PREDICTABILITY OF PRIMARY SUCCESSIONAL WETLANDS ON PUMICE, MOUNT ST. HELENS

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ABSTRACT

This study describes wetland vegetation developing on young volcanic surfaces at Mount St. Helens. Canonical correspondence analysis (CCA) revealed that habitat types reflecting moisture regimes were the best predictors of species composition and that elevation and geographical position were also significant predictors. Explained variation was significant and had increased from 19% to 31% in the five years since these wetlands were first sampled. Ten community types derived by TWINSPAN were cohesive when mapped in the CCA space. They represent more developed versions of community types previously identified in the study area. Understories of plots with over 70% *Salix* cover were internally more similar than those with less than 10% *Salix* cover, suggesting that biotic effects may be reducing variation. Similarity among plots connected by rapidly moving water was higher than that among plots supported by seeps and among drier plots. This suggests that dispersal limitations continue to influence understory species composition in isolated vegetation. The results of this study suggest that wetland vegetation is beginning to demonstrate deterministic effects due to competition and stronger coupling to moisture regimes. (From Madroño, 1999, 46:177-186)

INTRODUCTION

Wetlands forming on newly emplaced substrates are unusual. Those forming on Mount St. Helens offer an opportunity to test basic hypotheses about community assembly. Davey and Rothery (1993) proposed that assembly in Antarctic sinkholes was stochastic, but vegetation had not developed sufficiently there to determine the long-term affects of chance establishment. Motzkin et al. (1999) demonstrated that forest development in New England was controlled largely by unique historical factors. Fort & Richards (1998) suggested that the lack of seeds in a barren playa inhibited succession and Fastie (1995) demonstrated that dispersal strongly affected the course of primary succession in glacier valleys. There are no long-term studies of wetland formation on primary substrates, so the situation on Mount St. Helens provides a unique opportunity to explore the potential transition from a stochastic assembly to vegetation controlled by more deterministic factors (cf., Walker 1993, 1999).

Colonization of newly formed substrates requires physical facilitation (Bjärnason 1991; del Moral 1993a) and eventual colonization (Kalliola et al. 1991; del Moral and Bliss 1993). If a site is sufficiently isolated, limited dispersal produces initially variable vegetation (Wood and del Moral 1988; Clarkson 1990; del Moral 1993b; del Moral and Grishin 1999). Titus et al. (1999) studied wetlands established after the 1980 eruption of Mount St. Helens on the Pumice Plain. They concluded that similar sites might develop different plant communities due to stochastic effects. They also found only weak interactions between environmental factors and species composition. Developing dominance was predicted to reduce variation between sites by altering the competitive environment and by reducing habitat variation (del Moral 1999; Dlugosch and del Moral 1999).

This study centers on a subset of the primary wetlands examined by Titus et al. (1999). The purposes are to determine if increasing *Salix* dominance has reduced floristic variation and whether links between vegetation and the environment have developed. Wetland vegetation has developed rapidly, so it is here that biotic factors should first become apparent on pumice. Earlier studies on Mount St. Helens suggested that homogeneity increases as species expand from the site of their initial establishment (del Moral 1998). However, there is as yet scant evidence that dominance reduces heterogeneity in early primary succession on Mount St. Helens. The relationship between the woody species and within-community variation was used to explore the putative shift from stochastic to deterministic control of vegetation. I will describe the relationships between species and their environment and explore the evidence that vegetation is responding deterministically to environmental or biotic factors.

METHODS

Study area. All wetlands were on the Pumice Plains of Mount St. Helens between the south shore of Spirit Lake and the lower slope of the cone. A wetland was defined by the presence of saturated soils during July. Elevations ranged from 1035 m to 1340 m. Plots were established as close to sites sampled by Titus et al. (1999) in 1993 and 1994 as could be determined from his map. Of the 79 plots sampled in this study, at least 68 were floristically similar to and within a few meters of sites studied by Titus et al. (1999). However, direct comparisons were not possible because I could not relocate the plots exactly. The factors of slope and aspect used in that study were not used, but were replaced by elevation, erosion and geographic position variables that incorporated the potential variation.

Environmental data. Each plot was located using a global positioning system device and the positions placed on a topographic map. Positions were divided into five categories in two dimensions each (rotated 30° from true north). Elevations were divided into nine segments with approximately equal numbers of plots. Erosion was determined in three categories: sediments being removed, little erosion, or sediments being deposited. Tsuyuzaki et al. (1997) showed that erosion strongly influenced seedling survival.

Composites of five subsurface soil samples were obtained from each plot between 2 and 8 cm. Soils were dried at 105ºC. Texture was estimated by sieving 100 g of each sample through 2 mm, 250 µm and 63 µm screens to form four fractions (gravel, coarse sand, sand and fines). Soil pH was determined from a 1:1 soil paste of a 50 g subset of each sample. Organic matter was determined from a 20 g subset by loss on ignition at 400ºC after 24 h.

