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TEN YEARS OF VEGETATION SUCCESSION ON A DEBRIS-FLOW DEPOSIT IN OREGON[1]

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ABSTRACT: We tracked vegetation succession on a debris-flow deposit in Oregon's Coast Range to examine factors influencing the development of riparian plant communities following disturbance. Plots were stratified across five areas of the deposit (bank slump, seep, upper and lower sediment wedge, log jam) the first growing season after debris flow. At six times during the next ten years we estimated cover of vascular plants and tallied density of woody plants. Plant colonization occurred within two years. Total cover increased two- to seven-fold on the five areas within three years. Red alder and salmonberry were the dominant species, although weedy herbs persisted where woody species were lacking. Ordination of cover data showed that the five areas remained floristically distinct over time, while undergoing similar shifts related to the increasing dominance of alder and salmonberry. Rapid height growth of alder allowed it to outcompete salmonberry and effectively capture most areas by the tenth year, even where sprouts from transported rhizomes gave salmonberry an early advantage. Our results suggest that successional patterns were influenced by substrate variability, species composition of initial colonizers, propagule sources and their distribution, and species life-history traits such as growth rate, competitive ability, and shade tolerance.

(KEY TERMS: debris flow; revegetation; riparian forest; succession; watershed management.)

INTRODUCTION

Debris flows can leave a lasting legacy on riparian environments. These sudden torrents of water, sediment, and organic debris can scour stream channels to bedrock (Swanson *et al.,* 1998) and lay down massive and heterogeneous deposits on valley floors (Swanson *et al.,* 1987). Vegetation in the path of the flow can be damaged, sheared off, uprooted, or buried (Costa, 1984). The removal and deposit of material can alter stream-channel gradients, shift the location of channel features, and modify valley-floor landforms (Benda, 1990). Although debris flows may occur only periodically along any given stream reach, they exert an important influence on aquatic habitat by routing sediment and wood through channel networks (Benda, 1990). In the process, they also transport plant propagules such as seeds and rhizomes to downstream locations (Adams and Sidle, 1987), and create a variety of new surfaces for plant colonization (Gecy and Wilson, 1990). The plant community that develops following debris flow affects habitat and stream ecological processes through shading, nutrient retention, and inputs of litter and woody debris (Gregory *et al.,* 1991). This functional linkage between the terrestrial and aquatic environments makes it essential to understand the patterns and processes that characterize vegetation succession after disturbances such as debris flows.

Plant succession following mass failure has been studied across a variety of ecosystems (e.g., Flaccus, 1959; Hull and Scott, 1982; Gecy and Wilson, 1990; Guariguata, 1990), although only a few studies that we know of employed repeated sampling of permanent plots. These include the long-term research on mudflows and debris avalanches after the 1980 eruption of Mount St. Helens (Dale, 1991), and a five-year study of 16 landslides in Puerto Rico (Myster and Walker, 1997). More typical are chronosequence studies, which substitute space for time by sampling different sites that experienced comparable disturbances at different times in the past. For example, Flaccus (1959) sampled vegetation on seven landslides in New Hampshire that spanned a range of 9 to 72 years since disturbance. In the western Cascade Range of

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Oregon, Miles and Swanson (1986) studied plant recovery on 25 landslides aged 6 to 28 years. Like these studies, most research on succession after mass failure has focused on hillslope disturbances such as landslides, slumps, and debris avalanches, rather than on in-channel debris flows. An exception is the work of Gecy and Wilson (1990), who examined first-year vegetation response after debris flows along three creeks in the Cascade Range of Oregon. Collectively, this research has identified several factors influencing vegetation development after mass failure. Among these is species composition of the adjacent, intact vegetation, which serves as a source of seed and other propagules for colonization (Hull and Scott, 1982; Miles and Swanson, 1986). Substrate stability and the nutrient status and organic matter content of the soil may affect both the composition and distribution of colonizing species (Walker *et al.,* 1996). Species life-history traits, such as potential growth rates, longevity, and mode(s) of reproduction may be important as well. Finally, the rate of revegetation may be slower in areas of scour than in areas of deposition or where there are patches of relatively undisturbed ground that harbor mycorrhizal fungi, an intact seed bank, or residual vegetation that can resprout (Flaccus, 1959; Gecy and Wilson, 1990; Guariguata, 1990; Walker *et al.,* 1996).

In the Coast Range of Oregon, debris flows are important in shaping the morphology of stream channels and valley floors (Swanson and Lienkaemper, 1978; Benda, 1990). It follows that their influence on riparian vegetation could be equally important, however, the response of vegetation to debris flow is not well understood in this region. Most information on plant succession in riparian areas of the Coast Range comes from chronosequences of riparian forests with red alder (*Alnus rubra*) and salmonberry (*Rubus spectabilis*) (Henderson, 1978; Hibbs and Giordano, 1996). [Note: Plant nomenclature follows Hitchcock and Cronquist (1973). Latin names are provided on first mention of a plant's common name.] These species frequently dominate the plant community along streams in the Coast Range (Pabst and Spies, 1998; 1999), yet the mechanisms by which they achieve dominance following catastrophic disturbance have not been fully explored. Similarly, there is essentially no information from this region on the fine-scale temporal and spatial dynamics that occur in riparian plant communities in the years immediately following disturbance. To that end, we studied vegetation succession for ten years in permanent plots on a debris-flow deposit in the Oregon Coast Range. Our specific objectives were to examine: (1) the modes and timing of plant establishment, (2) how successional patterns are mediated by variation in the physical characteristics of the deposit, and (3) how initial species composition influences longer-term development of riparian plant communities.

METHODS

Study Site

The study took place in the central Coast Range of Oregon in the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness, 1973). This region is characterized by steep terrain deeply dissected by a dense network of stream channels. Underlying geology is primarily uplifted marine sediment (mostly sandstone and siltstone) from the Eocene epoch (Baldwin, 1981). Annual precipitation averages about 250 cm (Ruffner, 1985), with most falling as rain from October through April. Occasionally, intense or multi-day storms drop from 15 to more than 50 cm of rain, triggering landslides and debris flows.

