Forest development following mudflow deposition, Mount St. Helens, Washington

Marc H. Weber, Keith S. Hadley, Peter M. Frenzen, and Jerry F. Franklin

Abstract: Volcanic mudflows are locally important disturbance agents in the Pacific Northwest rarely studied within the context of forest succession. We describe 18 years (1981–1999) of forest development on the Muddy River mudflow deposit following the 1980 eruption of Mount St. Helens using permanent plot data collected along two transects traversing the Cedar Flats river terrace. We analyze changing forest structure over the study period and compare results with mudflow deposition using correlation and pairwise comparisons, as well as ordination (detrended correspondence analysis) and cluster analysis. Our results show a statistically significant relationship between mudflow deposition and forest change. Following mudflow deposition, the site consisted of patches of high tree mortality caused by deep mudflow deposits in abandoned river channels as well as patches of accelerated regeneration of surviving understory trees in areas of more shallow mudflow deposition and partial overstory mortality. Mudflow deposition at the site initiated multiple stages of stand development with (1) early-colonizing red alder (*Alnus rubra* Bong.) dominating deep deposition sites with fewer surviving trees, (2) gap recruitment and establishment by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) on intermediate to deep deposition sites with more postburial surviving trees, and (3) late-seral conditions and accelerated succession on shallow burial sites, where tree mortality was low. The initiation of differing succession trajectories, as well as variability in the extent and timing of tree mortality following mudflow deposition, demonstrates a dynamic response to disturbance in relation to small-scale gradients of mudflow deposition.

Résumé : Localement, les coulées de boue volcanique sont des agents de perturbation importants dans le Pacific Northwest qui ont rarement été étudiés en lien avec la succession forestière. Les auteurs décrivent l'évolution de la forêt pendant 18 ans (1981–1999) sur les dépôts de boue de la rivière Muddy formés lors de l'éruption du mont Saint Helens en 1980 à l'aide des données provenant de placettes-échantillons permanentes et collectées le long de deux transects qui traversent la terrasse alluviale de Cedar Flats. Ils ont analysé l'évolution de la structure de la forêt pendant toute la période d'étude et ils ont mis en relation ces résultats avec les dépôts de boue en effectuant des corrélations et des comparaisons par paires et en ayant recours aux techniques d'ordination (analyse des correspondances redressée) et à l'analyse de groupement. Leurs résultats montrent qu'il y a une relation statistiquement significative entre les dépôts de boue et l'évolution de la forêt. À la suite des dépôts de boue, le site était caractérisé par des parcelles où la mortalité des arbres était élevée à cause de l'épaisseur des dépôts de boue dans les lits de rivière abandonnés ainsi que des parcelles de régénération accélérée grâce aux arbres qui ont survécu en sous-étage dans les endroits où les dépôts de boue étaient plus minces et où la mortalité dans l'étage dominant était plus faible. Dans cette région, les dépôts de boue ont déclenché plusieurs stades de développement du peuplement caractérisés par : (1) la présence d'une espèce pionnière précoce, l'aulne rouge (*Alnus rubra* Bong.), qui domine les sites avec des dépôts épais et où peu d'arbres ont survécu; (2) le recrutement dans des trouées et l'établissement de la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et du douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) sur les dépôts moyens à profonds dans les sites où un peu plus d'arbres ont survécu après avoir été ensevelis; (3) des conditions de fin de succession et de succession accélérée dans les sites peu ensevelis où la mortalité était faible. Le déclenchement de différentes trajectoires de succession, ainsi que la variation dans l'ampleur et le moment de la mort des arbres à la suite des dépôts de boue sont la manifestation d'une réaction dynamique à une perturbation en relation avec des gradients à petite échelle de dépôts de boue.

[Traduit par la Rédaction]

Introduction

Volcanism plays an important role in shaping Pacific Northwest ecosystems, where eruptions and associated hydrologic events occur at ecologically relevant time scales and have significant impacts on regional succession patterns (Franklin et al. 1985; Dale et al. 2005). Volcanic mudflows are often associated with eruptions in the Cascade Range (Crandell

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1971) and occur relatively frequently, providing an excellent opportunity to study how this type of disturbance affects forest development (e.g., Halpern and Harmon 1983; Adams and Dale 1987; Frenzen et al. 1988). Nonetheless, studies of vegetation succession on mudflows are scarce prior to the 1980 eruption of Mount St. Helens (but see Beardsley and Cannon 1930; Frehner 1957; Heath 1967). Following the 1980 eruption of Mount St. Helens, several studies examined succession on a variety of volcanic substrates, including tephra, pyroclastic flows, and mudflows (e.g., Halpern and Harmon 1983; Adams et al. 1987; Halpern et al. 1990; del Moral 1998; Fuller and del Moral 2003). Most of these studies focus on primary succession of herbaceous communities rather than long-term forest succession on volcanic substrates, for which little information is available (Kroh et al. 2000). This study focuses on overstory response to disturbance, since trees are the dominant life-form, are long-lived, and influence other forest processes that may influence succession. Other studies at the site, however, focus on understory response to disturbance (see Frenzen et al. 2005).

Mechanisms of tree mortality following mudflow inundation are not completely clear. Insufficient oxygen supply to roots, cambial damage, and moisture stress can lead to tree mortality as well as contribute to secondary processes such as water freezing around roots in mudflow deposits (Beardsley and Cannon 1930; Frehner 1957; Adams and Dale 1987). A specific study on the effect of mudflow sediment on gas exchange by tree root systems found that mudflow sediment asphyxiated root systems through reduced gas exchange in the rhizosphere, but that mortality rate was variable depending on sediment thickness (Tominaga and Kikuchi 2003). Mortality-related responses to burial are likely species specific, since species tolerances to varying degrees of moisture stress and root aeration vary as well. The time it takes for trees to die, or whether they die at all following mudflow deposition, is not well understood, and it is not clear whether most trees die instantly following mudflow burial or survive for a certain period of time (Yoshida et al. 1997).

Comparison of background mortality rates with specific episodic mortality rates from particular disturbance types, such as mudflow deposition, is important in developing an understanding of both present forest community patterns and in predicting future community development (Urban and Shugart 1992; Mast and Veblen 1994). Episodic mortality following disturbance usually entails many trees dying within a short period (several years to decades), and it involves a rate of tree death usually several times greater than the average or background mortality rate (Mast and Veblen 1994). Background mortality of trees is an autogenic process, where trees die of their own intrinsic vulnerability, and background mortality rates for most trees are either generalized, highly site specific, or cover limited time spans (Franklin et al. 1987; Harcombe 1987; Mast and Veblen 1994). Rates of mortality (by species, size, time frame) following mudflow deposition have not been examined to our knowledge.

Although forests often undergo nearly complete removal of trees and mortality following mudflows, the severity of disturbance may vary, with sites of lesser mudflow deposition retaining significant standing snags and live trees. This retention of organisms, organic materials, and structure (biological legacies) following differing levels of mudflow deposition influences seed availability and competition among surviving plants as well as creating substrate, microclimate, and successional heterogeneity (e.g., Frenzen et al. 1988; Dlugosch and del Moral 1999). Biological legacies consist of “organisms, organic materials, and organically generated environmental patterns that persist through disturbance and are incorporated into the recovering ecosystem” (Franklin et al. 2000). Landscape legacies such as old river channels also influence postdisturbance community organization within this context. While the complexity of successional responses to disturbance is widely recognized (e.g., Connell and Slatyer 1977; Oliver 1981; Foster and Boose 1992), specific examples of heterogeneous successional responses to disturbance are poorly developed in the literature in part because of the lack of long-term monitoring of successional processes (Fastie 1995).

