creek; also found in less disturbed sites by Ghost and Meta Lakes and Coldwater Creek.	*Alnus sinuata* *Anaphalis margaritacea* *Carex mertensii* *Epilobium watsonii* *Juncus mertensianus* *Mimulus lewesii*	These areas are often species rich with more than 30 species in a plot.

TABLE 2, Continued.

Plant Community[1]	Occurrence	Common Species[2]	Notes
10. Primary Successional *Salix sitchensis/Equisetum arvense* wetlands (Type A)	Occurs across the Pumice Plain in several habitats, usually on moist substrates.	*Agrostis exarata* *Carex limnophila* *Carex mertensii* *Epilobium watsonii* *Juncus mertensianus*	Other species at low cover; understory differs from the secondary successional *Salix sitchensis/Equisetum arvense* type.
11. Primary Successional *Salix sitchensis / Equisetum arvense* wetlands (Type B)	Common in the northern part of the Pumice Plain; occurs most commonly along permanent streams.	*Anaphalis margaritacea* *Epilobium watsonii* *Hypochaeris radicata*	Contains upland invasive species.
12. *Salix sitchensis* dominated primary successional wetlands	Common across the Pumice Plain, usually on the banks of permanent streams; also occurs in the crater.	*Anaphalis margaritacea* *Epilobium angustifolium* *Epilobium watsonii* *Hypochaeris radicata* *Petasites frigidus*	*Equisetum arvense* is not present or only present in trace amounts.
13. *Salix sitchensis/Carex mertensii* wetlands	Occurs in the northern part of the Pumice Plain on ephemeral moist substrates.	*Agrostis exarata* *Alnus sinuata* *Anaphalis margaritacea* *Aruncus sylvester* *Lupinus latifolius* *Luzula parviflora* *Penstemon cardwellii* *Saxifraga ferruginea*	Understory differs from other *Salix sitchensis* types with a greater cover of upland invasive species.
14. *Equisetum arvense* wetlands	Occurs only in the northern part of the Pumice Plain and is the most common wetland type on the Plain.	*Agrostis exarata* *Epilobium watsonii* *Hypochaeris radicata* *Salix sitchensis*	Large areas of wet silt sediments are dominated by monocultures of *Equisetum arvense*; with infrequent occurrences of other species. This vegetation type occurs most frequently in moist and standing water habitats.
15. *Juncus bufonius* wetlands	Low diversity *Juncus bufonius* wetlands cover extensive ephemeral moist areas in the northern part of the Pumice Plain.	*Agrostis exarata* *Equisetum arvense* *Epilobium watsonii*	Often located on moist silt deposits.
16. *Juncus articulatus* wetlands	Habitat is similar to *Juncus bufonius* wetlands.	*Epilobium watsonii* *Equisetum arvense* *Juncus bufonius*	*Juncus bufonius* and *Equisetum arvense* are often co-dominants.
17. *Juncus drummondii* wetlands	Habitat is similar to *Juncus bufonius* wetlands.	*Juncus bufonius*	*Juncus bufonius* is co-dominant.
18. *Juncus tenuis* wetlands	Habitat is similar to *Juncus bufonius* wetlands.	*Equisetum arvense* *Juncus bufonius* *Salix sitchensis*	*Equisetum arvense* is often co-dominant and *Juncus bufonius* is usually common.
19. *Juncus ensifolius* wetlands	Occurs on the north end of the Pumice Plain in ephemeral moist habitats and in standing water and along streams.	*Carex mertensii* *Epilobium watsonii* *Equisetum arvense* *Salix sitchensis*	Not strongly associated with the other *Juncus* species.
20. *Typha latifolia* wetlands	Occurs in standing water on primary successional substrates in the Pumice Plain, and in secondary successional areas along the shores of several of the ponds.	*Epilobium watsonii* *Equisetum arvense* *Juncus bufonius* *Juncus ensifolius* *Salix sitchensis*	This type occurs across the disturbance spectrum. Secondary successional sites are similar to primary successional sites in richness, but are less diverse.

TABLE 2, Continued.

Plant Community[1]	Occurrence	Common Species[2]	Notes
21. *Scirpus americanus* wetlands	Occurs infrequently in standing water across the Pumice Plains.	*Eleocharis palustris* *Epilobium wasting* *Equisetum arvense* *Juncus bufonius*	Associated with hot water springs.
22. *Epilobium watsonii* wetlands	Occurs along both permanent and ephemeral streams on the Pumice Plain.	*Equisetum arvense* *Juncus bufonius* *Salix sitchensis*	The preponderance of *Epilobium watsonii* and the streambank habitat separate this from *Equisetum arvense* and *Juncus bufonius* wetlands.
23. *Epilobium angustifolium* wetlands	Occurs along both permanent and ephemeral streams on the Pumice Plain.	*Anaphalis margaritacea* *Carex mertensii* *Epilobium watsonii* *Mimulus lewesii* *Salix sitchensis*	Occurs in drier habitats and contains more upland invasive species than *Epilobium watsonii* wetlands.
24. *Calamagrostis canadensis* wetlands	Occurs along permanent streams on the Pumice Plain.	*Anaphalis margaritacea* *Epilobium angustifolium* *Epilobium watsonii* *Salix sitchensis*	Diverse primary successional community; this type is composed of both upland and wetland species.

---

[1] Vegetation types not discussed are as follows: moss-dominated wetlands occur patchily across the Pumice Plains; *Merchantsia* patches occur in seepage areas; *Hypochaeris radicata* dominated wetlands occur on the Pumice Plain and in the crater; patches of *Petasites frigidus* occur in some of the secondary successional areas; algal mats are common along both hot and cold spring runs and in the lakes.

[2] Species composition of each plant community available from the first author upon request.