The study site is a debris-flow deposit on the valley floor of an unnamed second-order stream (44.54°N, 123.89°W), which is a tributary of Horse Creek in the northern Alsea River watershed. The debris flow initiated in the winter of 1989-90 in a bedrock hollow (a concave depression on the upper hillslope) (Figure 1a). From the hollow it traveled about 350 m along a steep, first-order channel (Figure 1b) to the confluence with the lower-gradient, second-order channel, where it deposited roughly 1000 m^3 of material for a length of about 120 m on the valley floor (Figure 1c). The valley floor in this reach ranges from 10 to 20 m wide; it is oriented in a north-south direction, with the stream flowing southward. The deposit is characterized by a log jam at its downstream end, behind which piled up a collection of unsorted sand, gravel, and cobbles along with organic debris (Figure 1c and Figure 2). This collection of sediment and debris is referred to here as a "sediment wedge." The debris flow also appeared to cause the lower hillslope to slump at the confluence of the two channels. The slumped material, containing rhizomes of salmonberry and sword fern (*Polystichum munitum*) and possibly other vegetative propagules, formed a raised mound on the valley floor upstream of the sediment wedge. Between the bank-slump deposit and the west hillslope was a seep area covered by freshly deposited sediment from the debris flow.

The stream channel through the deposit reach is about 2 m wide. It is a fish-bearing stream, although intermittent and dry (or perhaps subsurface) in summer. The portion of the channel through the upstream

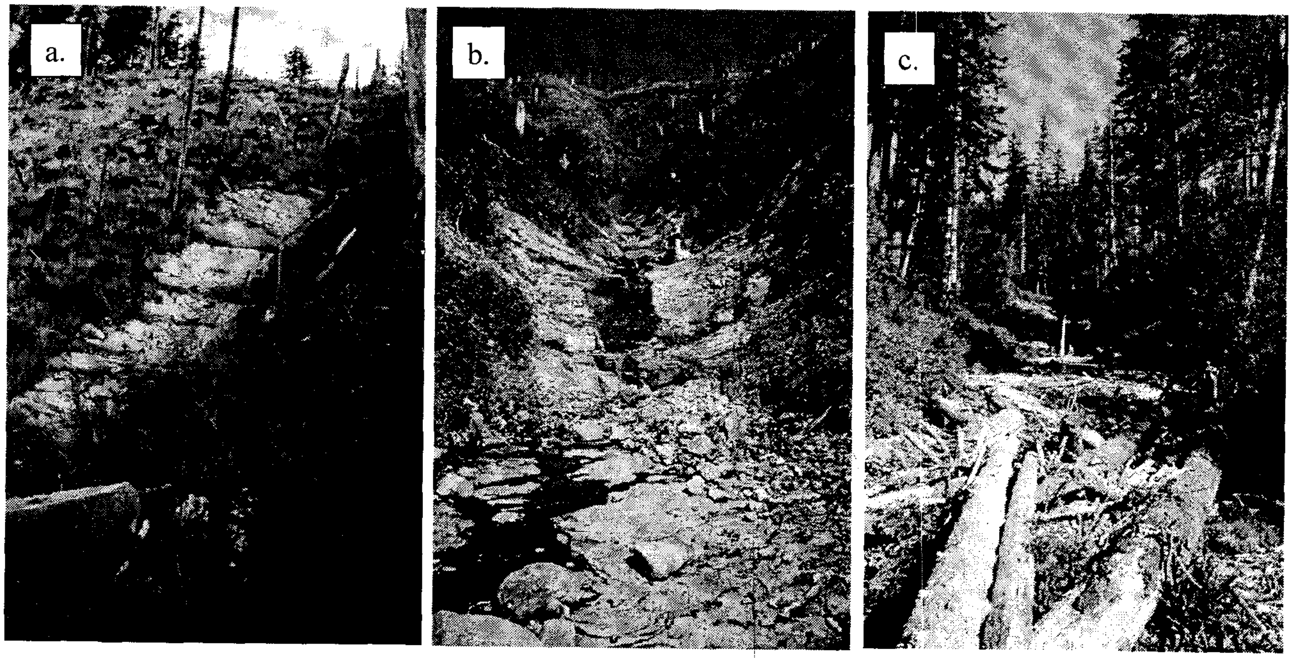


Figure 1. Site of the Debris Flow in 1990: (a) Initiation in Bedrock Hollow; (b) Scoured First-Order Tributary; and (c) the Debris-Flow Deposit, Looking Upstream From the Log Jam.

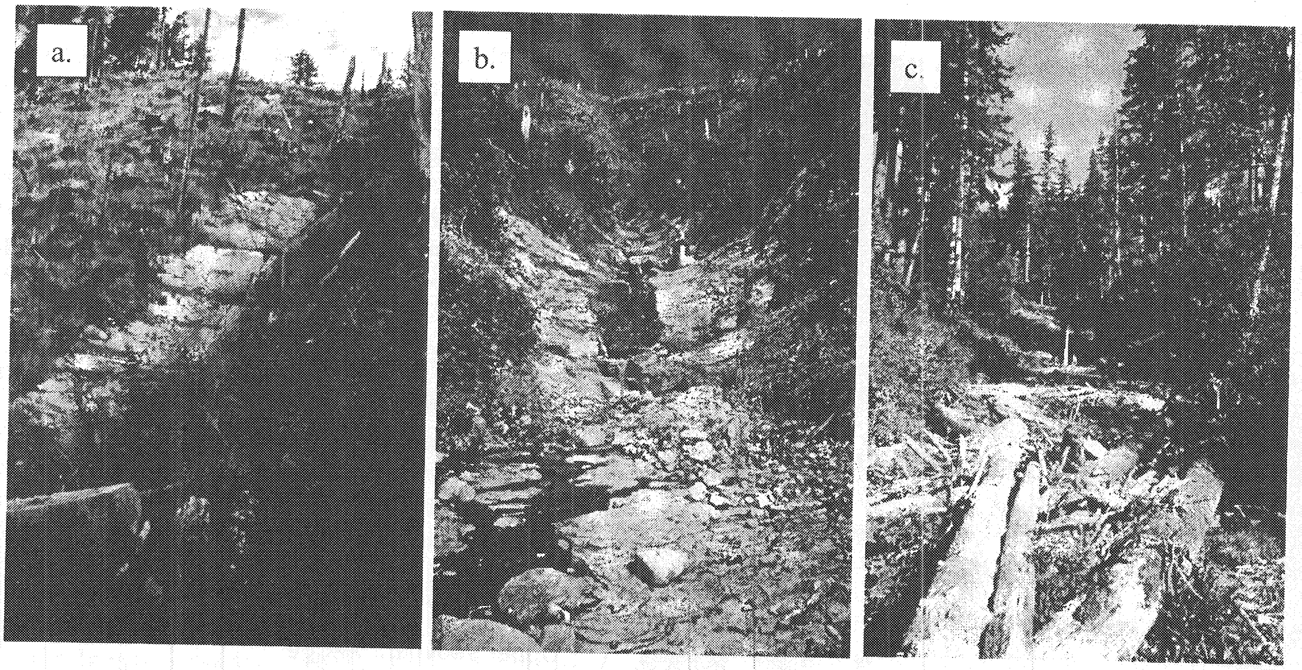
half of the deposit is constrained by its incision into the deposit and the hillslope to the east. From the west, a small, low-gradient ephemeral drainage enters the deposit reach near the seep area (Figure 2). The channel in the lower portion of the deposit is shallow and braided, possibly making this part of the valley floor more prone to flood disturbance during high flows. The character of the stream and valley floor changes both up- and downstream of the deposit. Upstream the valley floor is narrow, whereas downstream it is wider and has been altered by beaver dams and associated flooding.