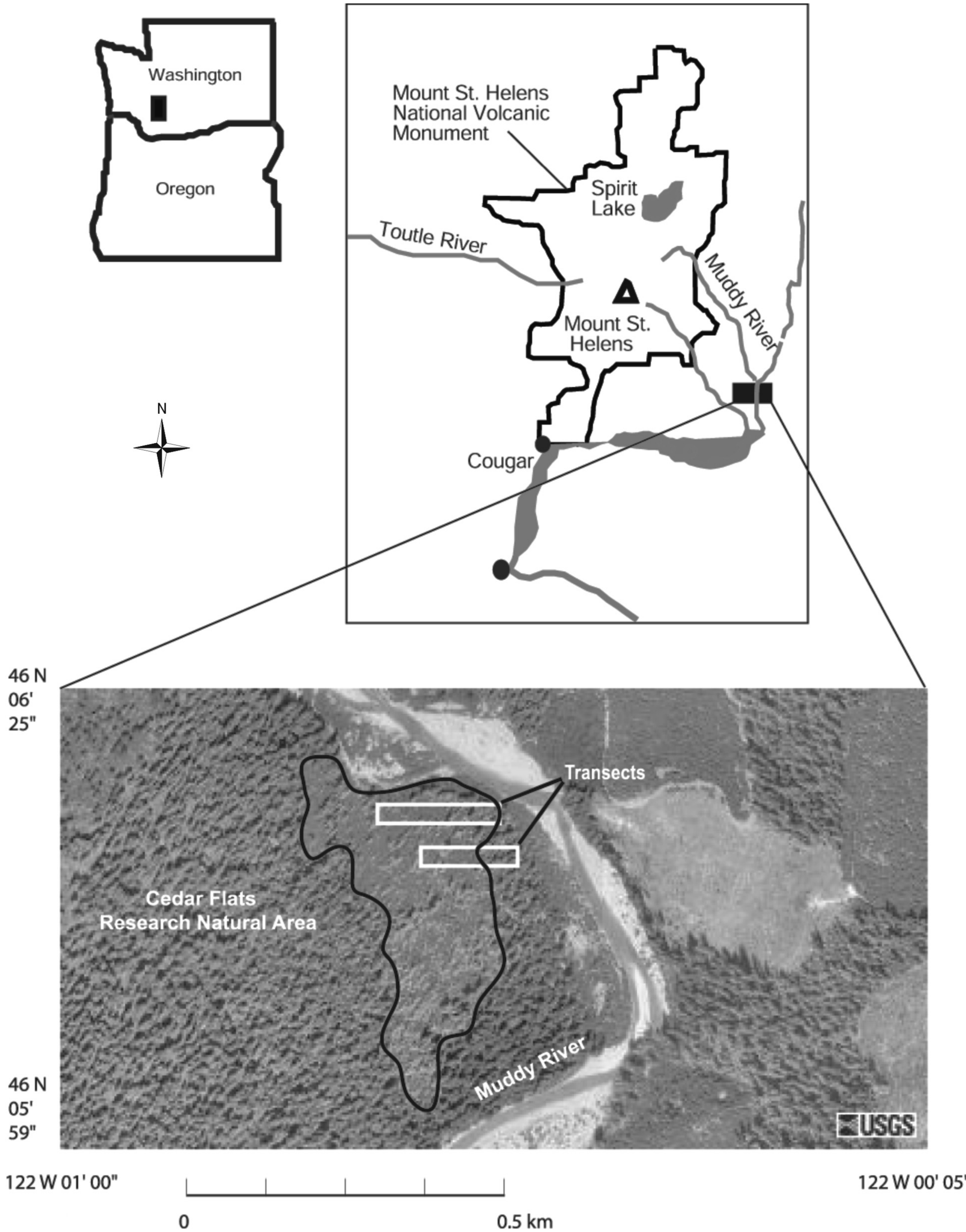
During the 18 May 1980 eruption of Mount St. Helens, mudflows were generated as hot pyroclastic debris melted snow and glacial ice on the upper portion of the volcano (Janda et al. 1981). The Muddy River valley on the southeast slopes of Mount St. Helens was inundated by two mudflows. These mudflows deposited from 10 to >120 cm of sediment on a forested terrace at Cedar Flats Research Natural Area. The purpose of our study is to describe postmudflow forest development in relation to mudflow deposition using 18 years of permanent plot data collected at Cedar Flats following the 1980 eruption of Mount St. Helens. Cedar Flats is an ideal location for studying the effects of mudflow burial on forest development because (1) trees at the site have been monitored since the time of mudflow deposition and (2) variability in mudflow deposition led to varying levels of tree mortality across the study site. We specifically address the following questions: (1) How do tree species at the site respond to mudflow deposition in level and timing of mortality? (2) How is forest structure and succession at the site affected by mudflow deposition? (3) How does forest development following mudflow deposition differ from other types of disturbance and compare with different models of succession, since mudflows are fairly common occurrences in volcanically active regions with unique disturbance effects?

Materials and methods

Study site

Cedar Flats Research Natural Area lies within the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest zone (Franklin and Dyrness 1988). Undisturbed terrace sites are dominated by large (>1 m diameter) Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western redcedar (*Thuja plicata* Donn ex D. Don), and western hemlock, with some grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and western white pine (*Pinus monticola* Dougl.) (Frenzen et al. 2005). Understory species include *Mahonia nervosa* (Pursh.) Nutt., *Rosa gymnocarpa* Nutt., *Rubus* spp., *Chimaphila* Pursh. spp., *Sorbus sitchensis* M. Roemer, *Lupinus latifolius* Lindl. ex J.G. Agardh, *Lupinus lepidus* Dougl. ex Lindl., *Tiarella trifoliata* L. var. *unifoliata* (Hook.) Kurtz, *Vancouveria hexandra* (Hook.) Morr. & Dcne., *Viola* L. spp., and Polypodiaceae. Riparian areas adjacent to abandoned river channels are dominated by red alder (*Alnus rubra* Bong.), black cottonwood (*Populus*

Fig. 1. Location of the Cedar Flats Terrace study site. Outlined areas on the aerial photograph indicate the locations of the sample transects (white) and approximate extent of the 1980 mudflow deposit on the terrace (black).



balsamifera L. subsp. *trichocarpa* (Torr. & Gray ex. Hook.) Brayshaw), and big leaf maple (*Acer macrophyllum* Pursh.).

The study area is located at 366 m elevation on a river terrace (650 m × 350 m), adjacent to the Muddy River 15 km southeast of Mount St. Helens in the Gifford Pinchot National Forest (Fig. 1). The terrace is bounded by a large bend in the river to the east and steep valley walls to the west. The terrace is part of a larger deposit of layered mudflow, pyroclastic flow, and alluvial deposits identified as the Cedar Flats fan of the Pine Creek volcanic assemblage (Crandell and Mullineaux 1973). This assemblage was formed during the late Pleistocene and Holocene in a series of eruptions of old Mount St. Helens, an eruptive center that predates the present volcanic cone (Veerhogen 1937).

Two mudflows originating in the headwaters of the Muddy River and Pine Creek drainages on 18 May 1980 deposited from 10 to >120 cm of sand- to cobble-sized sediments on the terrace, where the mudflows overtopped the riverbank and spilled across the terrace. In general, deposition was greatest on the upstream edge of the terrace where the mudflow entered the stand and in abandoned river channels located near the western valley wall. Deposit depth, while varied across the site, generally decreases in the downstream direction and east of the abandoned river channels.

Cedar Flats Research Natural Area is characterized by a maritime climate of cool, wet winters and warm, dry summers. Mean annual temperature at Pine Creek Work Center (335 m elevation), 5 km south of the study area, is 10 °C, with a mean daily low of –3 °C in January and a high of 30 °C in July. Average annual precipitation is 221 cm, with 134 cm falling from November through February and 67 mm from June through August (Gifford Pinchot National Forest GIS Data Clearinghouse 2001, data period 1937–1950).