Habitats were assigned to one of five categories: rapidly moving spring-fed streams (Spring), slow, low volume seep-fed courses (Seep), snow-fed stagnant trickles (Stagnant), habitats isolated from moving water (Isolated) and drier sites (Drier). Both springs and seeps remain active throughout the growing season. Stagnant habitats are low-gradient sites that often dry out during late summer. Isolated wetlands form in depressions that may be supported by ground water. Drier sites were either alluvial, with little to no stream flow, or rocky and narrow.

Vegetation sampling. Sites were sampled during July and August 1998 using 5 by 20 m plots established within the wetland. Sites were selected using a map of previously sampled sites and composition compared to field data collected by Titus et al. (1999). Woody species cover was determined directly over the whole plot by visual estimate. Mean herb layer cover was determined from five 1-m^2 quadrats placed regularly along the long axis of the plot adjacent to any surface water. R. N. Fuller and I sampled the first 20 plots together to ensure comparability in cover determinations and species identification. Thereafter, we each sampled plots independently, but calibrated our determinations frequently. Species not sampled but within the 5 by 20 m plot were given a value of 0.1%.

Vascular plant nomenclature follows the Integrated Taxonomic Information System (found at: www.itis.usda.gov). Two wetland mosses were sampled and could be distinguished in the field. Based on Vitt et al. (1988), photographs and consultation with Paul Yurky (pers. comm.), the two dominant mosses were identified as *Philonotis fontana* and *Brachythecium* sp. (either *B. rivulare* or *R. frigidum*), widely distributed highland mosses. *Cratoneuron* spp. are found along streams in this area, but were not sampled. Upland mosses encountered on dry margins of some samples included *Racomitrium* spp., *Polytrichum* spp. and *Oligotrichum*. Species were assigned to one of five wetland indicator categories based on Reed (1988) to assess the degree to which communities reflected wetland conditions. Hydrophytic species are defined as those that always (obligate), usually (facultative wetland) or often (facultative) occur in wetlands. Species that seldom (facultative upland) or rarely (upland) occur in wetlands suggest dry conditions. Nonvascular plants reported here are assumed to be hydrophytic based on their occurrence in saturated soil.

Classification. The plots were classified with two-way indicator species analysis (TWINSPAN; Hill and Gauch 1979), comparable to the previous study (Titus et al. 1999). I used cut-levels of 0, 2, 5, 10 and 20%, five divisions and deleted species with fewer than four occurrences (see McCune and Mefford 1997 for details.)

Indirect ordination. Patterns within the data were sought by detrended correspondence analysis (DCA; Hill and Gauch 1980). I used untransformed percent cover, deleted species with fewer than four occurrences and down-weighted species whose frequency was less than 20%. Axes were rescaled and divided into 26 segments for detrending. Nonmetric multidimensional scaling (NMS; Minchin 1987) gave similar results and is not reported. NMS showed that the matrix was three-dimensional. I used a multiple regression of the environmental values to predict DCA axis scores and to provide an estimate of their relationship to species patterns.

Direct ordination. I used canonical correspondence analysis (CCA; McCune and Mefford 1997) to evaluate relationships between environmental factors and species cover. CCA determines the least squares linear regression of environmental variables on plot scores determined by correspondence analysis. New plot scores are calculated by a multiple regression of the environmental scores. I used eigenvalues, Pearson correlations between species and environmental axes and correlations of variables to each axis to describe the results. I used *t*-values associated with the regression coefficient of environmental factors using CANOCO 4.0 (ter Braak and Šmilauer 1998) only to help assess the importance of each variable rather than to test hypotheses. Monte Carlo simulations (n=1000) were used to assess significance of eigenvalues and of species-environment correlations.

These continuous variables were used: elevation, erosion, soil pH, percent organic matter, gravel, coarse sand, sand and fines (silt and clay). In addition, the X and Y coordinates, in five geographic categories along northwest to southeast and northeast to southwest transects, were used. As described above, five categorical variables were used to characterize the habitats: spring, seep, stagnant, isolated and drier. Categorical values were treated as a set of binaries (ter Braak 1986). In order to avoid high variance inflation values (which occur when a set of variable are internally constrained), I eliminated “fines” and “isolated habitat” from the CCA.

Statistics. Plot structure (richness, percent cover, Shannon diversity and evenness were calculated with PC-ORD (McCune and Mefford 1997). Richness is the number of species, percent cover is the total cover of species in the plot, Shannon diversity is H', the information theory statistic and evenness is H'/ln Richness. Evenness approaches 1.0 as dominance decreases. Descriptive statistics were calculated with Statistix 4.1 (Analytical Software 1994). Comparisons among multiple means were conducted by Bonferroni comparisons after any significant analyses of variance. I used percent similarity to assess relationships within groups of plots. It was calculated using MVSP 3.0 (Kovach 1998).

RESULTS

Classification. Ten community types (CTs) were identified with TWINSPAN. Table 1 summarizes the species composition of the more common species. Species are ordered so that their weighted mean cover shifts diagonally down the table. Values are the mean percent cover. The number of samples in each CT is given within parentheses. Characteristic species, those found in all samples of a CT, are in bold. These species may be common or rare, but they occur in all samples of a CT. Mean species richness, mean percent cover, Shannon diversity (H') and evenness are summarized in Table 2 by habitat and in Table 3 for each CT. Wetland indicator status is shown and total percentage of hydrophytic species is summarized in Table 3. In these tables, all values within a column that share the same superscript are not significantly different ($P < 0.05$) from each other as determined by the conservative Bonferroni multi-comparison test.