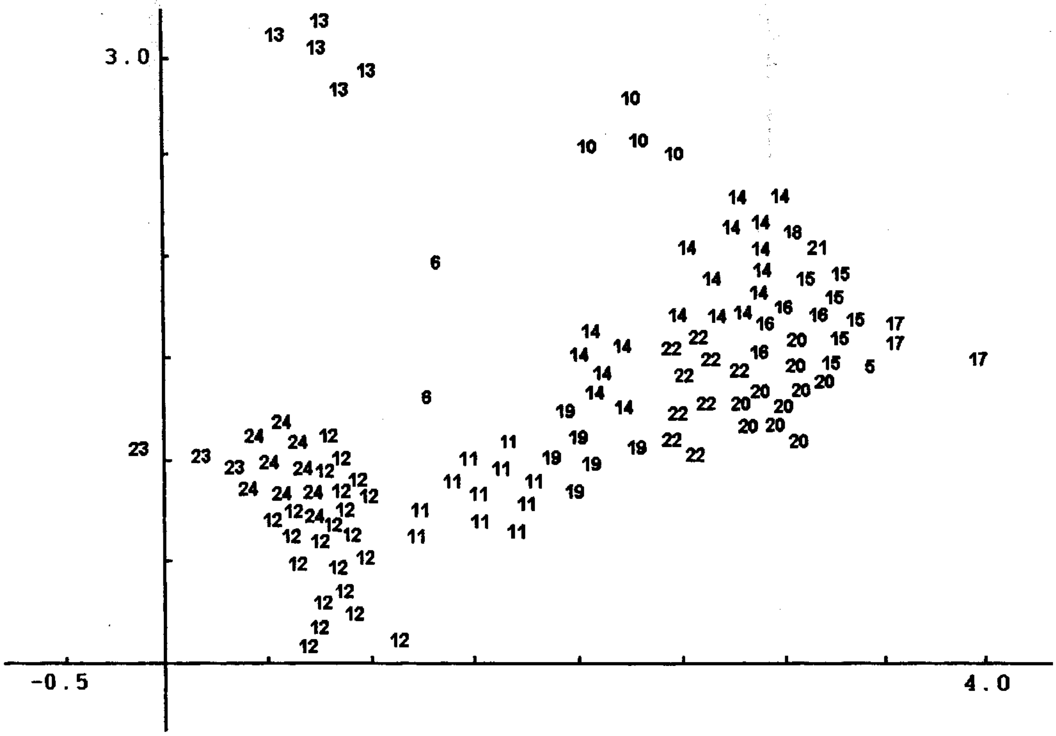

Figure 2. Detrended Correspondence Analysis of primary successional plots. Numbers correspond to communities in Tables 1 and 2.

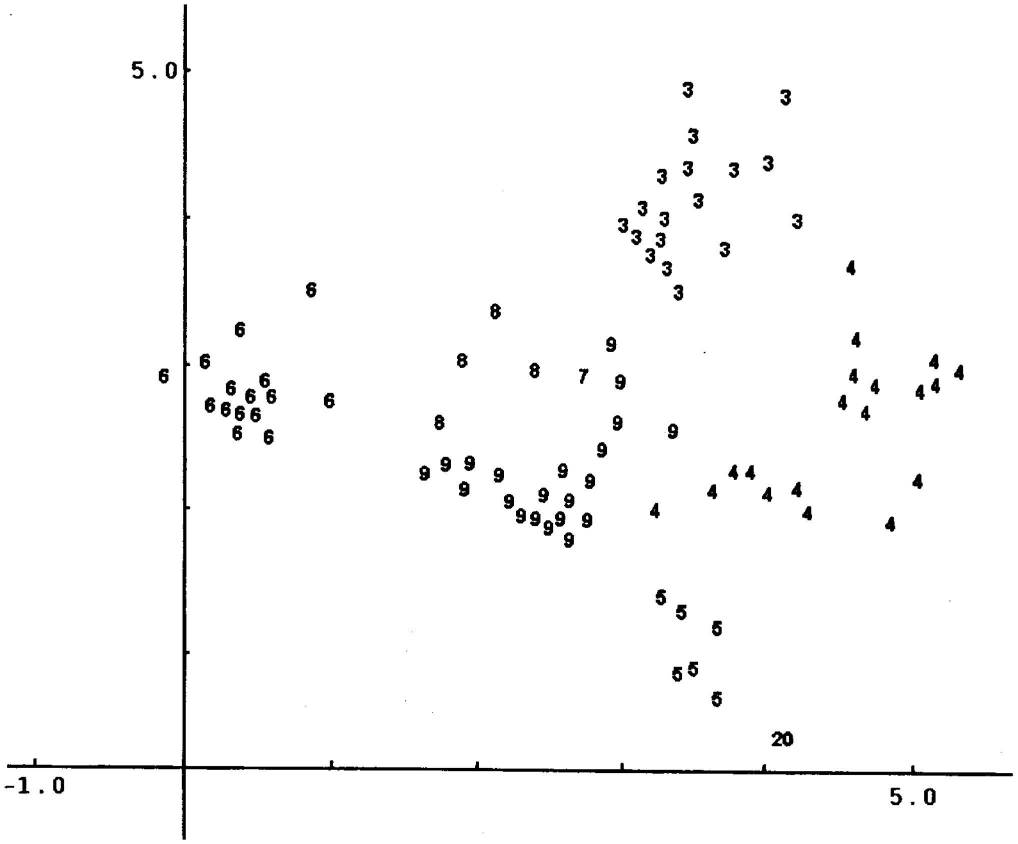

Figure 3. Detrended Correspondence Analysis of secondary successional plots. Numbers correspond to communities in Tables 1 and 2.

Correlations between Vegetation of the Wetland Types

Spearman rank correlations among primary successional wetland types show modest, but significant correlations (Table 3). Vegetation in wetlands with permanent shallow standing water is not significantly correlated to vegetation along ephemeral streams, which contains many upland species. In secondary successional environments wetland types are not correlated, with the exception of ephemeral streams, which are primarily found in heavily impacted sites. If the heavily impacted secondary successional sites (Disturbance Level 3) are removed from the analysis, the relationships do not change; however, the ephemeral stream group then has an insufficient sample size.

Canonical Correspondence Analysis

Entire Data Set. Aquatic plots were distinctive and were removed from the analysis. Of the variability in species composition of the plots, 24.7% can be explained by the environmental variables. For the entire data set, both axis I and the trace are significant as analyzed by the Monte Carlo test (P=0.01); that is, the relationship between the species and environmental data is stronger than randomly generated relationships.

Wetland communities did not segregate in the CCA biplot, indicating that they are not characterized by a consistent combination of environmental variables. The most important environmental variable on axis I, based on interset correlations (Table 4) and t-values, was disturbance level (t = 19.76). Axis II has its strongest relationships with elevation (t = 10.53) and the nominal variable "ephemeral stream" (t = 10.08). Also on axis II, the nominal variable "wet stream", although not highly correlated with axis II, was significant (t = 8.78).