Study design

We identified changes in tree density, basal area, and species composition between 1981 and 1999 using data collected along two parallel (east–west) belt transects (1.5 and 1 ha) placed ≈75 m apart and perpendicular to the direction of mudflows (Fig. 1). Each transect is two 25 m × 25 m plots wide for a total of 40 plots on the terrace (Fig. 2). Individual 25 m × 25 m plot data were used to compare burial depth, tree mortality, and changes in stand structure between the two transects. In 1999, we employed a stratified random sampling technique to select ten 25 m × 25 m plots (six plots in transect 1 and four plots in transect 2) for additional sampling of mudflow burial depth and age structure (Fig. 2).

To document forest development and mortality after 1980 at Cedar Flats, all live and dead trees (n = 3034) with diameter at breast height (DBH, at 1.37 m) ≥5 cm were marked with numbered aluminum tags and recorded on stem maps in 1981. DBH for all live trees was recorded during the initial mapping, and mortality was recorded in 1982, 1984, 1991, 1995, and 1999; in addition, diameters were measured in 1991, 1995, and 1999. Rooting medium (i.e., log, root wad, mineral soil) was also recorded for trees in 1982, 1984, and 1991, to determine influence of biological legacy on tree survival and regeneration. All new trees with DBH ≥5 cm were tagged and added to stem maps during our measurements. Because the density of young red alder was very high during field sampling in 1999 (up to 1000 stems/ha), we restricted our tagging of red alder to trees with DBH ≥10 cm.

Mudflow deposition and mortality

In 1992, we measured deposit depths along the center of each transect at 5 m intervals using a soil auger (Fig. 2). Two additional burial depth measurements were taken 8 m north and 8 m south of the transect center at 25 m intervals to ensure center-line sampling included the range of local variability. We also examined variations in burial depth at each of 10 intensively sampled plots during field sampling in 1999. Five soil pits were excavated at each of these 10 plots; one pit was located at the center of each plot and the four others were placed 5 m from the center in each cardinal direction.

We examined the relationship between deposit depth and mortality by using correlation analysis to compare our 1992 depth measurements with tree mortality along each transect. We used the average depth measurements along the center of each transect corresponding with mortality records for adjacent plot pairs for comparison (Fig. 2). We repeated this procedure for depth measurements and mortality on the 10 plots where burial depths were measured in 1999 to confirm our findings. We examined mortality rates for different tree species at the site for each sample date following burial and measured mortality for western hemlock on raised substrates versus those rooted on mudflow-inundated mineral soil to examine affects of biological legacies on mortality.

Changes in forest structure

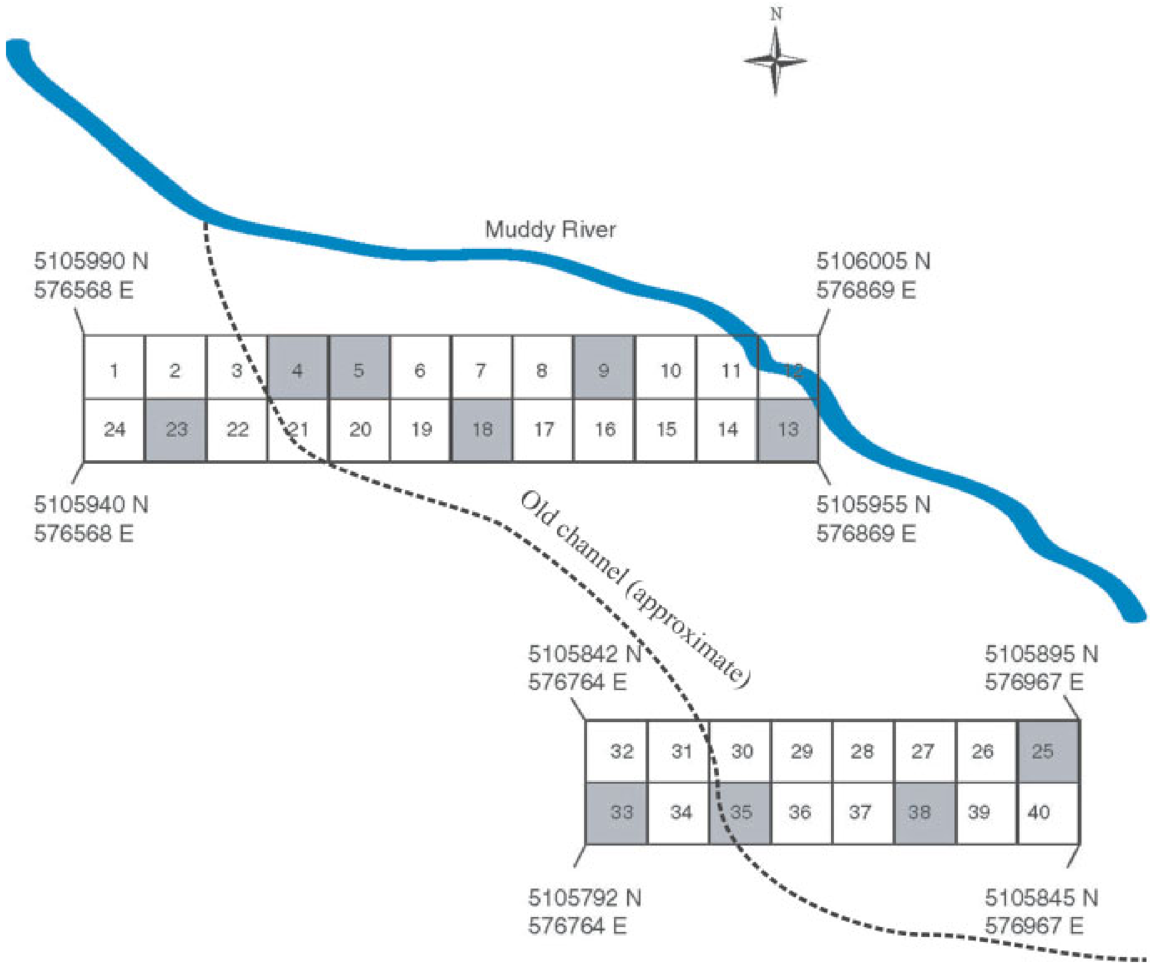
We examined changes in forest composition and structure between 1981 and 1999 by comparing stand structure measures to burial depth. We based these comparisons on (1) changes in live and dead basal area by species against burial depth through time, (2) changes in size class distributions of live and dead trees through time, and (3) testing the relationship between changes in live and dead basal area and burial depth using Spearman rank correlation (SPSS 1999). We calculated importance values for dominant tree species on each plot as the sum of relative basal area and relative density × 100 (maximum = 200).

We examined overall trends in dominance across the site by performing ordination analysis on species importance values for all plots in 1981, 1991, 1995, and 1999 using detrended correspondence analysis (DCA; Hill and Gauch 1980), a modified reciprocal averaging technique, in CANOCO (ter Braak 1988). We then identified compositional groupings through use of cluster analysis with Euclidean distance as the similarity measure and Ward's method of linkage, using PC-ORD (McCune and Mefford 1999). We tested the contribution of burial depth and tree mortality to compositional variability represented by ordination results by correlating them with DCA axis scores for all 40 plots for each sample year (see Weber 2001) using Spearman rank correlation (SPSS 1999). Transect comparisons were based on burial depths and structural measure (basal area, density, and importance value) differences (Mann–Whitney U test).