Hydrophytic species dominated all CTs and accounted for between 80.9% and 99.9% of total cover. No upland or *facultative* upland species was prevalent, but some were common along the margins of CTs with less developed canopies.

A. *Salix sitchensis/Epilobium luteum/*mixed mosses CT—This CT occurs in stagnant sites with moderate pH and organic matter. Soil has a low gravel fraction and moderate fine material. *Salix* dominance is strong, *Philonotis fontana* and *Brachythecium* are abundant and *Epilobium luteum* and *Equisetum arvense* are common. Species richness is very low and cover is very high.

B. *Salix sitchensis/Aruncus dioicus/Carex mertensii* CT—This CT is moderately eroded with coarse soils and *moderate* organic matter. It occurs along seeps, some of which may dry out. This CT occurs at lower elevations near Spirit Lake. *Salix* remains small and open, while *Alnus* and non-hydrophytic herbs such as *E. angustifolium*, *Anaphalis* and *L. latifolius* occur on the margins of this type. Cover is moderate and richness relatively low.

C. *Salix sitchensis/Epilobium ciliatum-Calamagrostis canadensis*/mixed mosses CT—All plots are sustained by seeps with moderate to low erosion. Soils are coarse and lack fines. *Salix* is scattered, while *Epilobium* occurs consistently. Though there is constant low water flow, which helps support *Philonotis* and *Brachythecium*, the soil has poor water retention and late summer drought is likely. Richness is intermediate and cover is relatively low.

D. *Salix sitchensis*/mixed herbs/mixed mosses CT—This CT occurs at higher elevations with rapid stream flow. Soils are acid, with low organic matter. *Salix* is ubiquitous, but poorly developed. Characteristic species include the non-hydrophytic species *Lupinus lepidus*, *Anaphalis* and *Hypochaeris*, though these are not common and are confined to the wetland margins. *Philonotis* and *Brachythecium* are common in local stable patches. High species richness and diversity result from low cover by *Salix*. It appears that soil and snow movements frequently disturb this type and have retarded vegetation development.

E. *Salix sitchensis/Mimulus lewisii-E. ciliatum/Philonotis fontana* CT—These plots are eroded, with low organic matter, low pH and coarse substrates. They occur at higher elevations along streams or near seep sources with well-developed *Salix*. *Philonotis* and *Mimulus* characterize this type. The liverwort *Marchantia* is abundant where stream flow *is* high, but is otherwise lacking. The understory demonstrates high richness, cover and diversity.

F. *Salix sitchensis/Juncus* spp.*/Brachythecium* sp. CT—This CT occurs at lower elevations in stagnant habitats near Spirit Lake. The organic fraction and fines are low, while pH is moderate. Though structurally similar to CT E, CT F has a *more* open *Salix* layer, several *Juncus* species and dominance by *Brachythecium*. It lacks *Petasites*, has little *Mimulus* or *Philonotis*, species normally associated with moving water. Richness and diversity are low and cover moderate.

G. *Salix sitchensis/Juncus* spp.-*E. ciliatum*/*Cratoneuron commutatus* CT—This CT occurs at lower elevations in dry and isolated habitats with little erosion. Soil pH is high and texture is coarse. *Salix* cover is low, but developing, and rushes are abundant in the wetter parts of this type. Cover is low, but richness and diversity are high.

H. *Salix sitchensis/Equisetum arvense-Juncus* spp. CT—This CT occurs primarily in dry and isolated sites at low elevations where erosion is nil. Organic matter is low, pH is high and fines are moderate. This CT is similar to CT G, but *Equisetum* is more abundant and *Brachythecium* is rare. Richness and diversity are intermediate.

I. *Salix sitchensis/Equisetum arvense* CT—This CT occurs in *depositional* sites at low elevations. Sites have high organic matter, moderate pH and a high level of fine material. *Salix* and *Equisetum* dominate, but sites are open. Richness and diversity are very low and various *Juncus* species occur sporadically.

J. *Typha latifolia-Juncus bufonius* CT—This CT occurs in narrow *seeps* with little erosion. *Typha* dominates and *Juncus bufonius* is abundant, but plots remain open. The margins contain a variety of upland species such as *Epilobium angustifolium*, but richness is moderate. One plot had an abundance of *Epilobium ciliatum*, but was otherwise similar to the other plots in CT J.

Vegetation structure. The richness and cover of plots in each of the five habitat types are variable. Springs are significantly richer than all other habitats. Diversity within habitats varies considerably, but Drier sites are significantly lower (Table 2). The habitats do not differ significantly in cover or evenness.