The deposit is bordered partially on both sides by mature trees left to buffer the stream from timber harvests on the adjacent slopes. Tree species in the buffer strip are Douglas-fir (*Pseudotsuga menziesii*), red alder, and western hemlock (Figure 2), all of which were capable of producing seed at the time of the debris flow. Estimated diameters of these trees range from 50 to 120 cm for the Douglas fir, 20 to 70 cm for the red alder, and about 40 cm for the lone western hemlock. Most of the buffer trees are clustered in two locations: east of the upper third of the deposit, and west of the middle third (Figure 2). Young plantations of Douglas fir grow upslope of the buffer on both sides of the stream.

Data Collection and Analysis

In 1990, the first growing season after deposition, we installed grids of 0.25 m^2 circular plots in four distinct areas of the deposit (Figure 2): bank slump (16 plots, four of which were disjunct from the main area), seep (14 plots), sediment wedge (48 plots), and log jam (15 plots). Plots were arranged 2 m apart within rows that were 5 m apart, except for the disjunct plots of the bank slump. We subsequently split plots on the sediment wedge into two areas, upper and lower, based on the abundance of red alder seedlings (generally lacking on the lower sediment wedge). We also established nine plots in intact vegetation on the adjacent hillslope and along the channel upstream of both the deposit and the tributary from which the debris flow originated to inventory species composition in less disturbed areas.

Sampling was conducted during late July to August in 1990, 1991, 1992, 1993, 1996, and 1999. At each sampling date we visually estimated absolute percent cover of all vascular plants in each plot, as well as various ground-cover attributes: exposed mineral soil (particles ≤ 2 mm), rocks (gravel, cobbles, boulders), litter (leaves and twigs), logs, and moss. The majority of plants were identified to species, although some only to genus because of uncertainty in identification. For this reason we use the term "taxa." With the exception of the crowns of mature trees in



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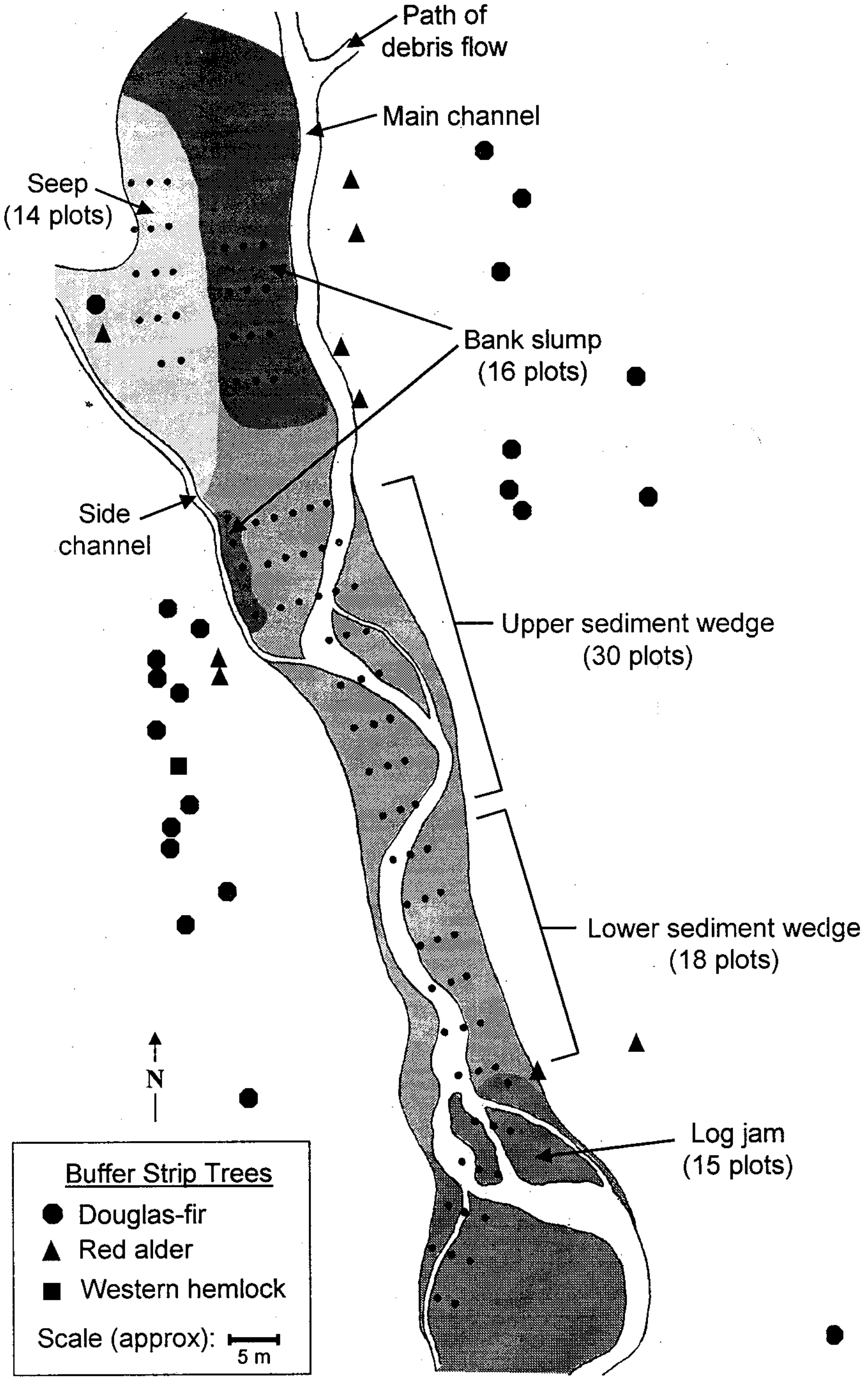