Primary Successional Plots. The CCA of plots on primary successional substrates is shown in Figure 5. Of the variability in species composi-

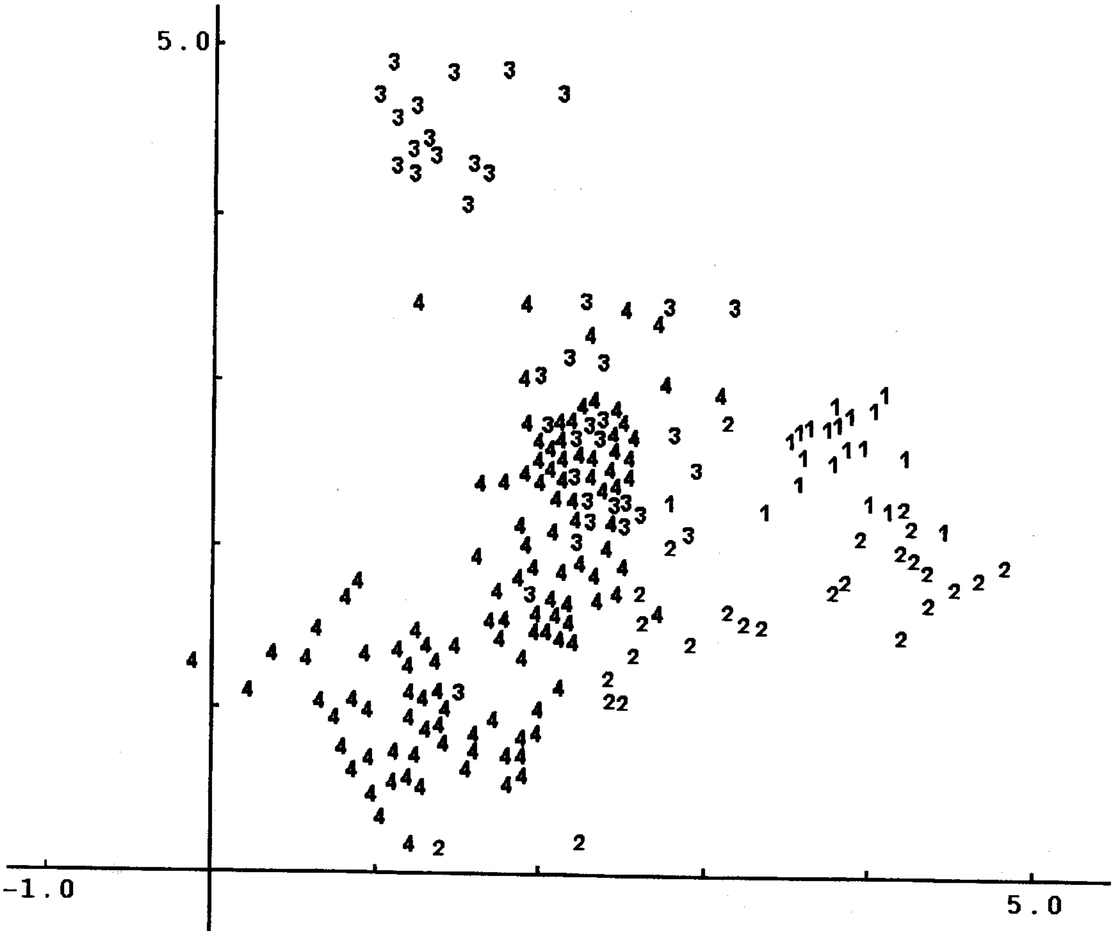

Figure 4. Detrended Correspondence Analysis of all plots. Numbers are the Disturbance Levels. 1=low impact; 2=moderate impact; 3= heavily impacted secondary succession; 4=primary succession.

TABLE 3. Spearman rank correlations between wetland types. The cover of each species in the plots comprising a wetland type were averaged, ranked, corrected for ties in the ranks, and then tested by Spearman's test. A significant result (in bold) indicates that the two wetland types have vegetation that is significantly correlated. In primary successional wetland types, pond was not tested due to small sample size, and in secondary successional wetland types, standing water was not tested due to small sample size.

Wetland Type	Primary Successional	Secondary Successional
moist vs. standing water	**r=0.366 p<0.005**	—
moist vs. ephemeral stream	**r=0.316 p<0.02**	**r=-0.419 p<0.001**
moist vs. permanent stream	**r=0.597 p<0.001**	r=0.170 p>0.1
moist vs. pond	—	r=0.046 p>0.5
standing water vs. ephemeral stream	r=0.174 p>0.1	—
standing water vs. permanent stream	**r=0.555 p<0.001**	—
ephemeral stream vs. permanent stream	**r=0.550 p<0.001**	r=-0.038 p>0.5
ephemeral stream vs. pond	—	**r=-0.258 p<0.01**
permanent stream vs. pond	—	r=0.167 p>0.05