CTs do differ in vegetative structure (Table 3). For each measure of vegetation structure, an initial one-way ANOVA was conducted. Despite large differences in evenness between CTs, the ANOVA was not significant due to high variance. Significant differences occurred among the other parameters. Subsequent Bonferroni comparisons indicated that there were four overlapping richness groups. Richness was greatest in the high elevation, eroded habitats found along faster moving streams (CTs D and E) and least in stagnant or dry sites (CTs A and I). Vegetation cover was high in protected, stagnant sites (CT A) and along seeps and streams (CT E) where *Salix* was well *developed*. Low cover is associated with high elevation, eroded sites (CT D) that, though similar to CT E, occur in narrower streambeds and lack *Salix* dominance. Low cover also occurs in depositional habitats where *Juncus* or *Typha* are common, but incompletely developed. The lowest diversity and least equitability occur in CT I, formed in a depositional habitat that is dominated by *Salix* and *Equisetum*. CT F, dominated by *Salix* and *E. ciliatum*, also has low richness, diversity and equitability. The more diverse CTs are those that have yet to develop a dense canopy and which have an open herb layer (e.g., CTs D, G and H). The less diverse CTs occur in more stable habitats where dominance has developed (CTs A, F and I)

Indirect ordination. Species composition was analyzed by DCA using percent cover. The eigenvalues for the first three axes were 0.348 (8.4%), 0.216 (5.2%) and 0.170 (4.1%), respectively. Each habitat type (not plotted) tends to occur in a distinct portion of the graph, but plots overlap considerably, particularly in only two dimensions. This implies that there is only a modest relationship between species composition and habitat type. The trend along DCA-1 is from plots along rapidly moving streams, through seeps to drier or depositional habitats (Fig. 1). Along DCA-2 a less pronounced trend is from stagnant to drier habitats. Isolated habitats overlap drier ones and seeps, suggesting that habitat classifications do not completely capture moisture effects. Along DCA-1, CTs D and E form one extreme and CT J the other. (One sample of CT J was unique in that it contained a high concentration of *Epilobium ciliatum*, a short-lived herb.) This reflects a gradient from *Salix* dominated sites with rapid stream flow and strong erosion to sites dominated by *Typha* and *J. bufonius* in isolated or depositional habitats. Along DCA-2, the trend is from CT F, dominated by *Salix*, Moss B and *Marchantia* to CT B, seep sites with margins dominated by upland species such as *Aruncus, C. mertensii* and *E. angustifolium* and CT H, dominated by *Salix*, *Equisetum* and *Juncus* spp.

DCA species patterns offer little additional insight. Inspection of the species graph from DCA shows that *Equisetum* and *Typha* dominate depositional wetlands. *Juncus ensifolius*, *J. articulatus* and *J. bufonius* are typical of some low-energy wetlands. In contrast, the upland species *J. parryi* is common along stream margins, as are such typically upland species as *Agrostis pallens*, *Carex mertensii*, *Hieracium albiflorum* and *Luzula parviflora*.

Simple correlations of environmental factors to DCA scores (cf. Gauch 1982) suggested spatial correlations. The X-position value increased with DCA-1 (r = 0.70; $P < 0.01$) and decreased with elevation (r = -0.65; $P < 0.01$). Low DCA-1 scores were associated with Springs (r = -0.57; $P < 0.01$), while higher DCA-1 scores were associated with Drier sites (r = 0.52), Isolated sites (r = 0.42) and higher soil pH (r = 0.59). DCA-2 was weakly correlated with a gradient of Stagnant (r = -0.37) to Drier sites (r = 0.28, $P < 0.05$) and with fine soil (r = 0.45). A multiple regression of the environmental factors with DCA scores implied the relative strength of correlations of environmental factors to species patterns. Two analyses were conducted. First, without spatial variables, DCA-1 was predicted by these factors (multiple r = 0.82): stagnant ($P < 0.001$), fresh ($P < 0.001$), drier ($P < 0.004$) and seep ($P < 0.02$) habitats, soil pH ($P < 0.003$) and gravel ($P < 0.03$). The second analysis, with spatial factors included, was slightly better (multiple r = 0.86). The location in the X-position ($P < 0.001$) was the strongest predictor of the DCA-1 score of a plot, followed by stagnant ($P < 0.002$), pH ($P < 0.005$) and drier ($P < 0.01$). DCA-2 was unaffected by spatial factors. The regression (multiple r = 0.68) was associated with elevation ($P < 0.02$) and seeps ($P < 0.04$).

Direct ordination. CCA was applied to the species and environmental data (excluding fine texture and isolated habitats to eliminate co-linearity). Table 4 summarizes the standardized canonical coefficients and intraset correlations. The constrained plot ordination (community types) is overlain by the vectors to indicate relative importance of environmental variables (Fig. 2). The vectors are exaggerated two-fold. The Pearson correlation between plot positions determined by correspondence analysis and those predicted by a multiple regression of environmental values were 0.861, 0.746 and 0.732, respectively. The variances (eigenvalues) associated with each axis were 0.348, 0.216 and 0.170, respectively. These measured variables explained 30.4% of the species-environment correlation. These eigenvalues and species matrix to environment matrix correlations were significant (1000 Monte Carlo simulations, $P < 0.001$).