Age distributions and growth response

Age distributions were reconstructed on 10 intensively sampled plots to examine postmudflow colonization in comparison with historic stand structure at the site (Fig. 2). We considered age structure in addition to examining size structure at the site, since size alone cannot differentiate between postmudflow colonization and growth or development of already established understory trees that survived deposition. Age structure also provides evidence of historic species recruitment in contrast to postmudflow regeneration. We collected increment cores from all live conifers with DBH ≥5 cm and all live red alder with DBH ≥10 cm in each of our 10 intensive plots. All cores were collected at ≈30 cm height to avoid basal swelling; for larger trees coring heights of 50 or 75 cm were used and noted as necessary. Cores were mounted on wooden holders and sanded until cell structure was visible using a binocular microscope (Stokes and Smiley 1968). Ages are reported as age at coring height and in 20-year age-classes. We identified tree growth responses to mudflow burial by noting growth releases during counting, since abrupt changes in ring width can provide both evidence for and a measure of a particular disturbance event (Lorimer 1984). We defined

Fig. 2. Permanent transects showing the layout of individual plots. Shaded plots indicate intensive study plots used in 1999 for soil sampling and obtaining tree ages.



growth release as an increase ≥250% over a 5-year period compared with the mean ring width of the prior 5 years (Veblen et al. 1991). Nineteen (4%) of our cores were excluded from age analysis because of missing centers, missing sections, or other anomalies.

Results

Mudflow deposit thickness and tree mortality

Deposit thickness following the 1980 eruption varied over short distances across the terrace (Fig. 3). Deposit thickness (based on 1992 depth measurements) was generally greater in transect 1 (upstream, average depth ≈71 cm) than in transect 2 (downstream, average depth ≈50 cm) and reached a peak roughly midway through each transect. Patterns of deposit thickness measured in 1992 and 1999 (Fig. 3), while varying slightly, show no significant difference (P = 0.853) in results of a Mann–Whitney U test (SPSS 1999) between sample dates.

Tree mortality varied with burial depth across the study area (1992 burial measurements, r_s = 0.593, P < 0.001, Fig. 4). Correlations using burial measurements in 1999 on selected plots verify this relationship (r_s = 0.607, Fig. 4); however, the low number of measured plots (n = 10) does not meet a level of significance for this test (P = 0.063) using 1999 burial data. Stand monitoring frequency at Cedar Flats did not allow us to establish the exact year of mortality following deposition, but mortality rates were calculated based on the average of a given census period (Fig. 5). The complacency of rings, deterioration of outer rings of snags, and small sample size of cores from surviving trees precluded accurate dendrochronological reconstruction of mortality timing.

The presence of locally elevated substrates decreased mudflow deposition for many understory trees (i.e., trees with DBH <25 cm). Roughly one-quarter of western hemlock understory trees were rooted on logs at the time of burial, some of which were covered with a thin veneer of sediment and others of which appear to have shifted as they floated to the surface of the mudflow deposit. By the fifth growing season following burial, mortality for understory (DBH <25 cm) western hemlock on transect 1 was 10% for stems rooted on downed logs versus 50% for stems rooted on mudflow-inundated mineral soil; in transect 2, mortality was 30% (logs) and 90% (mudflow).

Tree mortality, while highest initially, continued at varying levels for different species during the years following mudflow deposition (Fig. 5). At the time of the first site measurement in 1981, 16 months following mudflow burial, 52% of the trees were dead (26% of total basal area;

Fig. 3. Burial depth profile for both transects. Shaded gray area represents depth measurements collected every 5 m down the center of each transect in 1992; circles with range bars represent depth samples collected on intensive study plots in 1999 showing median and range of five depth pits from a given location.

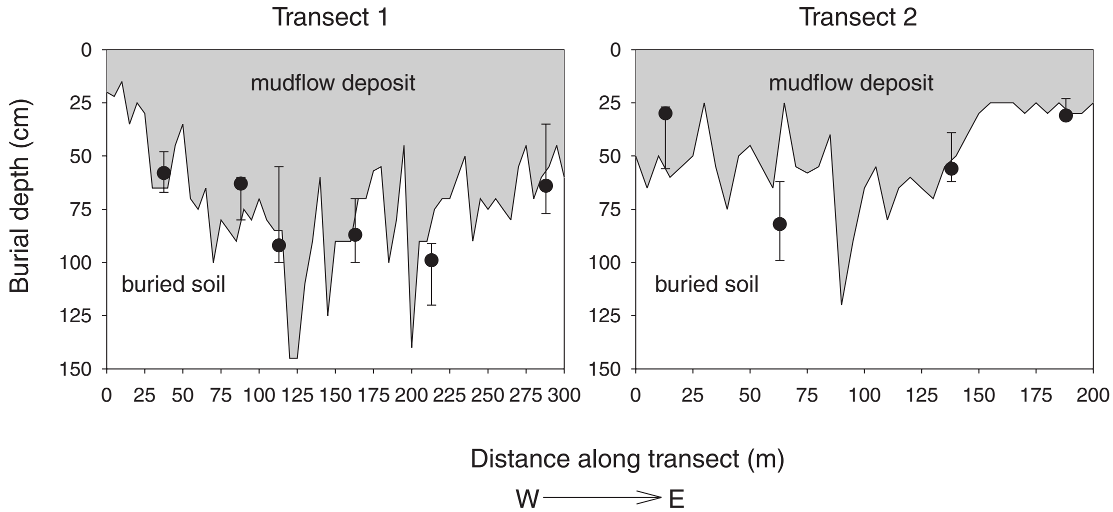
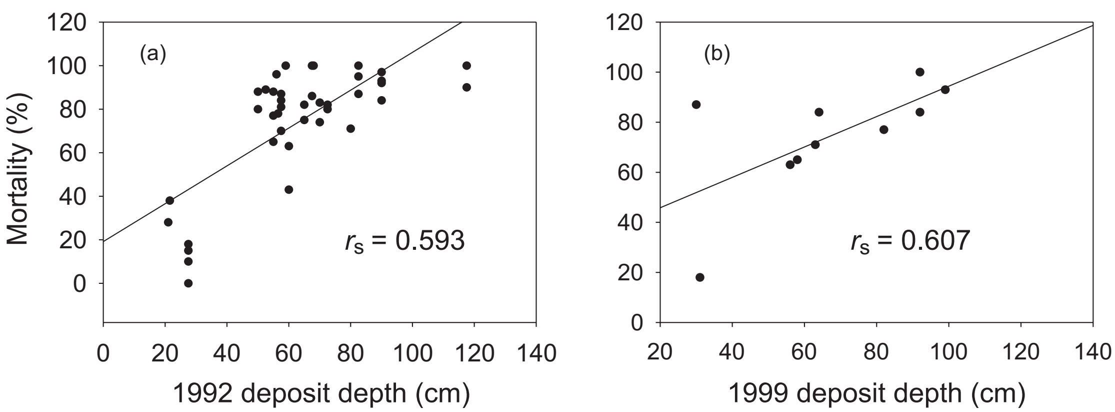


Fig. 4. Variation in burial depth compared with mortality (number of dead trees / total number of trees) per plot for (*a*) 1992 burial depth measurements and (*b*) 1999 burial depth measurements on intensive study plots. Each data point represents value at a given plot.



135 m^2/ha). Overall mortality in the same plots was 58% in 1982 and 71% in 1984. By 1991, 11 years following deposition, overall mortality had leveled off to 76% and only increased to 78% by 1999. Tree species differed in their levels of mortality following mudflow deposition and also differed in mortality levels by size class (Fig. 5; Weber 2001). Red alder experienced the highest mortality of all species at 87% in 1981. Among major conifer species, western hemlock had the highest initial mortality (52% in 1981), while Douglas-fir and western redcedar showed significant delayed mortality (increasing from 20% each in 1981 to 62% and 59%, respectively, by 1991). Delayed mortality for large overstory Douglas-fir averaged 41% in 1981 and averaged between 2% and 5% until 1991 (Fig. 5). Other species such as western hemlock and Pacific silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) experienced delayed mortality for several years following disturbance across all size classes (Fig. 5).