Figure 2. Sketch of Plot Locations (n = 93) in Five Areas of the Debris-Flow Deposit and the Approximate Locations of Mature Trees in the Adjacent Buffer Strip.

the buffer strip, cover estimates included plants that overhung the imaginary three-dimensional cylinder of the plot. Total plant cover on a plot could exceed 100 percent since estimates were made independently for each taxa. We also tallied the number of woody plants rooted in each plot. In 1990 we were able to distinguish salmonberry and stink currant (*Ribes bracteosum*) seedlings from stems that had resprouted from buried rhizomes, the latter of which had larger leaves and greater stature. This distinction became more difficult over time, thus counts for seedlings and sprouts of these species were lumped after 1990. It appeared that all other shrubs were of seedling origin. Finally, we photographed each deposit area from two fixed points at the time of data collection to create a visual record of change over time.

Temporal trends in the occurrence of taxa were evaluated by calculating constancy, or frequency of occurrence, across all the plots on the site, and determining an annual rate of turnover in taxa composition using Wilson and Shmida's (1984) "beta turnover" (β_T) (M. Wilson, pers. comm.):

$$\beta_T \text{ rate} = [(g_t + l_t) / 2\alpha] / i$$

where g and l are the number of taxa gained and lost, respectively, during sample period t; α is the average number of taxa found across all sampling dates; and i is the time interval in years between sampling periods.

For each of the five deposit areas, we summarized average yearly cover of plants by life form (forbs, graminoids [grasses, sedges, rushes], shrubs, trees) and origin (native, nonnative), and calculated the average number of taxa per plot. We also examined changes over time in the density of red alder and salmonberry.

Nonmetric multidimensional scaling (NMS) (Mather, 1976), an ordination technique, was used with data from all sample years to analyze compositional change over time. NMS is recognized as a robust method for ordination of community data (Minchin, 1987). Percent cover data were reduced to a "composite" (average) sample representing each area of the debris-flow deposit at each point in time, and then transformed with an arcsine-squareroot transformation (Sokal and Rohlf, 1981). Four species that occurred a single time were excluded from the ordination to reduce noise. An evaluation of "stress" (Kruskal, 1964), an inverse of the measure of fit, indicated that three dimensions (axes) would provide the best solution to the ordination. Two-dimensional scatterplots of ordination scores for the composite samples were used to portray successional change over time (trajectories) by connecting points representing successive years for each deposit area. We present scatterplots from Axes 1 and 2 and from Axes 1 and 3. The plot of Axes 2 and 3 did not add to the interpretation of the ordination and is not shown. Interpreting the ordination axes was aided by correlating sample scores with cover of individual taxa and overlaying taxa abundance on the ordination scatterplots. In addition, we quantified changes in taxa composition and abundance in each area from 1990 to 1999 with the Bray-Curtis coefficient (Bray and Curtis, 1957) using untransformed, composite cover data. This coefficient is a measure of ecological distance or dissimilarity among the composite samples. Its calculation and the NMS ordinations were carried out in PC-Ord, version 4.14 (McCune and Mefford, 1999).

RESULTS

General Patterns and Trends

There were substantial first-year differences in ground-cover attributes among the five areas of the deposit (Figure 3). Rocks occupied over 40 percent of the surface on the upper and lower sediment wedge (Figure 4a) compared to 4 to 10 percent elsewhere. Litter cover was highest on the bank slump and log jam, and, not unexpectedly, cover of logs was higher on the log jam than on other areas.

Numerous forbs, graminoids, shrubs, and trees colonized the debris-flow deposit, resulting in a mosaic of herbaceous and woody plants interspersed with openings of exposed mineral soil, rock, and woody debris (Figure 4b). Over the ten-year period of study, we recorded 61 taxa, including four trees, 11 shrubs, 15 graminoids, and 31 forbs (Table 1). By the second year (1991), 84 percent of these (51/61) had been documented, and more than two-thirds were still present in 1999. Twelve of the taxa – mostly forbs and graminoids – were nonnative. The total number of taxa recorded did not vary greatly from year to year, ranging from 39 in 1990 to 49 in 1996. Of the 26 taxa observed in plots in the adjacent undisturbed vegetation, all but one were present on the debris-flow deposit.

Temporal trends in constancy were highly variable among taxa (Table 1). Some such as tooth-leaved monkeyflower (*Mimulus dentatus*) were most common in the first and second years. For several weedy taxa, including foxglove (*Digitalis purpurea*), willow-weed (*Epilobium* sp.), groundsel (*Senecio* sp.), and ryegrass (*Lolium* sp.), constancy peaked in 1992 or 1993, then declined. Conversely, candyflower (*Montia siberica*) and starwort (*Stellaria crispa*) were initially common, disappeared by 1992 or 1993, and then reappeared. Constancy of sword fern and youth-on-age (*Tolmiea menziesii*), both native forbs, increased steadily over time, whereas other native species such as Dewey's sedge (*Carex deweyana*), Mexican hedge-nettle (*Stachys mexicana*), and salmonberry occurred at relatively stable levels over the entire ten-year period. The annual rate of taxa turnover (β_T/year) generally declined over time, from a high of 17.7 percent from 1990 to 1991 to a low of 3.7 percent from 1996 to 1999 (Figure 5). This was due primarily to a reduction in the number of species gained.