Significant canonical coefficients for CCA-1 (estimated from *t*-tests) were for the variables Stagnant ($P < 0.001$), Seep ($P < 0.01$), Spring ($P < 0.01$), X-position ($P < 0.05$) and pH ($P < 0.05$). Significant CCA-2 canonical coefficients were for Seep ($P < 0.001$), Drier ($P < 0.01$) and Elevation ($P < 0.05$). Intraset correlations indicate the degree to which a variable is correlated with the species axes. Bi-plot positions of environmental variables illustrate the strong effects of habitats, elevation, erosion and position. Soil pH is the only significant soil factor. The overall relationships between these two axes and the environmental factors were relatively strong. The CTs segregate well in this space (Fig. 2), indicating that the environmental factors capture a significant portion of the species variation.

In order to test the hypothesis that *Salix sitchensis* was a deterministic factor that structured vegetation, a second CCA was completed, with *Salix* transferred to the environmental matrix. Inclusion of *Salix* altered the canonical regression because it is correlated with elevation. Pearson correlations improved to 0.926, 0.852 and 0.773 for the first three axes, respectively. The variances associated with these axes increased to 0.573, 0.314 and 0.256, respectively (34.1% of the species-environment variation). The significant regression coefficients along CCA-1 were Stagnant ($P < 0.001$), X-position ($P < 0.001$) and Seep ($P < 0.05$). *For* CCA-2, Seep ($P < 0.001$), *Salix* ($P < 0.01$), X-position ($P < 0.01$) and Drier ($P < 0.05$) were significant.

Plot similarity. Another analysis was used to determine if *Salix* reduced between-plot heterogeneity by constraining understory species composition. Plots were categorized by *Salix* cover as follows: < 10% cover (n=23 plots); 10 to 20% cover (n=18); 21 to 50% (n=13); 51 to 70% (n=12); and > 70% (n=13). Cover of *Salix* and *Alnus* was removed since their inclusion guarantees that similarity will be relatively high and obscure understory relationships.

Mean similarity among *Salix* cover groups, from low to high, was: 14.7%, 19.3%, 17.8%, 14.4% and 21.0%. The only significant difference in mean similarity was between low *Salix* plots and high *Salix* plots ($P < 0.05$, Bonferroni comparison of all means).

Studies of uplands on the Pumice Plain (del Moral and Wood 1993) indicated that species established by nucleation, then expanded from initial foci. If wetlands form similarly, then there may be a negative relationship between the degree of isolation and similarity. Plots in the five habitats were studied for internal similarity. Analyses were conducted with all species and also with all tall woody species excluded (Table 5). If dispersal limited homogeneity development, then high similarities occur found in plots along active streams and low similarities in dry and isolated plots. Including shrub species, only Seeps were significantly less similar than Springs. Without shrubs, each of the habitat types displays low mean internal similarity. Springs had the highest values while Seeps and Dry habitats had the least internal similarity.

DISCUSSION

The present study suggested that significant changes have occurred during the five-year interval since the Titus et al. (1999) study. The rate of community development where erosion is strong is lower than where water flows are limited. Stable environments have developed dense shrub or dense ground layers, often both. The community types described in this study were floristically similar to those previously identified by Titus et al. (1999, see also Tu et al. 1998), but were more developed.

Each CT is variable (Fig. 1) and all plots now contain some *Salix*. While Titus et al. (1999) noted four CTs dominated by different species of *Juncus* with little or no *Salix*; here all *Juncus* plots had substantial willow. *Juncus* species were also common subordinates in several CTs. Many species generally not found in wetlands were common in the earlier study, particularly in open and seasonally wet habitats. Titus et al. (1999) predicted that species such as *Agrostis* spp., *Anaphalis margaritacea*, *Epilobium angustifolium*, *Lupinus lepidus*, and *Hypochaeris radicata* would decline in wetlands, and in fact they have.

The matches between the extant CTs and those previously defined are moderate. Differences due to willow maturation and my inclusion of mosses and liverworts make it impractical to match community types closely. There were 81 species in this study, compared to 104 in the more extensive study of Titus et al. (1999). Richness changed little between studies, from 14.8 to 15.2 species per plot. The continued species accumulation in open plots was balanced by the reduction in richness in plots that developed closed canopies. Cover in the 86 comparable plots in the earlier study was 46% compared to 66% in the 79 plots of this study. Cover increased dramatically in CTs A, B, C, E, F, H and I, due mostly to tall shrubs. CTs D and J had lower cover. The latter resulted because we did not sample any dense *Typha* communities. Mean species richness declined in CTs A, B, C and E, which had large cover increases due to *Salix* and *Alnus*. This suggests that dominance suppressed species richness.

The relationship between CTs and their environment remains weak, but detectable. The CTs segregated efficiently in DCA. The species-based ordination is correlated with measures of the environment. DCA-1 reflects species changes from sites with rapid stream flow and less acid soils to sites that are isolated or drier, and which may accumulate organic matter. As these habitats develop, I predict that the relationships will strengthen.