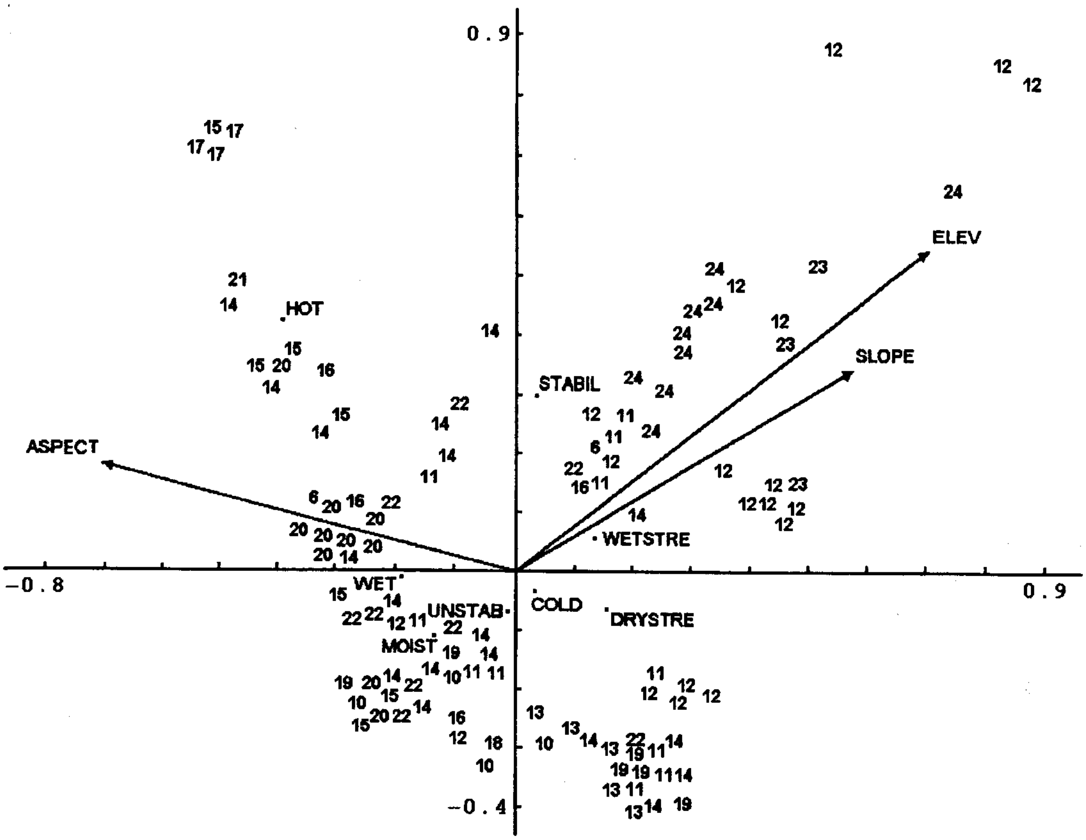

Figure 5. Canonical Correspondence Analysis plot-environment biplot of primary successional plots. Numbers correspond to communities in Tables 1 and 2. Abbreviations of environmental variables are defined in Table 4. See text for interpreting the diagram.

tion of the plots, 19.0% can be explained by the environmental variables. Note that disturbance level is not included in this analysis since all plots are primary successional. Both axis I and the trace are significant (P=0.01, Monte Carlo test). In the ordination biplot diagram, nominal environmental variables are represented by points and continuous environmental variables are represented by vectors. The direction of a vector represents the direction of maximum change of the environmental variable across the diagram and the length of a vector is proportional to the magnitude of change in that direction. The environmental variables that have long arrows are more closely correlated to the vegetation than those with short arrows and are usually more important in influencing community variation. The vector should also be considered as extending back through the origin. A point that represents a plot can be related to each vector by drawing a perpendicular from the line of the vector up to the point representing the plot. Plots with their perpendicular projections near to or beyond the tip of the vector will be strongly correlated with and influenced by that environmental variable, those near the center will be less affected. Also, the position of a vector with respect to an axis indicates how closely correlated the axis is with that environmental factor (Kent and Coker 1992).

Based on t-values for Axis I, the variables elevation, permanent stream and hot water contribute the most to vegetation structure. Elevation, slope and aspect have the highest correlations with axis I (Table 4). Although slope and aspect contribute significantly to the pattern, they are less important than some of the wetland types and water temperature. Axis II is not strongly correlated with any environmental variable, nonetheless elevation and substrate stability contribute the most to this axis. Slopes increase and exposure decreases (i.e.,

TABLE 4. CCA interset correlations of environmental variables with the canonical axes. All analyses were conducted with aquatic vegetation removed. Scores are times 1000. Variables that contribute strongly to the ordination (t>3.0) are in bold. Variables that have high correlations with CCA axes do not necessarily contribute significantly to observed patterns. Thus, large interset correlation values are not necessarily significant.

	All Plots		Primary Successional		Secondary Successional	
Variable	Ax 1	Ax 2	Ax 1	Ax 2	Ax 1	Ax 2
Elevation-ELEV	**106**	**647**	**612**	**369**	**786**	**84**
Slope-SLOPE	110	**403**	507	250	359	86
Aspect-ASPECT	**-334**	-227	**-601**	138	-463	-112
Moist Site-MOIST	-109	**-122**	**-209**	-134	-218	**494**
Wet Site-WET	**281**	-320	**-389**	-6	-107	97
Ephemeral Stream-DRYSTRE	**184**	**455**	144	-50	**771**	**74**
Permanent Stream-WETSTRE	**164**	**256**	436	135	**106**	**152**
Pond-POND	**-494**	**-246**	—	—	**-399**	**-578**
Hot Water-HOT	222	**-266**	**-378**	**338**	—	—
Cold Water-COLD	-222	266	378	-338	—	—
Stable Substrate-STABIL	-294	298	77	393	609	25
Unstable Substrate-UNSTAB	294	-298	-77	**-393**	-609	-25
Disturbance Intensity-DIST	**865**	**-120**	—	—	**-720**	**-503**

more northern aspects) with increasing elevation. Wet and moist sites generally occur at lower elevations, whereas streams occur at higher elevations.

Most of the communities do not segregate in the CCA biplot, indicating one or more of the following: plots comprising each plant community do not belong to a similar set of environmental variables; vegetation is responding to unmeasured variables; and/or, vegetation patterns are stochastic, i.e., the patterns in the vegetation are due to random factors rather than environmental variables. Weak species-environment patterns were further reflected by the common species, in that most of the common species were located near the center of the biplot (not shown), which indicates that they inhabit a variety of environments. Weak tendencies, such as the affinity of *Equisetum arvense* for moist areas and *Salix sitchensis* for seasonal streams, were apparent. Most *Juncus* species cluster around the wet substrate variable.

Secondary Successional Plots. The CCA of plots on secondary successional substrates, including non-aquatic pond vegetation (i.e., emergent vegetation near a pond shore), is shown in Figure 6. Of the plot variability in species composition, 34.7% can be explained by environmental variables. Both Axis I and trace are significant (*P*=0.01, Monte Carlo test).

Axis I is correlated with elevation (t = 13.19), ephemeral streams (t = 11.50), disturbance (t=7.79), and permanent streams (t = 9.15); substrate stability is not significant (Table 4). Axis II is correlated with ponds, disturbance and moist areas. It is clear from Figure 6 that, with increasing elevation, slope increases, whereas exposure and substrate stability decreases; ephemeral streams are the most common wetland type at higher elevations. Thus, the "disturbed stream" vegetation type is found in a portion of the diagram that illustrates higher elevation, unstable substrate, steep slopes, and ephemeral character.