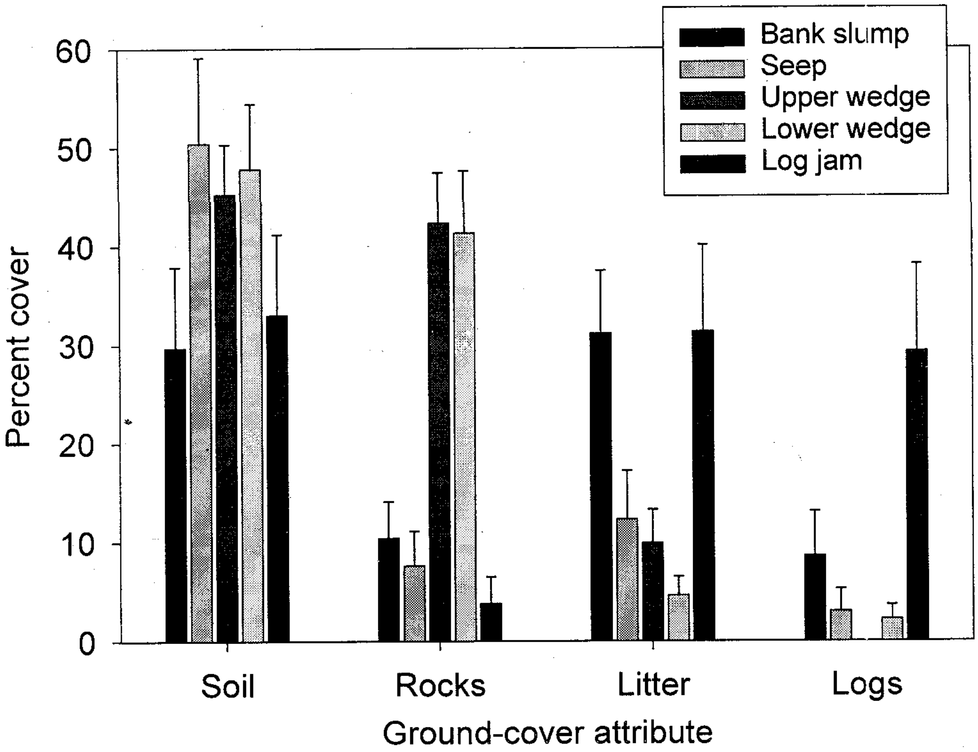

Figure 3. Mean Percent Cover of Ground-Cover Attributes in 1990 in Five Areas of the Debris-Flow Deposit. Error bars are standard errors. Soil includes particles ≤ 2 mm. Rocks include gravel, cobbles, and boulders. Moss was absent in 1990.

Dominance of Red Alder and Salmonberry

Red alder and salmonberry were the dominant species. Average cover of alder increased throughout the study, from 1 percent in 1990 to 74 percent in 1999 (data not shown). Salmonberry averaged 11 percent cover in 1990, by far greater than any other taxa that year, and ranged from 18 to 25 percent thereafter. In comparison, no other taxa exceeded 15 percent average cover in any year, with the vast majority averaging less than 2 percent. Among the higher-cover herbaceous taxa, Mexican hedge-nettle peaked at 5 percent cover in 1991, while foxglove (10 percent), Dewey's sedge (6 percent), common velvet-grass (*Holcus lanatus*) (5 percent), and groundsel (4 percent) peaked in 1992 or 1993. Thimbleberry (*Rubus parviflorus*) and stink currant, the most common shrubs besides salmonberry, attained an average cover of 5 percent in 1996. Prominent species in the last year of study included youth-on-age (14 percent) and sword fern (9 percent).

Red alder established from seed, most of which germinated in the first two years. Alder seedlings were abundant on the bank slump, seep, and upper sediment wedge, with an average density of 16 to 20 seedlings/m^2 in 1990 (Figure 6a). These seedlings developed into a thicket of small trees that thinned over time to a density of less than 2/m^2 by 1999 (Figure 6a and Figure 4c). In contrast, alder seedling density on the lower sediment wedge and log jam was never greater than 1/m^2 in any year. Despite differences in initial density among deposit areas, cover of alder was comparable among all areas by 1999 (Figure 6b), when cover ranged from 60 to 85 percent and alder trees were 4 to 8 m tall.

Salmonberry germinated from seed, resprouted from plants sheared off and buried in place, and sprouted from rhizomes entrained in the debris flow or transported with the bank slump. Vegetative regrowth from the rhizomes and buried plants was generally rapid in the first year, producing cover that far exceeded that produced by salmonberry seedlings. In 1990 (when we were able to differentiate sprouts from seedlings), sprout clumps were most abundant on the bank slump (7.3/m^2) and seep (4.6/m^2). These areas also had the highest combined density of seedlings and sprout clumps (Figure 6a). In comparison, sprout-clump density in 1990 was less than 1/m^2 on the upper and lower sediment wedge. The initial abundance of salmonberry on the seep did not translate into a rapid increase in salmonberry cover, as it did on the bank slump, where cover exceeded 50 percent from 1991 to 1993. Also, salmonberry density on the seep declined steadily after 1991, unlike other areas where clear trends in density were not evident (Figure 6a). Salmonberry cover decreased sharply from 1993 to 1996 on the bank slump and log jam, during which time there was a corresponding increase in cover of red alder (Figure 6b). On the bank slump, these changes coincided with alder overtopping the 1.0 to 1.5 m tall salmonberry canopy. Seedling establishment of salmonberry, like red alder, appeared to be greatest in the first two years. However, we observed ongoing establishment of salmonberry seedlings during the course of the study, even in the shade of red alder trees in places where the ground surface was disturbed from localized flooding.

Area-Specific Patterns: Life Forms, Origin, and Richness

Despite widespread dominance of red alder and salmonberry, there were distinct differences in total vegetative cover and in the abundance of life forms across the five areas. Total cover in 1990 was 40 to 50 percent on the seep and bank slump, compared to 8 to 23 percent on the other areas (Figure 7a). Forbs were more abundant on the seep than elsewhere, reaching a ten-year high of about 60 percent cover in 1993. In each year on the lower sediment wedge, graminoids comprised a greater proportion of total cover than on other areas. Shrubs accounted for the majority of cover on the bank slump and log jam from 1990 through 1996, due in large part to vegetative sprouts of salmonberry as well as vine maple (*Acer circinatum*) on the log jam. Tree cover increased in each area over time, although there was a pronounced lag in this trend on the lower wedge and log jam. The only tree species to establish besides red alder were three Douglas fir and two western hemlock on the upper sediment wedge, none of which survived beyond 1996, and a Sitka spruce on the lower sediment wedge, which was nearly 2 m tall in 1999.