In contrast to the previous study of Pumice Plain wetlands, community types also segregated well in CCA space. CTs D and E occur along fast-moving streams (Spring), while CTs B and C occur in Seeps and CT F tends to form in Stagnant habitats. CT A is a variant found in Stagnant habitats characterized by *Epilobium luteum*. Isolated habitats contain CTs G and H, and are dominated either by *Juncus* spp. or by *Equisetum arvense*. Finally, Drier habitats are a mix of CTs I and J, with some examples of G and H. CT J, with the highest scores of CCA-1, is plots dominated by *Typha latifolia*, with *J. bufonius* and little *Salix*. The other CTs found in drier habitats are dominated by wind-dispersed species (i.e., *Salix*, *Epilobium angustifolium, E. ciliatum, Juncus* spp. and *Equisetum arvense*). Weak tendencies towards the association of certain species with particular habitats noted by Titus et al. (1999) have strengthened. *Salix* has developed and expanded, while *Equisetum* and *Juncus* have become more restricted. These changes are consistent with expected patterns of early primary succession.

Titus et al. (1999) noted a large stochastic element within Pumice Plain wetlands. Their analysis accounted for only 19% of the species-environment variation. In this study, 30% of the variation was associated with environmental factors. Including *Salix*, 34% of the variation was associated with the regression. This increase occurred despite the exclusion of unique warm-water or high elevation sites and of complex spatial parameters. *Salix* cover developed from 10% in the previous study to 28% in this one.

Investigations of plot similarities provided evidence for developing deterministic control of vegetation structure. Plots with strong *Salix* dominance were significantly more homogeneous than those with low *Salix* cover. Understory species do not dominate sufficiently to reduce between plot similarity because there is substantial open space in the understory of most plots.

The interaction between degree of isolation and degree of similarity is complex. Spring habitats were consistently the most similar. This reflects their connectivity and the ability of species to be dispersed along stream corridors. Seep habitats do not readily disperse seeds along the watercourses and dispersal of species with poor wind dispersal is constrained. Dry habitats are variable in composition due to a substantial stochastic effect. Stagnant and Isolated habitats are intermediate. The species common in isolated habitats (e.g. *Juncus* spp., *Eleocharis macrostachya*, *Equisetum* spp. and *Epilobium ciliatum*) are wind dispersed so that these habitats, though hydrologically isolated, may not be dispersal limited.

Several of the CTs described in this study have rough analogs throughout the region (Titus et al. 1996, 1998; Christy and Titus 1997), though these differ in structure from described associations owing to their immaturity. Associations dominated by *Salix sitchensis* are widespread (Kunze 1994), with a variety of understories, but none of the understories is recognized. A *S. sitchensis*/*Equisetum arvense-Petasitis frigidus* association was described by Christy (2000), and CT A could be assigned to this type. CT H and I are similar, but without *Petasitis*. A *Marchantia polymorpha-Philonotis fontana* association was described for sites in Oregon and British Columbia (Christy 2000). CT E may be similar to this type, but with willows and *Mimulus lewisii*. *Typha latifolia* associations are widespread. Here it is joined by *Juncus bufonius* an early pioneer species. None of the CTs described in this study have exact analogs elsewhere in the region. However, unlike the case in the adjacent uplands (del Moral et al. 1995), none is so different from described associations that it would be surprising for them to develop into recognized associations. The wetland CTs remain poorly correlated with their environment and are internally variable, yet each is recognizable. This paradox may result because most wetland CTs developed from only a few predominantly wind-dispersed species that quickly occupied these habitats. Because the initial colonization was stochastic, similar habitats may have received dissimilar colonists, for example one of several possible *Juncus* species. Subsequent invasions may be limited by infertile soils, poor dispersal or by competition from existing plants, thus perpetuating low similarity among vegetation in similar habitats. Due to the gradual development of an overstory, slow spread of better-adapted species (Fuller 1999) and competitive interactions, vegetation in these wetlands is becoming more predictable.

An initially stochastic pattern has begun to develop such that mechanisms that structure vegetation are becoming more prevalent. The principle structuring mechanisms in this study are the moisture regime, which permits rapid development of plant biomass, and the competitive effects of *Salix*. Vegetation should become more predictable as species come into closer equilibrium with these factors and competitive effects among the herbs develop more fully.

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TABLE 1. SPECIES COMPOSITION OF PRIMARY WETLANDS. Species listed as determined by TWINSPAN two-way table. Species values in bold indicate 100% frequency. t=< 0.1% cover. Less common species are omitted. "Wet" indicates the wetland indicator value of the species: OBL (obligate, always in wetlands); FACW (facultative wetland, usually in wetlands); FAC (facultative, indifferent to wetland conditions); FACU (facultative upland, usually not in wetlands); and UPL (upland, rarely in wetlands). Numbers in parentheses after Community Type designation are the number of samples in the CT.