Plots are strongly clustered in several parts of the CCA biplot (Figure 6). Many communities retain their coherence in the CCA biplot, indicating that the plots comprising each community belong to a similar set of measured environmental variables. *Carex* meadows occupy the left part of the biplot and vary along axis II. *Carex* meadows are usually associated with ponds, except *Carex interrupta* meadows, which often occur in wet areas not associated with ponds. There is a clear distinction between heavily impacted streamside sites and *Carex* meadows, because *Carex* meadows occur in environments that suffered relatively little disturbance from the eruption. Unlike the primary successional CCA, *Salix sitchensis* and *Equisetum arvense* do not occur in such a

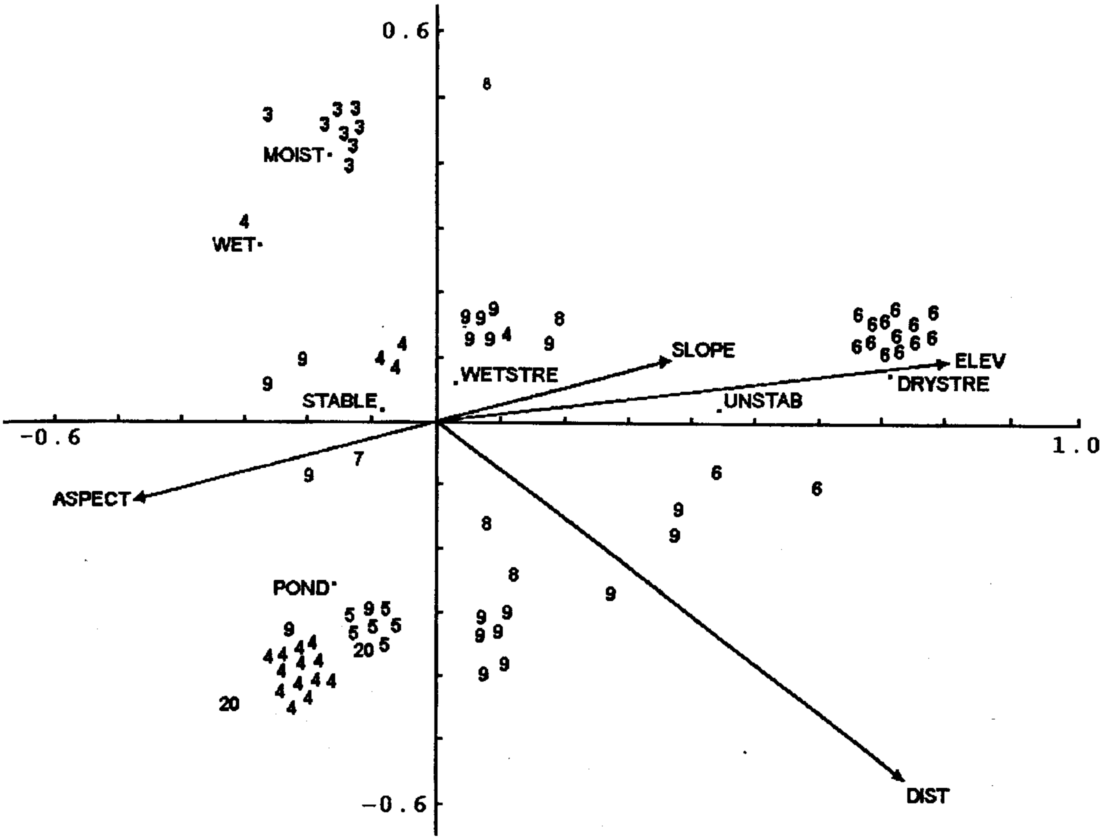

Figure 6. Canonical Correspondence Analysis plot-environment biplot of secondary successional plots. Numbers correspond to communities in Tables 1 and 2. Abbreviations of environmental variables are defined in Table 3. See text for interpreting the diagram.

wide array of environments and are not in the center of the biplot.

Wetland Types in CCA. CCAs were conducted on primary and secondary successional data using only wetland type as the environmental variable. Results were tested by the Monte Carlo test. In both primary and secondary successional communities, wetland type was significant (primary successional first axis P=0.01, trace P=0.01; secondary successional first axis P=0.01, trace P=0.01). This indicates that the relationship between wetland type and species distribution is different from a random distribution, and that there is a significant relationship between wetland type and vegetation patterns.

Spatial Analysis. For the three data sets (complete, primary successional and secondary successional), forward selection indicated that most spatial variables were significant. Although the amount of variability explained by spatial variables was not large, it was comparable to the variability explained by measured environmental factors alone (Table 5). However, multicollinearity between the spatial variables was high. "Inflation values" >20 in the CCA output indicate high multicollinearity between environmental variables. If only those spatial variables which have low multicollinearity are used, explained spatial variability is reduced by about one-half. If inflation values are reduced below 20, the following spatial variables are retained: Y, X^3 and XY^2 for the complete data set; X^3, X^2Y and Y^3 for the primary succession data set; and Y, X^3 and XY^2 for the secondary successional data set. If only X and Y are used, explained spatial variability is considerably reduced.

In these analyses environmental, spatial, and spatially-structured environmental sources of

TABLE 5. Variance partitioning of wetland vegetation from Mount St. Helens. The variation due to environmental factors after removing the effect of the geographical matrix, the variation due to the geographical matrix after removing the effect of the environmental variables, spatially structured environmental variation, and the remaining unexplained variation are partitioned. Spatial variables used were determined by forward selection. Spatial variables were: all plots (X ,Y, X^2, XY, Y^2, X^3, X^2Y, XY^2), primary successional (X ,Y, X^2, Y^2, X^3, X^2Y, Y^3), secondary successional (X ,Y, X^2, XY, Y^2, X^3, X^2Y, XY^2, Y^3).

	% Variance partitioned		
Source of Variation	All Plots	Primary Successional	Secondary Successional
environmental	11.7	11.2	18.5
spatial	13.4	17.1	16.6
spatially structured environmental	11.0	10.5	16.3
unexplained/stochastic	64.0	61.2	48.7

variation account for 35-50% of vegetation structure. Measured environmental factors are more important in the secondary successional vegetation than in the other analyses. Unexplained variation is high in all three analyses, although it is less than 50% in the secondary successional analysis. Unexplained variation includes variation due to unmeasured environmental factors and stochastic factors, such as seed dispersal.

Discussion

Communities

Wetland communities in the less impacted areas of this study also occur at similar elevations throughout the region where there is suitable substrate (Franklin and Dyrness 1988, Kunze 1994, Titus et al. 1996, Christy and Titus 1997). Likewise, vegetation similar to the primary successional wetland communities on the Pumice Plain is found in highly disturbed wet areas from sea level up to the elevation of the Pumice Plain throughout the region (Titus et al. 1996, J. Titus, pers. obs.). For example, wetlands dominated by *Epilobium watsonii* and *Salix sitchensis* occur in wet, logged sites, *Juncus bufonius* and *J. tenuis* are found along logging roads, and *Equisetum arvense* occurs in wet areas around road construction.