Cover of nonnative taxa was generally low, although there were area-specific differences in its abundance and persistence. Nonnative cover was higher, peaked later (1993), and persisted longer on the lower sediment wedge than on other areas (Figure 7b). In addition, it was about equal to native plant cover on the lower wedge through 1993, unlike other areas where non-natives comprised a smaller proportion of total cover.

Richness, expressed as the number of taxa per plot, was highly variable across deposit areas in 1990 and tended to converge over time (Figure 8). It was highest on the seep from 1990 to 1993, after which it declined. Richness steadily increased on the log jam, from an average of 2.7 taxa/plot in 1990 to 8.3 taxa/plot in 1999.

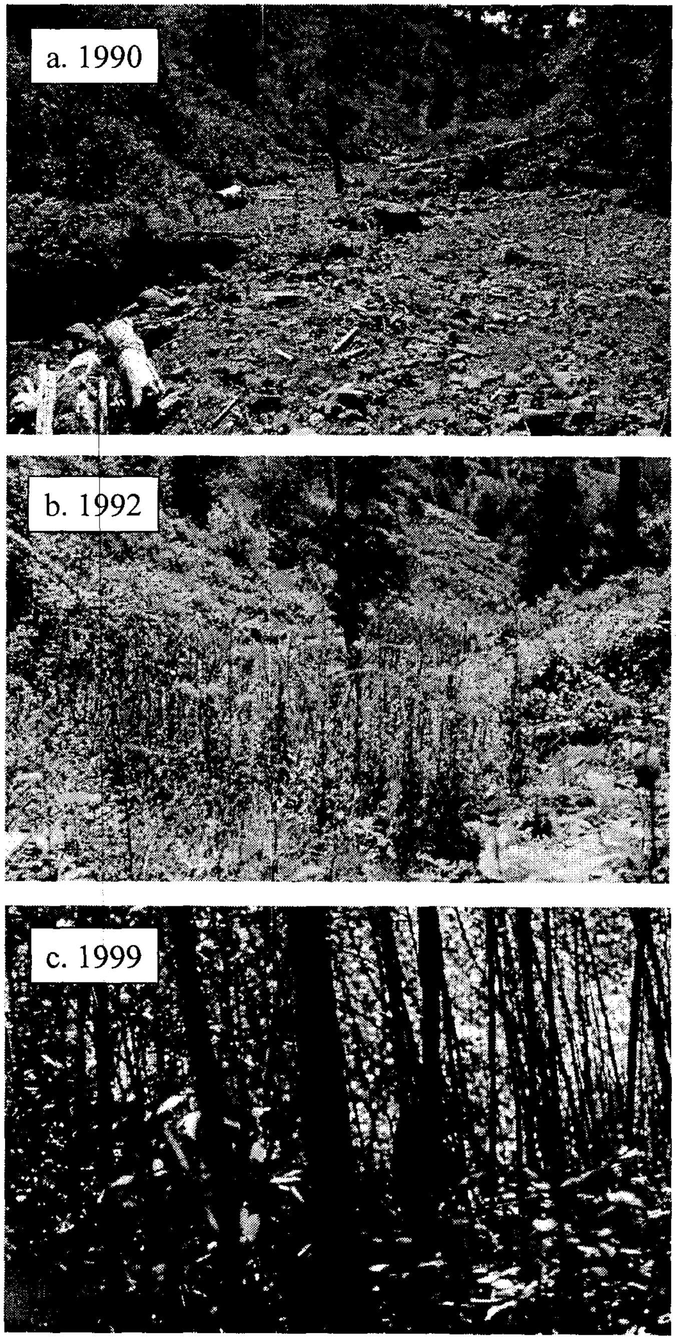

Figure 4. Photographic Time Series of Plant Succession on the Upper Sediment Wedge in (a) 1990, (b) 1992, and (c) 1999. The photograph in 1990 was taken with a 35 mm lens and the other two with a 50 mm lens.

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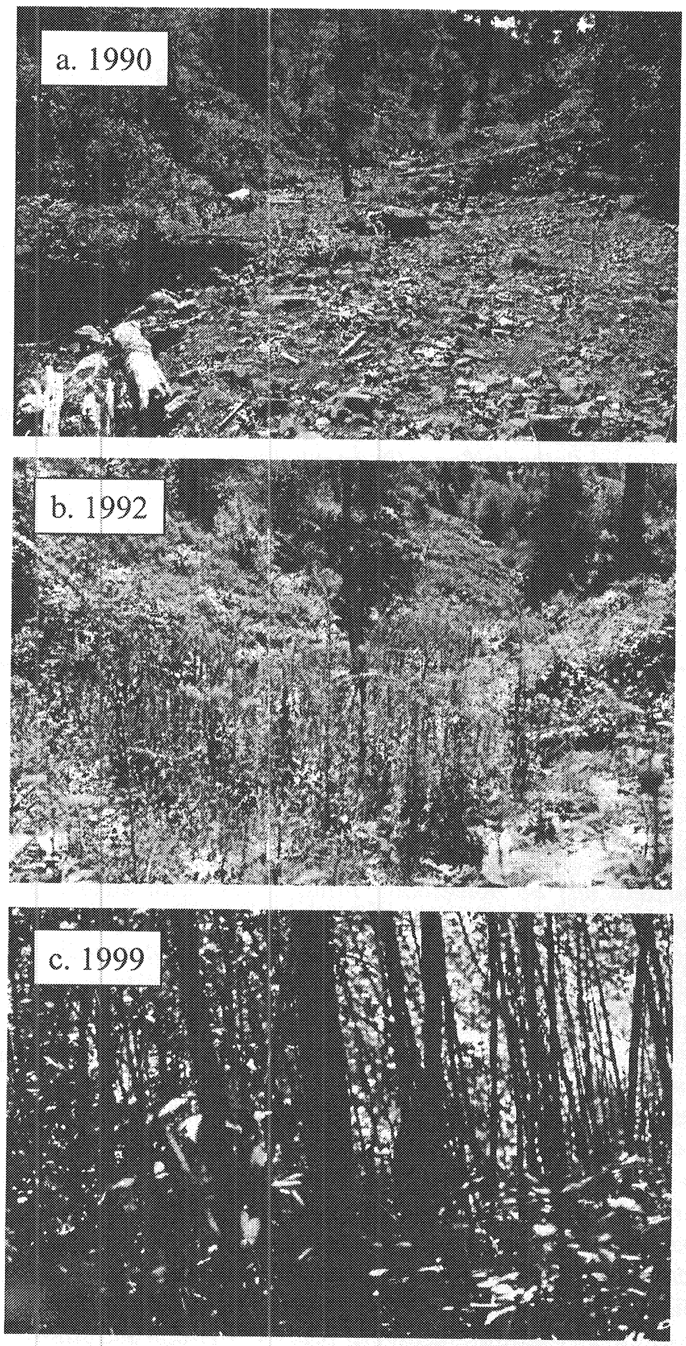

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TABLE 1. Taxa Constancy (percent), or Frequency of Occurrence, Across All Deposit Areas by Year. Nonnative taxa are indicated by an asterisk (*). Total number of taxa for each year is shown at bottom.