Changes in forest structure

Forest structure at Cedar Flats changed significantly during the 18-year study period as a consequence of mudflow deposition. In 1981, the site was dominated by large (>100 cm) surviving Douglas-fir and western redcedar (Fig. 6). The ratio of live to dead basal area of Douglas-fir at the site decreased dramatically between 1981 and 1999, resulting from mortality of overstory trees in areas of deeper burial (>60 cm, Fig. 7). The ratios of live to dead basal areas also decreased for western hemlock and western redcedar (Fig. 7). Pacific silver fir, primarily an understory species at the site, showed little change in basal area through time. Basal area of red alder increased following burial, driven by an increase in density of smaller (DBH <15 cm) trees (756 stems/ha, Figs. 6 and 7). There was also an increase in density of small-diameter (DBH <15 cm) Douglas-fir (275 stems/ha) and western hemlock (366 stems/ha) following deposition.

The upstream transect (transect 1) with deeper mudflow deposition exhibited a greater reduction in live basal area between 1981 and 1999 than was observed at the downstream, shallower deposit transect (transect 2) (Table 1, Fig. 7). Basal area for live trees differed little between transects in 1981 but was significantly higher for dead trees in transect 1 (Table 1). Live tree density in transect 2 was twice that of transect 1 during our first census (1981) following mudflow

Fig. 5. Annualized mortality rates for primary tree species at Cedar Flats by census period and diameter class. The number of trees that were present in 1981 (live and dead) at time sampling began are shown in parentheses above each figure.

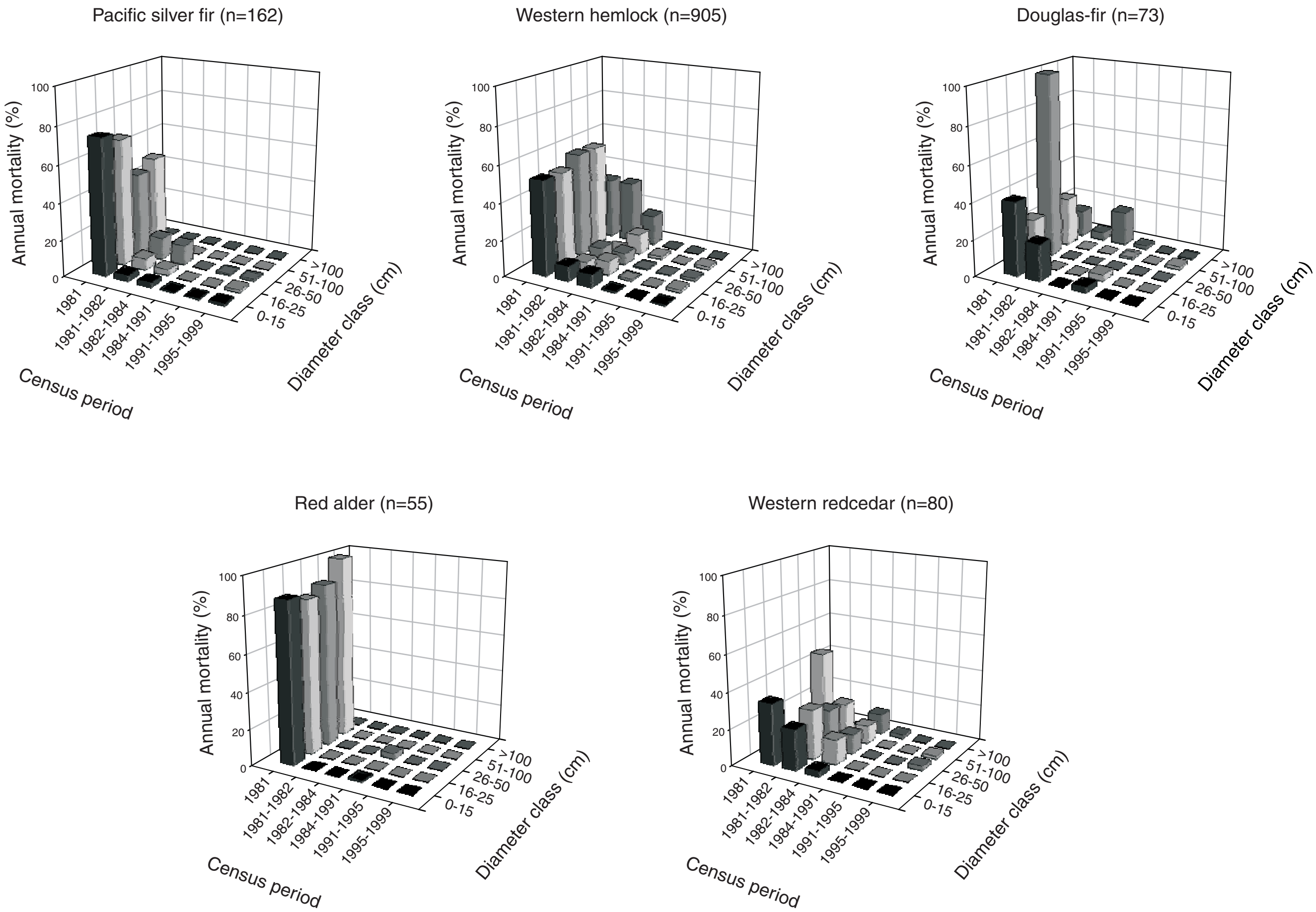


Fig. 6. Number of live (hatched bar) and dead (hollow bar) trees by diameter class for all plots in both transects combined. Tree size distributions for three sample dates (1981, 1991, and 1999) are displayed by increasing diameter class from top to bottom for major tree species at Cedar Flats.

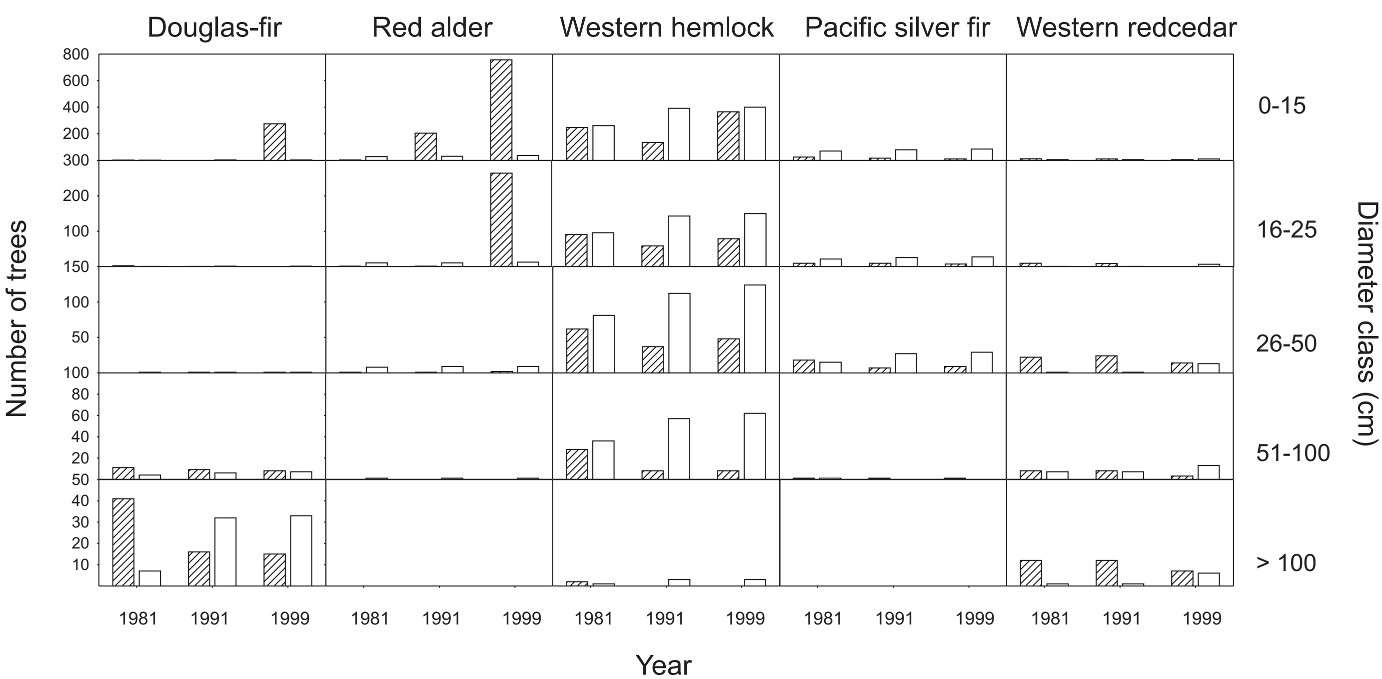


Fig. 7. Change in basal area between 1981 and 1999 for live and dead trees by burial depth for major tree species at Cedar Flats. Note differing *y*-axes for the different species.