The most species rich and diverse communities found in this study are the secondary successional *Alnus, Salix/Equisetum,* and *Rubus spectabilis* thickets. This is due to the rich assemblage of understory herbaceous species. These communities are located in disturbance prone sites, such as streambanks, and both early and late successional species occur in the understory. Primary successional *Salix* communities are less diverse because they contain fewer understory species, i.e., the later successional species are not present. The *Salix sitchensis/Carex mertensii* community is more diverse than the other primary successional *Salix* communities because of the occurrence of both upland and wetland pioneer species in the understory; this is due to the fact that *Salix sitchensis/Carex mertensii* occurs in drier substrates than the other *Salix* communities.

Many pioneer species most commonly found in uplands colonized both wet and dry areas across the Pumice Plain. These species have wide ecological amplitudes and can inhabit many different kinds of sites if the site is unoccupied (Grime et al. 1988, del Moral et al. 1995, Titus et al. 1998). These species are represented in high densities in the seed rain (del Moral and Bliss 1993, del Moral and Wood 1993a). For example, wet areas in high impact sites often contain species such as *Anaphalis margaritacea, Epilobium angustifolium* and *Hypochaeris radicata*, however, it is unlikely that these will persist in Pumice Plain wetlands. These species are less common in wetlands in the low impact areas. The preponderance of *Equisetum arvense* dominated wetlands on the Pumice Plain may be due to the aggressive clonal spread of this species combined with substrate instability, which make *E. arvense* sites difficult for other species to colonize. No information regarding the density of *E. arvense* spores in the seed rain is available, probably because the spores are too small to be documented in most seed traps.

A major difference between primary and secondary successional areas is the predominance of *Juncus* dominated wetlands on the Pumice Plain and the predominance of *Carex* dominated wetlands in less disturbed areas (Table 1 and 2). *Carex* species form wet meadows in relatively undisturbed areas throughout the Cascade Range. *Juncus* species, with the exception of *J. ensifolius*, generally vegetate wetlands in disturbed sites throughout the region. It is possible that the *Carex* species have not invaded Pumice Plain wetlands due to dispersal limitations, but upland *Carex* species, *e.g.*, *Carex mertensii* and *Carex limnophila*, are widespread across the Pumice Plain (Titus et al. 1998). Thus, it is more likely that the characteristics of Pumice Plain wetlands, such as high substrate instability, are not amenable to wetland *Carex* species.

Disturbance Level

The intensity of disturbance from the eruption strongly influenced species composition within our study area. During the eruption, vegetation was completely destroyed in primary successional sites and heavily impacted in Disturbance Level 3 secondary successional sites. Since the eruption, some primary successional sites have developed vegetation that resembles that of heavily impacted secondary successional sites and the boundary between these two disturbance levels (levels 3 and 4) overlaps in the DCA ordination (Figure 4). This overlap is caused by primary successional *Salix* thickets that resemble heavily-impacted secondary successional *Salix* thickets. Nevertheless, most primary successional sites differ from heavily impacted secondary successional sites; this is primarily due to later successional and forest species that sprouted from rootstock that survived the eruption (del Moral et al. 1995, Titus et al. 1998) and differences in substrate features. Many Disturbance Level 3 secondary successional sites are ephemeral streams on steep slopes, whereas the Pumice Plain is relatively flat and offers a wider variety of wetland types. Disturbance Level 2 plots are often floristically similar to Disturbance Level 1 plots, particularly those dominated by *Carex* species.

Wetland Types

Wetland types were found to be more important in structuring the vegetation in secondary successional plots than in primary successional plots (Table 3). This may be a result of wide ecological amplitudes of many primary successional species that can occupy any moist site. For example, several species (e.g., *Agrostis exarata, Equisetum arvense*, and *Juncus bufonius*) are prevalent in plots across all wetland types, and their inclusion prevent wetland types and communities from segregating clearly in the DCA ordination (Figure 2). As succession proceeds, it is likely that these widespread species will become restricted to certain environments or disappear. Species such as *Juncus bufonius* may become less common when substrates stabilize and other species invade. Wetland types in secondary successional sites differ from each other in species composition and the plant communities have few species in common. Species in these communities, when compared to those that dominate primary successional wetlands, appear to have relatively narrow distributions, i.e., these species occur in fewer communities.

Succession

Not all of the sites in this study are necessarily successional, rather some may be merely recovering from biomass removal. For example, *Carex* meadows are stable communities. These sedges apparently survived the eruption under ice and sprouted through accumulated ash. In contrast, highly disturbed sites with *Salix sitchensis* and *Alnus sinuata* thickets will probably change in the coming decades as shrub cover increases. Eventually, these communities may resemble the high shrub cover sites observed in low impact areas. Herbaceous wetlands on primary successional sites will change in ways that are difficult to determine at present. It is likely that *Typha latifolia* will dominate some sites and *Salix sitchensis* will eventually dominate others (Keddy 1989, Tu et al. 1998). Clonal species such as *Equisetum arvense* and *Typha latifolia* may retain site dominance indefinitely (Keddy 1989, Tsuyuzaki 1989, Prach and Pysek 1994). Unstable sites may continue to be dominated by *Equisetum arvense* and/or *Juncus bufonius* for many years if substrates do not stabilize. Thus at present, there is little evidence that primary successional wetland sites are undergoing directional succession towards relatively undisturbed wetland communities and little reason to believe that they soon will. Most of the Pumice Plain will eventually become forest that will resemble the pre-eruption Pumice Plain (Kruckeberg 1987). Because of the geologically unstable nature of the Pumice Plain, hydrologic changes may cause some substrates to become drier through time. Wetlands that remain may become *Thuja plicata* dominated forest, which occurs elsewhere in the region (Franklin and Dyrness 1988, Kunze 1994, Titus et al. 1996, Christy and Titus 1997). If the shore of Spirit Lake stabilizes, the vegetation may eventually resemble pond shore vegetation found in low impact sites, although there is no evidence of this at present.