Taxa	**Taxa Constancy (percent occurrence in all plots)**					
	1990	**1991**	**1992**	**1993**	**1996**	**1999**
Forbs						
Adiantum pedatum (maidenhair fern)	0	1	2	0	1	1
Anaphalis margaritacea (pearly everlasting)	0	3	1	1	0	0
Aquilegia formosa (red columbine)	0	1	2	1	3	1
Athyrium filix-femina (lady fern)	1	3	4	10	10	9
Blechnum spicant (deer fern)	0	1	9	9	9	9
Cardamine angulata (wood bittercress)	1	0	0	0	1	1
Cardamine oligosperma (western bittercress)	0	0	0	0	16	0
Cirsium sp.* (thistle)	2	8	2	1	0	0
Dicentra formosa (bleeding heart)	1	2	1	0	2	0
*Digitalis purpurea** (foxglove)	20	38	51	22	38	9
Epilobium sp. (willow-weed)	19	52	52	59	35	10
Equisetum arvense (common horsetail)	2	4	6	5	4	1
Galium aparine (goose-grass)	0	0	0	0	1	0
Galium triflorum (fragrant bedstraw)	13	20	10	5	8	6
*Hypochaeris radicata** (spotted cats-ear)	0	1	1	3	0	0
Hydrophyllum tenuipes (Pacific waterleaf)	1	0	0	0	0	0
Marah oreganus (bigroot)	1	6	1	2	8	10
Mitella caulescens (leafy mitrewort)	0	0	0	1	0	1
Mimulus dentatus (tooth-leaved monkey-flower)	22	17	2	0	1	2
Montia siberica (candyflower)	20	14	0	1	10	17
Oxalis oregana (Oregon wood-sorrel)	20	22	22	22	27	40
Phacelia sp. (phacelia)	1	3	2	2	0	0
Polystichum munitum (sword fern)	4	9	15	19	23	30
Scrophularia californica (California figwort)	3	5	14	15	4	1
Senecio sp.* (groundsel)	11	35	34	40	16	5
*Sonchus asper** (prickly sow-thistle)	0	8	16	13	0	0
Stellaria crispa (crisped starwort)	13	3	1	0	1	9
Stachys mexicana (Mexican hedge-nettle)	39	37	43	35	34	27
Tellima grandiflora (fringecup)	0	3	6	5	10	9
Tolmiea menziesii (youth-on-age)	40	46	54	56	63	72
*Vicia spp.** (vetch)	1	1	0	0	0	0
Graminoids						
Agrostis exarata (spike bentgrass)	15	30	27	12	9	8
Bromus vulgaris (Columbia brome)	5	11	25	33	32	29
Carex deweyana (Dewey's sedge)	33	42	51	48	55	46
Carex hendersonii (Henderson's sedge)	0	4	14	9	10	4
*Dactylis glomerata** (orchard-grass)	0	2	0	1	0	0
Deschampsia elongata (slender hairgrass)	5	8	16	11	4	1
Elymus glaucus (blue wildrye)	1	0	0	0	4	8
Festuca sp. (fescue)	4	13	19	19	22	18
Glyceria elata (tall mannagrass)	0	1	2	1	1	3
*Holcus lanatus** (common velvet-grass)	2	5	27	39	29	18
Lolium sp.* (ryegrass)	0	13	12	19	5	0
Luzula sp. (woodrush)	19	23	23	13	8	13
Melica subulata (Alaska oniongrass)	0	0	1	0	2	2
*Poa trivialis** (roughstalk bluegrass)	1	4	12	12	15	25
Trisetum sp. (trisetum)	0	3	10	4	1	0

TABLE 1. Taxa Constancy (percent), or Frequency of Occurrence, Across All Deposit Areas by Year. Nonnative taxa are indicated by an asterisk (*). Total number of taxa for each year is shown at bottom (cont'd.)

Taxa	Taxa Constancy (percent occurrence in all plots)					
	1990	**1991**	**1992**	**1993**	**1996**	**1999**
Shrubs						
Acer circinatum (vine maple)	1	1	1	1	1	2
Holodiscus discolor (ocean spray)	0	0	1	1	2	2
Ribes bracteosum (stink currant)	20	25	28	18	26	30
*Rubus discolor** (Himalayan blackberry)	0	0	0	0	3	10
*Rubus laciniatus** (evergreen blackberry)	0	0	0	0	2	1
Rubus leucodermis (black raspberry)	0	0	1	1	0	0
Rubus parviflorus (thimbleberry)	9	14	27	28	34	25
Rubus spectabilis (salmonberry)	67	66	59	65	69	74
Rubus ursinus (trailing blackberry)	0	0	2	0	10	19
Salix sp. (willow)	2	1	2	2	1	0
Sambucus racemosa (red elderberry)	2	0	0	0	0	0
Trees						
Alnus rubra (red alder)	52	48	54	55	78	98
Picea sitchensis (Sitka spruce)	0	0	0	0	0	1
Pseudotsuga menziesii (Douglas fir)	3	2	2	2	1	0
Tsuga heterophylla (western hemlock)	2	2	2	2	2	0
Total Number of Taxa	39	47	48	45	49	43