		Percent Cover in Community Type									
Species	**Wet**	**A(3)**	**B (9)**	**C (7)**	**D(15)**	**E(12)**	**F (6)**	**G (7)**	**H (8)**	**I (7)**	**J (5)**
Aruncus dioicus	FACU		**4.1**							t	
Luzula parviflora	FAC		1.8		t	t				t	
Epilobium luteum	FACW	**8.1**	t			0.3					
Lupinus latifolius	UPL		1.9		1.2	t					
Hieracium albiflorum	UPL		t		0.1	0.1					
Mimulus lewisii	FACW		1.0	0.4	0.2	**6.4**	0.7				
Epilobium minutum	FACU	t	t	0.3	0.1	t	t	t			
Agrostis scabra	FAC			t	0.4				t		
Achillea millefolium	FACU				0.1	0.5	t	t			
Agrostis pallens	UPL				0.3	0.4		t			t
Marchantia polymorpha	FACW	1.3	t	0.3	0.2	8.7	5.9	0.6	0.7		
Philonotis fontana	FACW	**42.4**	2.1	**5.0**	**6.9**	**26.5**	6.4	2.1	4.0	t	t
Alnus viridis	FACW	3.3	3.3	0.5	1.3	0.8	0.2	t	0.4	t	
Epilobium angustifolium	FACU	**4.6**	5.8	0.9	0.1	5.2	t		0.2	t	11.8
Petasitis frigidus	FACW	2.8	0.5	0.3	t	1.0			0.4		
Brachythecium sp.	FACW			1.6	2.1	8.8	**34.6**	**10.5**	3.3		
Lupinus lepidus	UPL			t	**0.7**	0.5	t	0.1	t	t	t
Anaphalis margaritacea	UPL		2.3	0.7	**0.7**	1.4	0.1	0.1	0.1	0.1	0.3
Carex mertensii	FACW		**3.2**	1.1	0.5	**1.0**	0.5	**0.8**	0.4	0.3	
Carex microptera	FAC		0.4	t	t	t	t	0.1			
Agrostis exarata	FACW	t	0.8	0.5	**0.2**	0.9	0.1	0.1	1.1	0.5	0.9
Hypochaeris radicata	UPL		1.2	0.3	**0.2**	0.4	t	**0.5**	0.5	0.1	1.2
Salix sitchensis	FACW	**92.7**	**48.4**	**36.1**	**11.7**	**50.3**	**25.3**	**21.2**	**20.4**	**46.8**	**4.3**
Juncus mertensianus	OBL		0.1		0.1	0.5	2.2	0.1	1.2		
Calamagrostis canadensis	FACW		0.1	**1.1**	0.1	0.8				0.4	0.6
Epilobium ciliatum	FACW		0.4	**11.7**	**0.6**	**1.9**	**0.7**	**5.8**	**2.0**	0.1	**0.8**
Equisetum arvense	FAC	**2.5**	2.9	0.6	0.3	0.2	0.6	2.4	**19.8**	**18.9**	4.9
Juncus ensifolius	FACW				t	0.1	4.8	**4.3**	**2.4**	0.5	0.7
Juncus bufonius	FACW					0.2	0.5	**2.6**	**7.2**	0.7	**12.5**
Typha latifolia	OBL		t					0.1	1.7	0.1	**15.3**
Eleocharis macrostachya	OBL								4.9		0.1
Juncus articulatus	OBL						0.7	**4.5**	**2.0**	0.1	0.4

TABLE 2. STRUCTURE OF HABITAT TYPES. Richness is the mean number of species per plot in the habitat type; cover % is the mean total plant cover; H' is the mean Shannon diversity index; and E is the mean Simpson equitability. Values within a column with different superscripts (if any) are significantly different ($P < 0.05$, Bonferroni comparison).

Habitat type	Richness	Cover %	H'	E
Springs	20.7^{a}	65.7	1.65^{a}	0.55
Seeps	14.6^{b}	68.8	1.49^{a}	0.57
Stagnant	12.3^{b}	106.5	1.28^{a}	0.52
Isolated	13.1^{b}	55.5	1.68^{a}	0.64
Drier	11.9^{b}	82.7	1.10^{b}	0.46

TABLE 3. STRUCTURE OF COMMUNITY TYPES. Values within a column with different superscripts (if any) are SIGNIFICANTLY different ($P < 0.05$, Bonferroni comparison). Richness is the mean number of species per plot; cover % is the mean cover in the community type, H' is the mean Shannon diversity index of the CT, E is the mean evenness of the CT, and % Hydrophytic is the cover of species considered to be hydrophytes, e.g., obligate, facultative wetland, or facultative species (cf. Reed 1988).

C.T.	**Name**	Richness	Cover %	H'	E	% Hydrophytic
A	*Salix/Epilobium luteum/* mosses	10.0^{cd}	157.6^{a}	1.09^{ab}	0.484	97.9
B	*Salix/Aruncus-Carex mertensii*	13.7b^{cd}	83.7^{bc}	1.34^{ab}	0.508	80.9
C	*Salix/E. ciliatum-Calamagrostis/*mosses	13.0b^{cd}	67.5^{cd}	1.42^{ab}	0.596	96.4
D	*Salix/*mixed herbs/ mosses	20.5^{a}	28.9^{d}	1.68^{a}	0.562	91.5
E	*Salix/Mimulus-E. ciliatum/Philonotis*	19.6^{ab}	117.6^{ab}	1.61^{a}	0.540	92.6
F	*Salix/Juncus* spp.*/Brachythecium*	12.0^{cd}	85.5^{bc}	1.18^{ab}	0.481	99.9
G	*Salix/Juncus* spp.-*E. ciliatum*/*Brachythecium*	16.0^{abc}	57.2^{cd}	1.70^{a}	0.613	99.1
H.	*Salix/Equisetum arvense-Juncus* spp.	14.2^{bcd}	72.9^{bc}	1.67^{a}	0.633	99.2
I.	*Salix/Equisetum arvense*	8.3^{d}	73.0^{c}	0.79^{b}	0.387	99.7
J.	*Typha latifolia-Juncus bufonius*	12.8^{bcd}	52.6^{cd}	1.52^{ab}	0.603	97.2