Contribution of Spatial and Environmental Variables

In upland areas on Mount St. Helens, geographic position plays an important role in determining which species colonizes a site (del Moral and Bliss 1993). Spatial analyses enable a partition to be made between environmental, spatial, spatially structured environmental, and undetermined components (Borcard et al. 1992). In the complete and secondary successional analyses, disturbance intensity is highly correlated with both the X and Y factors. This is because disturbance decreases with increasing distance from the volcano in all directions. Likewise in these two analyses, spatial variables are highly correlated, which indicates that similar patterns are explained by both X and Y variables. However, forward selection indicated that, even with high correlations, a large number of spatial variables were significant in structuring vegetation patterns. A reason for this is the patchy distribution of wetland complexes across the landscape. Each of these wetland complexes was sampled by several plots, causing groups of vegetatively similar plots to be highly clumped in spatially scattered wetland locations. This clumping of vegetatively similar plots may cause a large number of spatial variables to exhibit significance. The amount of variation in the vegetation attributed to spatial variation is most likely due to this landscape effect. Thus, although a large number of spatial variables are significant, that does not mean that they are all important in structuring the vegetation. In any case, the amount of variation due to the spatial and environmental variables are similar and both are relatively unimportant in structuring the vegetation (Table 5). Unexplained variation (variation due to unmeasured environmental variables and/or stochastic factors) was found to explain 61.2% of the variation in the primary successional plots, as opposed to 48.7% for secondary successional plots (Table 5).

Environmental variables that are important in mature wetlands, such as soil chemistry, are unlikely to be important in early successional landscapes, where soils are extremely nutrient poor (Tu et al. 1998, Titus unpubl. data). Thus, it is likely that stochastic factors were initially important in the colonization of primary successional wetlands, i.e., a wetland is colonized by a particular species based upon the random chance of a propagule of that particular species landing in the wetland. At present, many of these wetlands are densely vegetated, much more so than most upland sites (del Moral et al. 1995) and therefore other factors, such as competition, are also important. However, in high-disturbance primary successional wetlands, such as unstable streambanks and areas of frequent sediment deposition, stochastic factors, such as seed dispersal, may still be important for establishment because open sites remain plentiful. In these areas chance would favor the locally prevalent species.

Stochastic factors are unlikely to be important in structuring low impact sites, because vegetation has occupied these sites for long periods of time and vegetative cover is high. Thus, it is probable that unmeasured pre-eruption environmental variables, rather than chance, are important in the low impact sites and are responsible for most of the unexplained variation.

In upland primary successional studies, it has been posited that initial species assemblages are *ad hoc* and may be novel. Invading species have broadly overlapping tolerances and therefore many species could potentially occupy a microsite (del Moral and Wood 1993b, del Moral et al. 1995). Establishment has been attributed to stochastic factors operating through a lottery model (Sale 1977, Lavorel and Lebreton 1992). Unlike upland primary successional sites, where species generally cannot exclude other pioneers from their vicinity (del Moral et al. 1995), in wetlands plants can exclude other pioneers. This is due to the rapid achievement of high cover in the wet environment via prolific seed production and clonal growth. Thus, it is unlikely that a carousel mechanism (van der Maarel and Sykes 1993), where different species successively occupy the same microsite, will occur.

In the wetlands studied here, most of the primary successional communities are not novel, but are similar to wetland species assemblages found in heavily disturbed sites throughout the region. If the unexplained variation in communities was largely determined by stochastic factors, would it be possible that similar assemblages would develop in disturbed sites throughout the region? On the Pumice Plain, initial species composition may have been stochastic from the pool of wetland species that have propagules in the seed rain, i.e., founder effects are important. That is, seed and clone production by locally established species would quickly outweigh any long distance dispersal by species not locally established (Moody and Mack 1988, del Moral and Bliss 1993, Stöcklin and Bäumler 1996). Thus, where a species establishes and subsequently becomes dominant is due to the chance processes of dispersal and not due to environmental variables. Because of the limited pool of wetland species in the seed rain, communities that emerge via the stochastic dispersal process are similar to wetland vegetation throughout the region. The particular location of an *Equisetum arvense, Salix sitchensis* or *Juncus bufonius* wetland is stochastic because these species can colonize a wide variety of sites, and because of the relatively small available species pool similar wetland assemblages occur elsewhere. Thus, these wetland communities are found throughout the region wherever a disturbance occurs. However, future changes in vegetation composition will be driven by factors such as environmentally mediated competition.

Conclusion

We conclude that environmental factors were not of great importance in the species assembly of wetland communities on the Pumice Plain. Stochastic factors are important on the Pumice Plain and are linked with a small species pool of potential dominants, which yield common and recognizable communities with little linkage to environmental factors. Thus, similar sites yield different communities. Vegetation development in the future will be strongly determined by initial founder effects. In low impact areas, unmeasured environmental variables appear to be of greater importance.

Acknowledgments

Thanks to S. Tsuyuzaki, J. Bishop and S. Moore for assistance in the field. J. Leps assisted with data analysis and the facilities of the Faculty of Biology, University of South Bohemia, Ceske Budejovice, Czech Republic were invaluable. J. Leps, P. Smilauer, J. Christy, E. Rykiel Jr., and an anonymous reviewer greatly improved the manuscript. Many species were identified by M. Arnot, A. Yen, S. Gage, S. Moore and J. Christy. A grant from the Washington Native Plant Society made this research possible. NSF Grants BSR-89-06544 and DEB-9406987 to R. del Moral helped support this research.

Literature Cited

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73:1045-1055.

Chesson, P.L. and T. J. Case. 1986. Overview: Nonequilibrium community theories: chance, variability, history and coexistence. *In* Diamond, J. and Case, T.J. (eds.) Community Ecology, Harper and Row, New York. Pp. 229-239.

Christy, J.A. and J. H. Titus. 1997. Classification and catalog of native wetland plant communities in Oregon — 1997 draft. Oregon Natural Heritage Program, Portland, OR.

Collins S.L. and S. M. Glenn. 1990. A hierarchical analysis of species abundance patterns in grassland vegetation. American Naturalist 135:633-645.

_________. 1991. Importance of spatial and temporal dynamics in species regional abundance and distribution. Ecology 72:654-664.

Collins S.L., S. M. Glenn, and D. W. Roberts. 1993. The hierarchical continuum concept. Journal of Vegetation Science 4:149-156.

Davey, M.C. and J. Rothery. 1993. Microalgal distribution on Antarctic soils. Journal of Ecology 81:335-344.

del Moral, R. 1993. Mechanisms of primary succession on volcanoes: a view from Mount St. Helens. *In* J. Miles and D. H. Walton (eds.) Primary succession on land. Blackwell Scientific Publications, London, UK. Pp. 79-100.

del Moral, R. and L. C. Bliss. 1993. Mechanisms of primary succession: insights resulting from the eruption of Mount St. Helens. Advances in Ecological Research 24:1-66.

del Moral, R., J. H. Titus, and A. M. Cook. 1995. Early primary succession on Mount St. Helens, Washington, USA. Journal of Vegetation Science 6:107-120.

del Moral, R. and D. M. Wood. 1986. Subalpine vegetation recovery five years after the Mount St. Helens eruption. *In* S. A. C. Keller (ed.) Mount St. Helens: Five Years Later. Symposium May, 1985. Eastern Washington State University Press, Cheney, WA. Pp. 215-221.