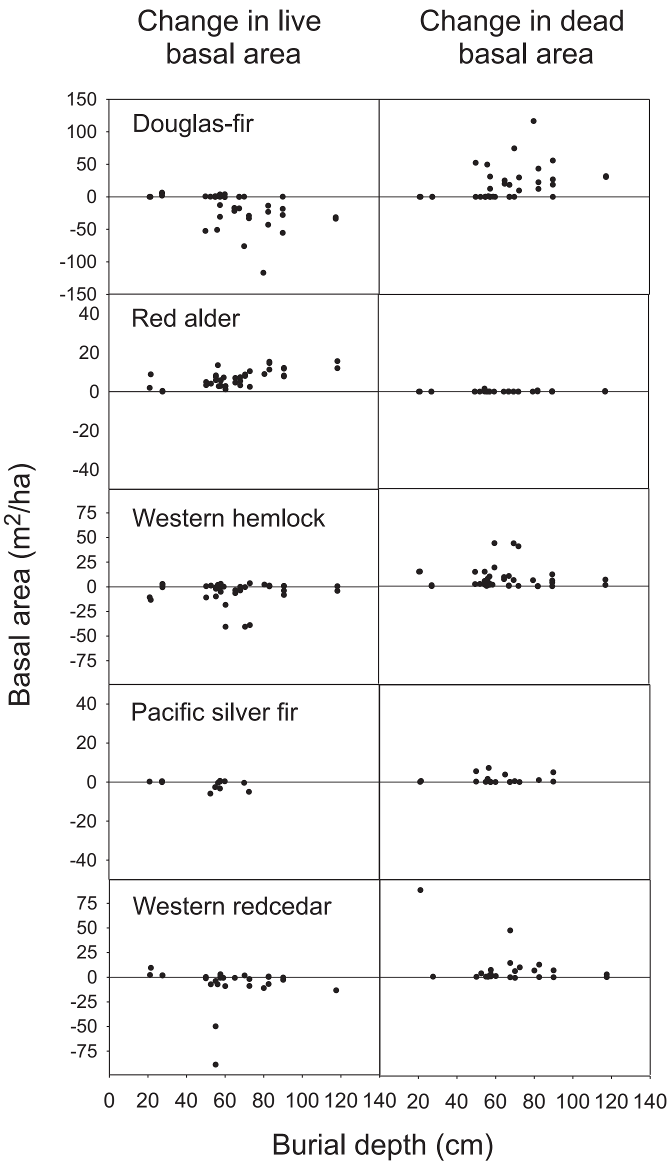


Table 1. Basal area and density for 1981, 1991, and 1999 for transects 1 and 2.

		Basal area (m^2/ha)		Density (stems/ha)	
Date	Transect	Live	Dead	Live	Dead
1981	1	51.84	25.4	193.3	272.0
	2	46.52	9.5	382.0	297.0
1991	1	15.38	63.9	240.7	376.7
	2	33.09	25.1	231.0	473.0
1999	1	22.22	64.4	818.7	383.2
	2	41.20	25.8	723.0	492.0

deposition. Total live tree density increased 4-fold in transect 1 and nearly doubled in transect 2 between 1981 and 1999 (Table 1). Mann–Whitney *U* tests (SPSS 1999) show significant differences between transects 1 and 2 in 1999 for dead tree basal areas ($P < 0.001$) and importance values for red alder, Douglas-fir, and western hemlock ($P < 0.001$, <0.001, 0.041, respectively). In 1981, only red alder showed a significant difference in importance values between transects ($P < 0.001$).

The effect of mudflow deposition on stand composition and differences in forest development following disturbance is illustrated by the grouping of site scores (importance values) using ordination and cluster analysis. The DCA ordination of species importance values separates plots by species composition (Fig. 8, Table 2). Using 1999 data, axis 1 of the ordination separates plots with a high Douglas-fir ($r_s = 0.96$, $P < 0.01$), western white pine ($r_s = 0.605$, $P < 0.01$), and western hemlock ($r_s = 0.488$, $P < 0.01$) component from those dominated by red alder ($r_s = -0.868$, $P < 0.01$). The second ordination axis reiterates this trend, separating plots with high red alder composition ($r_s = 0.885$, $P < 0.01$) from all other tree species, particularly western redcedar. Ordination analyses for other sample dates were not significant, suggesting low compositional sorting during the first 15 years following mudflow deposition (Weber 2001).

This separation of species importance values in ordination corresponds with variation in deposit thickness at the site (Fig. 8, Table 2). Axis 1 is negatively correlated with depth of mudflow deposition ($r_s = -0.453$, $P < 0.01$), and axis 2 is positively correlated with mudflow deposition ($r_s = 0.728$, $P < 0.01$); both axes are correlated with mortality (axis 1: $r_s = 0.526$, $P < 0.01$; axis 2: $r_s = 0.660$, $P < 0.01$). Cluster analysis grouped plots into three general categories. Plots in these groupings had sampled mudflow deposition values of (1) deep deposition (median = 91 cm, range 48–120 cm), (2) intermediate deposition (median 66 cm, range 35–99 cm), and (3) shallow deposition (median = 32 cm, range 23–62 cm) by 1999 (Fig. 8).

Age distributions and growth response

Age-class distributions for each of the three cluster groups (deep, intermediate, and shallow deposition) illustrate the ecological significance of biological legacy in the form of surviving trees opposed to the development of new post-mudflow cohorts. Plots in the first two cluster groups (1 and 2, thick and intermediate deposition groups) were composed primarily of a red alder dominated postmudflow cohort, with a smaller component of Douglas-fir and western hemlock (Fig. 9). Group 1 exhibits lower survivorship and fewer species than does group 2 (Fig. 9, Table 3). Group 2 plots had significantly more Douglas-fir seedlings, a greater number of postmudflow surviving trees, and more delayed mortality in the 4 years postdisturbance (26% vs. 15%) than did the group 1 plots (Table 3). Plots in group 3 show weakly defined postburial cohorts, a wide range of age-classes, and high species diversity.

Plots with shallow mudflow deposition also exhibited a higher number of growth releases than did plots with deep mudflow deposits (Fig. 10). Subcanopy, late-successional species (Pacific silver fir, western hemlock, grand fir) exhibited the majority of growth releases (78%) over a 5-year period following mudflow deposition.

Fig. 8. Detrended correspondence analysis ordination diagram of importance values for 1999 showing site scores delineated by cluster group affiliation. Species scores in the ordination are included to illustrate effect on ordination results.