TABLE 4. STANDARDIZED CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS BETWEEN ENVIRONMENTAL FACTORS AND CONSTRAINED ORDINATIONS. STATISTICAL evaluations are exploratory and based on *t*-tests. *a* = $P < 0.05$; *b* = $P < 0.01$; *c* = $P < 0.001$

	CCA-1	**CCA-2**	**CCA-1**	**CCA-2**
Variable	**Canonical Coefficients**		**Intraset Correlation**	
Erosion	0.10	0.05	-0.59	-0.13
pH	0.19^{a}	0.02	0.71	0.04
Gravel	-0.07	0.17	-0.25	-0.04
Coarse sand	0.02	0.09	-0.08	0.33
Fine sand	0.06	0.11	0.02	0.03
Organic	-0.10	-0.06	-0.10	-0.40
Elevation	0.07	-0.26^{a}	-0.72	-0.12
Spring	-0.52^{b}	0.04	-0.55	0.13
Seep	-0.40^{b}	-0.43^{c}	-0.14	-0.69
Stagnant	-0.42^{c}	0.01	-0.24	0.53
Drier	-0.09	-0.30^{b}	0.73	-0.17
X (NE to SW)	0.24^{a}	-0.02	0.77	0.14
Y (NW to SE)-	-0.12	-0.05	-0.45	-0.20

TABLE 5. PERCENT SIMILARITY WITHIN HABITAT TYPES. Parenthetical values are standard deviations. Values sharing a superscript in each row are not significantly different ($P < 0.05$, Bonferroni comparisons across each row).

Analysis	**Spring**	**Seep**	**Stagnant**	**Isolated**	**Dry**
All species	39.4 (18.9)^{a}	28.8 (19.6)^{b}	31.86 (19.7)^{ab}	36.1 (17.1)^{ab}	33.5 (23.0)^{ab}
No shrubs	32.5 (19.0)^{a}	15.9 (13.6)^{c}	24.7 (20.5)^{ab}	28.4 (20.9)^{ab}	18.6 (23.4)^{bc}

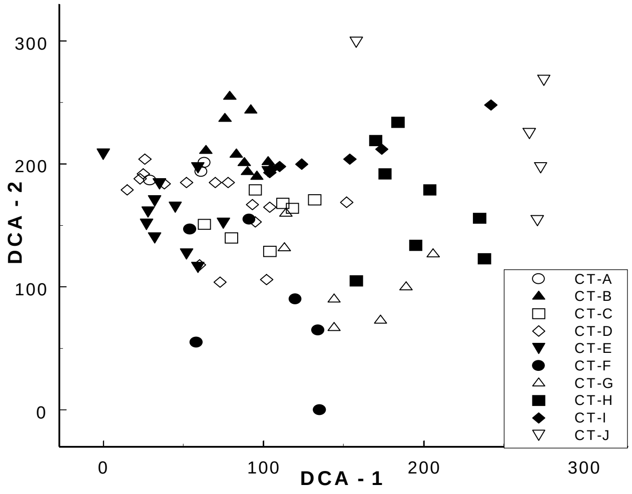

Fig 1. Detrended correspondence analysis ordination of 79 wetland plots. Symbols are keyed to the 10 community types (CT) identified by TWINSPAN classification. Axes are scaled in turnover units such that plots separated by 400 units have no species in common.

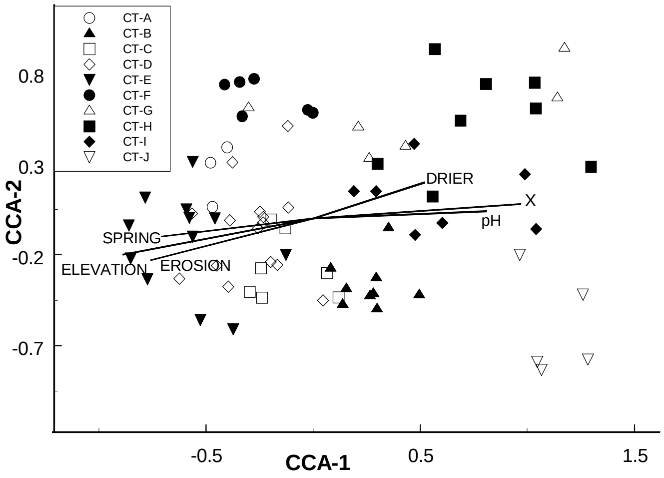

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Fig. 2. Canonical correspondence analysis 79 wetland plots using 13 environmental variables. Only the variables with strong predictive power are shown as vectors. The length of the vector is proportional to the effect of the variable in predicting the position of a sample (length of vectors has been exaggerated two-fold for clarity). Spring = spring-fed stream habitats; Drier = depositional habitats likely to dry during late summer; X = position on grid of samples, from northwest to southeast); Elevation = elevation class from high to low; Erosion = degree of erosion from high to low; and pH = soil pH, from low to high.