_________. 1993a. Early primary succession on the volcano Mount St. Helens. Journal of Vegetation Science 4:223-234.

_________. 1993b. Early primary succession on a barren volcanic plain at Mount St. Helens, Washington. American Journal of Botany 80:981-992.

Foxworthy, B. L. and M. Hill. 1982. Volcanic eruptions of 1980 at Mount St. Helens: the first 100 days. U.S. Geological Survey Professional Paper 1249.

Franklin, J. F. and C. T. Dyrness. 1988. Natural Vegetation in Oregon and Washington. Oregon State University Press, Corvallis, OR.

Grime, J. P., J. G. Hodgson, and R. Hunt. 1988. Comparative Plant Ecology: a Functional Approach to Common British Species. Unwin Hyman, London, UK.

Grishin, S. Yu., R. del Moral, P. V. Krestov, and V. P. Verkholat. 1996. Succession following the catastrophic eruption of Ksudach Volcano (Kamchatka, 1907). Vegetatio 127:129-153.

Halpern C. B., P. M. Frenzen, J. E. Means, and J. F. Franklin. 1990. Plant succession in areas of scorched and blowndown forest after the 1980 eruption of Mount St. Helens, Washington. Journal of Vegetation Science 1:181-194.

Hill, M. O. 1979. TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Dept. of Ecology and Systematics, Cornell University, Ithaca, NY.

Hill, M. O. and H. G. Gauch. 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio 42:47-58.

Hitchcock, C. L. and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, WA.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren. 1987. Data Analysis in Community and Landscape Ecology. Pudoc, Wageningen, The Netherlands.

Keddy, P. A. 1989. Competitive hierarchies and centrifugal organization in plant communities. *In* J. Grace and D. Tilman. Perspectives on Plant Competition. Academic Press, New York. Pp. 265-290.

Kent, M. and P. Coker. 1992. Vegetation Description and Analysis: A Practical Approach. CRC Press, Inc., Boca Raton, FL.

Kruckeberg, A. R. 1987. Plant life on Mount St. Helens before 1980. *In* D. E. Bilderback (ed.) Mount St. Helens 1980. University of California Press, Berkeley, CA. Pp. 3-23

Kunze, L. M. 1994. Preliminary classification of native, low elevation, freshwater wetland vegetation in western Washington. Washington Natural Heritage Program, Department of Natural Resources, Olympia, WA.

Lavorel, S. and J. D. Lebreton. 1992. Evidence for lottery recruitment in Mediterranean old fields. Journal of Vegetation Science 3:69-78.

Margalef, R. 1963. On certain unifying principles in ecology. American Naturalist 97:357-374.

Moody, M. E. and R. N. Mack. 1988. Controlling the spread of plant invasions: the importance of nascent foci. Journal of Applied Ecology 25:1009-1021.

Nuhn, W. W. 1987. Soil genesis on the 1980 pyroclastic flows of Mount St. Helens. M.S. thesis, University of Washington, Seattle, WA.

Pacific Northwest River Basins Commission. 1969. Climatological Handbook Columbia Basin States. Vol. 1, Part A and Vol. 2. Meteorology Committee, Pacific Northwest River Basins Commission, Portland, OR.

Prach K. and P. Pysek 1994. Clonal plants: what is their role in succession? Folia Geobotanica et Phytotaxonomica 29:307-320.

Primack, R.B. and S. L. Miao. 1992. Dispersal can limit local plant distribution. Conservation Biology 6: 513-519.

Sale, P. F. 1977. Maintenance of a high diversity in coral reef fish communities. American Naturalist 111:337-359.

Smilauer P. 1993. CanoDraw 3.0. Environmental Change Research Centre, University College, London, UK.

Stöcklin, J. and E. Bäumler. 1996. Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. Journal of Vegetation Science 7:45-56.

Talling, J. F. 1951. The element of chance in pond populations. Naturalist 839:157-170.

ter Braak C. J. F. 1990. CANOCO - a FORTRAN program for CANOnical Community Ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 3.10). Microcomputer Power, Ithaca, NY.

Titus, J. H., J. Christy, D. VanderSchaaf, and J. S. Kagan. 1996. Native Wetland, Riparian, and Upland Plant Communities and their biota in the Willamette Valley, Oregon. Report to Environmental Protection Agency, Region X, Seattle, WA, USA. Willamette Basin Geographic Initiative. Oregon Natural Heritage Program, The Nature Conservancy, Portland, OR.

Titus, J. H. and R. del Moral. 1998. Seedling establishment in different microsites on Mount St. Helens, Washington, USA. Plant Ecology 134:13-26.

Titus, J. H., S. Moore, M. Arnot and P. J. Titus. 1998. Inventory of the vascular flora of the blast zone, Mount St. Helens, Washington. Madroño 45:145-161.

Tsuyuzaki, S. 1989. Contribution of buried seeds to revegetation after eruptions of the volcano Mt. Usu, northern Japan. Botanical Magazine Tokyo 102:511-520.

__________. 1997. Wetland development in early stages of volcanic succession. Journal of Vegetation Science 8:353-360.

Tsuyuzaki, S. and J. H. Titus. 1996. Vegetation development patterns in erosive areas on the Pumice Plains of Mount St. Helens. American Midland Naturalist 135:172-177.

Tu, M., J. H. Titus, S. Tsuyuzaki, and R. del Moral. 1998. Composition and dynamics of the wetland seed bank on Mount St. Helens, Washington, USA. Folia Geobotanica et Phytotaxonomica 33:3-16.

van der Maarel, E. and M. T. Sykes. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. Journal of Vegetation Science 4:179-188.

Walton, D. W. H. 1990. Colonization of terrestrial habitats—organisms, opportunities and occurrence. *In* K. Kerry and G. Hempel (eds.) Antarctic Ecosystems: Ecological Change and Conservation. Springer-Verlag, Heidelberg, Germany. Pp. 51-60.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279-338.

Zar, J. H. 1984. Biostatistical Analysis. Second edition. Prentice-Hall, Inc., Englewood Cliffs, NJ.

Received 4 September 1998
Accepted for publication 18 June 1999