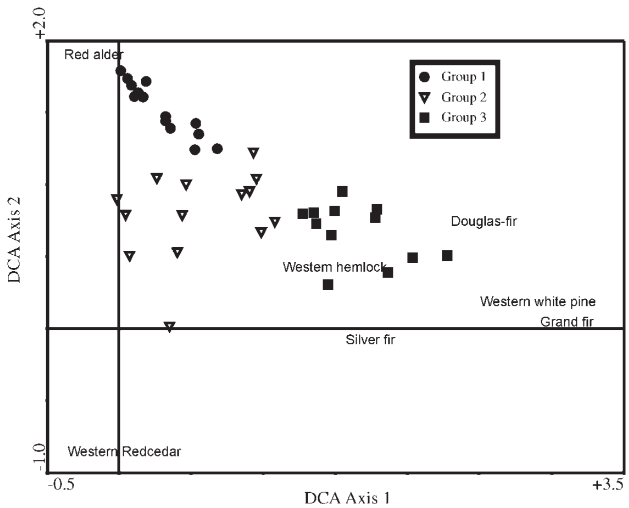


Table 2. Spearman rank correlation coefficients of species importance values (IV), mortality, and burial depth with detrended correspondence analysis axis scores (1999) for all 40 plots at Cedar Flats.

	Axis 1	Axis 2
Burial depth (1992)	–0.453*	0.728*
Mortality (%/plot)	0.526*	0.660*
Douglas-fir IV	0.926*	–0.419*
Red alder IV	–0.868*	0.885*
Western hemlock IV	0.488*	–0.363**
Western redcedar IV	–0.209	–0.541*
Pacific silver fir IV	0.450*	–0.595 *
Grand fir IV	0.154	–0.342**
Western white pine IV	0.605*	–0.393**

Note: *, $P < 0.05$; **, $P < 0.01$.

Discussion

Mudflow deposition at the Cedar Flats river terrace following the 1980 eruption of Mount St. Helens was highly variable and led to a range of stand responses at a fine spatial scale (<2.5 ha). Our results indicate a significant relationship between deposit thickness and tree mortality consistent with depositional thinning downstream from the breeched upstream edge of the terrace, infilling of abandoned river channels along the west edge of the terrace, and variable topography across the terrace. Before the 1980 eruptions, these former channels supported a black cottonwood – red alder – bigleaf maple community adapted to fluctuating water tables (Frenzen at al. 2005). Superimposed on these depositional patterns are localized raised substrates (rafted debris, logs, stumps, snags) that influenced plant survival and subsequent regeneration. Tree responses to differences in deposit thickness are evidenced by the species-specific timing of mortality and changes in basal area, density, and importance values. All species exhibited a strong relationship between depth of mudflow deposit and tree mortality, regeneration, and accelerated growth among surviving understory trees.

Mortality at Cedar Flats was episodic, stemming from exogenous disturbance by mudflow and did not relax to a typical background mortality level for several years following mudflow deposition. General mortality rates for Douglas-fir – western hemlock forests have been reported from several locations in the Pacific Northwest following long-term monitoring. Mortality values for these forests range from 0.52% to 0.75% annually as a percentage of total tree cohorts (Franklin et al. 1987). Average annual mortality rate in one study of a forest stand in the Wind River valley of southeast Washington was 0.75%, with 22% mortality over a 36-year study with 1002 trees (Franklin and DeBell 1988). At Cedar Flats, average annual mortality for all species the first year after disturbance was 46%, 8% in the second year, and 5% between 1982 and 1984 (annualized). These values suggest that an episodic level of mortality was maintained from several years to a decade following mudflow deposition.

Mortality was not checked in yearly intervals following this, but averaged 1% for all species from 1984 to 1991 and from 1995 to 1999. Rates of mortality for large overstory trees, in particular, were elevated beyond a typical background mortality level up to the 1984–1991 census period at Cedar Flats (Fig. 5), although there was a gap in mortality checks between 1984 and 1991. Rates of mortality for western hemlock, Pacific silver fir, and western redcedar were also elevated across size classes until 1984, demonstrating differing responses to mudflow deposition in overstory versus understory tree species as well as between early-seral species such as Douglas-fir and late-seral species such as western hemlock and Pacific silver fir. Life-history strategies of different species likely played a significant role in survival rates; for instance, adaptation of western redcedar to seasonal anaerobic conditions during flooding, growth of seedlings on nurse logs by western hemlock, growth of seedlings on root mounds of larger overstory trees by Pacific silver fir, and depth and extent of roots below mudflow deposit by larger overstory trees.

The increase in tree mortality between the second and fifth growing seasons following mudflow deposition observed at Cedar Flats is consistent with previous observations of flooding of bottomland hardwoods. In areas of continuous flooding, Green (1947) observed little mortality the first year, increasing mortality among flood-intolerant species the second year, and complete mortality the third year. The progressive nature of the physiological effects of flooding that contribute to delayed mortality has been documented in laboratory studies (Kozlowski 1984) and is the only similar disturbance causing delayed mortality that has received significant study of physiological effects on trees following the disturbance.

Disturbance severity often governs the rate and trajectory of succession by influencing the type and availability of propagules (e.g., Connell and Slatyer 1977; Connell 1978; Sousa 1984; Pickett and White 1985), the degree of biological legacy at a site (Franklin et al. 2000), and other initial site conditions. Close proximity to seed sources (<100 m) (e.g., Frehner 1957; Frenzen et al. 1988; del Moral 1998;

Fig. 9. Age-class distributions on 10 intensively sampled plots in 20-year age classes shown in three groups (1, 2, and 3) identified by cluster analysis (n = number of plots in group). Note differing y-axes (number of trees) for different species.

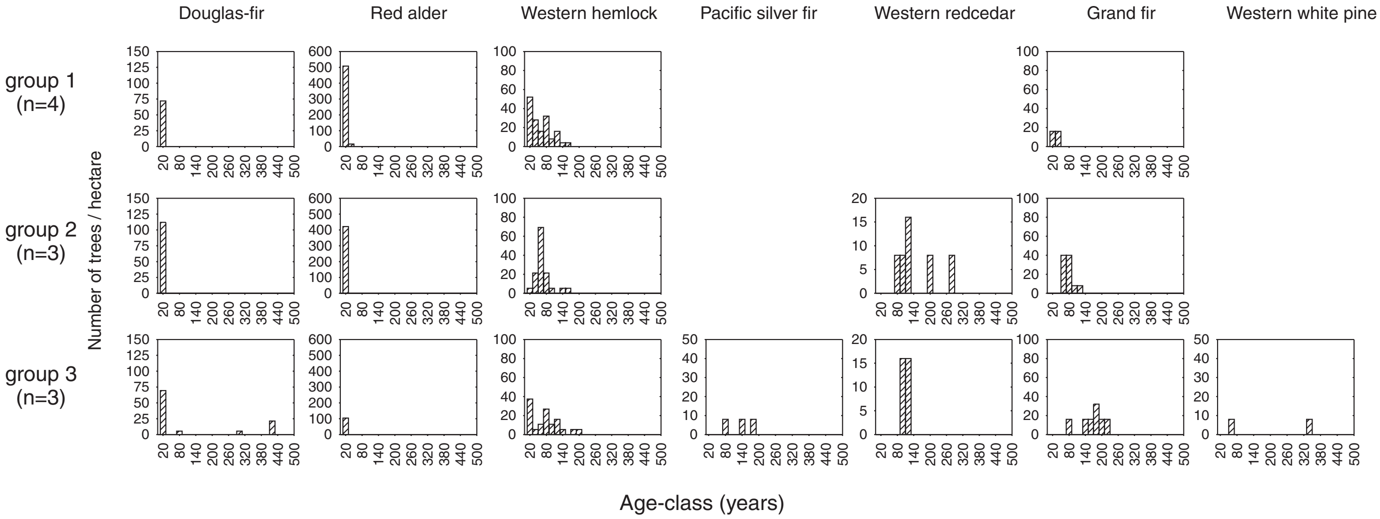
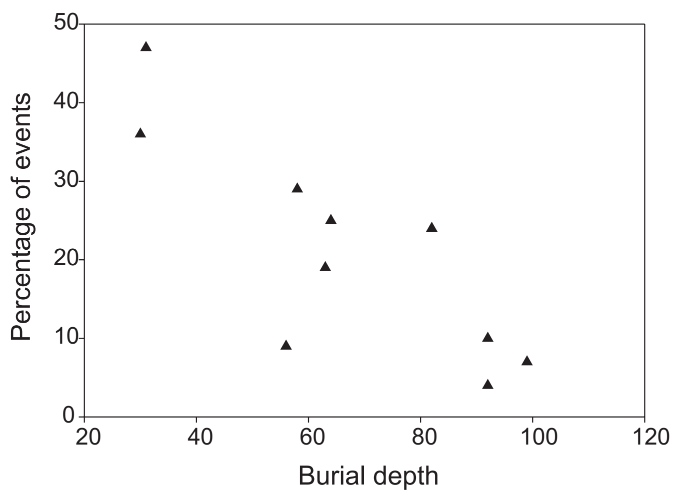


Table 3. Number of live trees in 1981, dead trees in 1999, and seedlings with DBH <20 cm in 1999 for the four dominant tree species at the site.

No. trees/ha	Red alder	Western hemlock	Douglas-fir	Western redcedar
Group 1				
Live, 1981	2	103	15	19
Dead, 1999	55	288	27	2
Seedlings, 1999	523	120	34	1
Group 2				
Live, 1981	5	181	13	37
Dead, 1999	11	327	9	23
Seedlings, 1999	430	199	117	2
Group 3				
Live, 1981	0	247	48	17
Dead, 1999	0	262	12	6
Seedlings, 1999	125	135	195	2

Fig. 10. A comparison of growth release events from 1980 to 1990 and burial depth. Growth releases are shown as percentages of dated trees on a given plot. Abrupt changes in ring width were examined on intensive study plots sampled in 1999, and burial depths correspond to 1999 sampled depths.



Kroh et al. 2000; Fuller and del Moral 2003; Frenzen at al. 2005) and biological legacies in the form of surviving trees, snags, and mudflow rafted logs (Frenzen et al. 1988) played an important role in postmudflow seedling establishment, recruitment, mortality, and subsequent forest composition on the terrace at Cedar Flats. These biological legacies help to determine the subsequent rate and successional pathways of forest development (Keeton and Franklin 2004). Mortality for understory western hemlock at Cedar Flats, for example, was significantly less on elevated substrates (such as logs and root wads) than on mudflow-inundated mineral soil. Red alder colonizing areas of high canopy mortality at Cedar Flats also depended initially on the arrival of propagules from surviving alder stands adjacent to the terrace and above the zone of mudflow burial and scour (Frenzen et al. 2005). Surviving canopy Douglas-fir, in contrast, provided seeds during the period of posteruption mortality, leading to a higher component of Douglas-fir and western hemlock in area experiencing partial or delayed canopy mortality.

The postmudflow stand structure and subsequent recovery reflects a range of disturbance intensities at the Cedar Flats terrace, suggesting that succession following heterogeneous disturbance may contain elements of several models of succession and may be difficult to encompass with any particular model (Clarkson 1990). The range of initial postmudflow conditions on the Cedar Flats terrace varied from a near total resetting of the successional sequence to largely unaltered late-succession conditions. By 1999, colonizing stands of nitrogen-fixing red alder had established on severely disturbed sites, initiating succession typical of severe disturbance events such as crown fires, landslides, and hurricanes (e.g., Oliver 1981) and which was consistent with relay floristics (Clements 1916) and facilitation (Connell and Slatyer 1977). Gap-phase recovery was common among intermediate deposition sites with infilling by young western hemlock and Douglas-fir. These areas also exhibit an initial floristics (Egler 1954) establishment pattern similar to that observed on landslidedisturbed sites (Whittaker 1975). Shallow deposition left the forest largely intact, resulting in few postmudflow changes in forest structure or composition typical of minor disturbances such as windthrow, selective cutting, and some types of insect disturbance (Glitzenstein et al. 1986; Abrams and Scott 1989; Veblen et al. 1989). In these sites, both initial floristics and regeneration of late-successional understory species occur along with the release of surviving, suppressed subcanopy trees. Trees that experienced growth releases at Cedar Flats were primarily shade-tolerant, late-successional species occupying subcanopy positions before the mudflow deposition, leading to accelerated succession, where the overstory consisted primarily of early-seral Douglas-fir.

Several studies describe patterns of disturbance-accelerated succession following windstorms, ice storms, logging, and insect damage (e.g., Glitzenstein et al. 1986; Abrams and Scott 1989; Veblen et al. 1989). To our knowledge, however, mudflow deposition has not been reported as an agent of accelerated succession. This is not surprising, since mudflows are cement-like slurries that typically remove riparian plant communities through scouring and deposit bare substrates. Accelerated succession and advanced regeneration are common following moderate levels of disturbance, causing partial destruction of forest overstories and releasing resources to surviving trees (Glitzenstein et al. 1986; Veblen et al. 1989). These conditions often result in canopy gaps where early- or late-successional species are promoted (Abrams and Scott 1989; Veblen et al. 1989), determining (1) regeneration success in many Pacific Northwest forests (e.g., Stewart 1986; Spies and Franklin 1989; Taylor 1990; Hadley and Savage 1996) and (2) development of replacement cohorts or patchy uneven-aged stand patterns (Oliver 1981).

On the mudflow-inundated terrace at Cedar Flats, differential deposition resulted in a heterogeneous mosaic of successional stages as a result of the interplay of disturbance severity and individualistic tree species responses to disturbance. Our findings are similar to those of Foster and Boose (1992), who note similar disturbance effects along hurricane-induced disturbance gradients in New England but where disturbance intensity varies across a landscape. They suggest that disturbance-induced gradients may be as important in contributing to landscape-level forest diversity as the combination of temporally differentiated disturbance events. At Cedar Flats terrace, deep deposition sites had low overstory survival and are now dominated by early-colonizing red alder, intermediate to deep deposition sites had more surviving overstory western hemlock and Douglas-fir trees, and shallow deposition sites had high overstory tree (Douglas-fir, western white pine, western hemlock) survival. Individualistic responses to disturbance included higher survival on elevated substrates by understory western hemlock, delayed mortality of large overstory Douglas-fir, and infilling of larger gaps by red alder and smaller gaps on mudflow-inundated substrate by Douglas-fir seedlings. Our results show both coarse-grain (stand level) and fine-grain (microtopographic) scale changes in forest structure following mudflow deposition and suggest a combination of gradient (continuous) and patch-scale analyses may be appropriate when examining similar types of disturbed landscapes (van Coller et al. 2000).

Multiple successional responses to disturbance (e.g., Cattelino et al. 1979; West et al. 1981; Abrams and Scott 1989) such as those observed at Cedar Flats may be present where several factors such as predisturbance vegetation type, disturbance type and severity, and microenvironment shape vegetation development (e.g., Watt 1947; Christensen and Peet 1984; Fastie 1995). In these cases, both deterministic and stochastic factors are likely to be important in shaping alternate successional pathways (Halpern 1988). Deterministic factors include life-history characteristics and competitive relationships following disturbance; stochastic factors include variation in timing, intensity, and frequency of disturbance, availability of species, and local environment. Specifically, forest development displays a disposition toward stochastic, multiple outcomes under conditions of intermediate mudflow deposition and follows more deterministic pathways under deep and shallow deposition. These conditions suggest that communities inundated by mudflow are sensitive to both initial (preburial) conditions and threshold phenomenon in forest development (cf. Savage et al. 2000). These outcomes provide an interesting context for forest development, where a single disturbance event may encompass a range of community-response thresholds that result in both stochastic and deterministic outcomes.

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