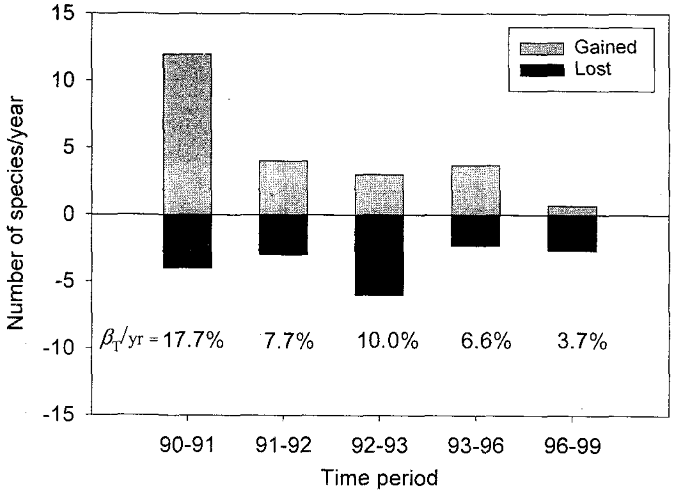

Figure 5. Number of Species Gained and Lost, on a Per-Year Basis, From One Sampling Year to the Next on the Debris-Flow Deposit. Annual rate of change in species turnover, using beta turnover (Wilson and Shmida, 1984), is shown as a percentage below each bar.

Successional Trajectories

NMS ordination of plant cover revealed several patterns underlying plant succession on the debris-flow deposit. The scatterplot of scores from Axes 1 and 2 illustrates gradual convergence of plant community composition over time (trajectories for deposit areas get closer together), yet the areas also remained compositionally distinct (trajectories tend not to intersect) (Figure 9a). Correlations between cover and scores for Axis 1 indicate that convergence was tied to increasing dominance of red alder (r = -0.85) and native forbs such as sword fern (r = -0.86) and youth-on-age (r = -0.80). Convergence is also demonstrated by the decline in dissimilarity among the five deposit areas, from an average of 62 percent (range 42 to 79 percent) in 1990 to 31 percent (range 16 to 45 percent) in 1999 (data not shown). Within individual areas, dissimilarity from 1990 to 1999 was 64 percent on the bank slump, 77 percent on the log jam, and from 85 to 90 percent on the seep and sediment wedge. Axis 2 distinguished first-year data from the log jam and sediment wedge from other years and areas. Taxa associated with Axis 2 scores were Dewey's sedge (r = -0.76), foxglove (r = -0.53), and thimbleberry (r = -0.51).

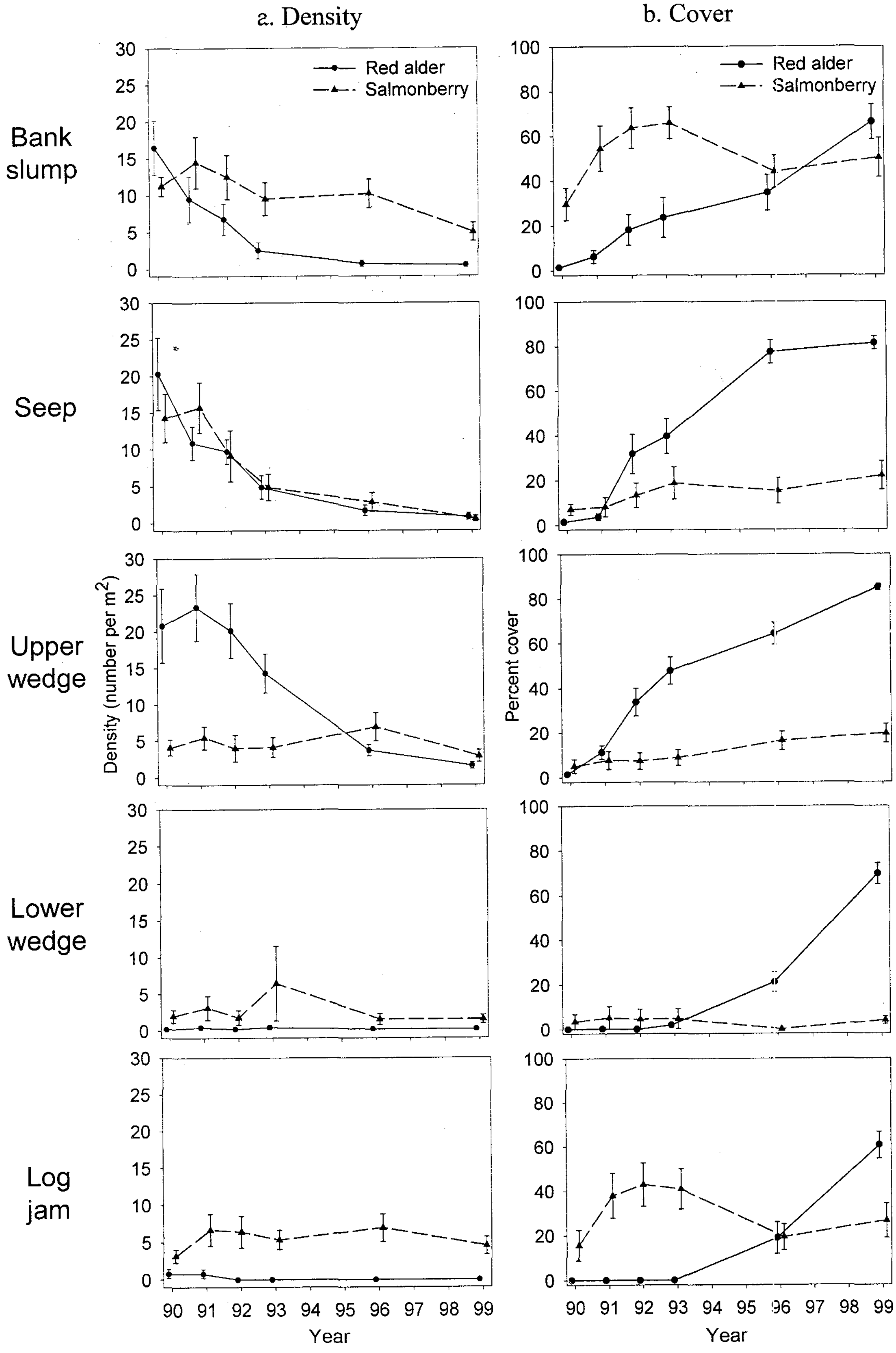

Figure 6. (a) Density (number/m^2) and (b) Cover (percent) of Red Alder and Salmonberry (seedlings and sprout clumps combined) in Five Areas of the Debris-Flow Deposit.

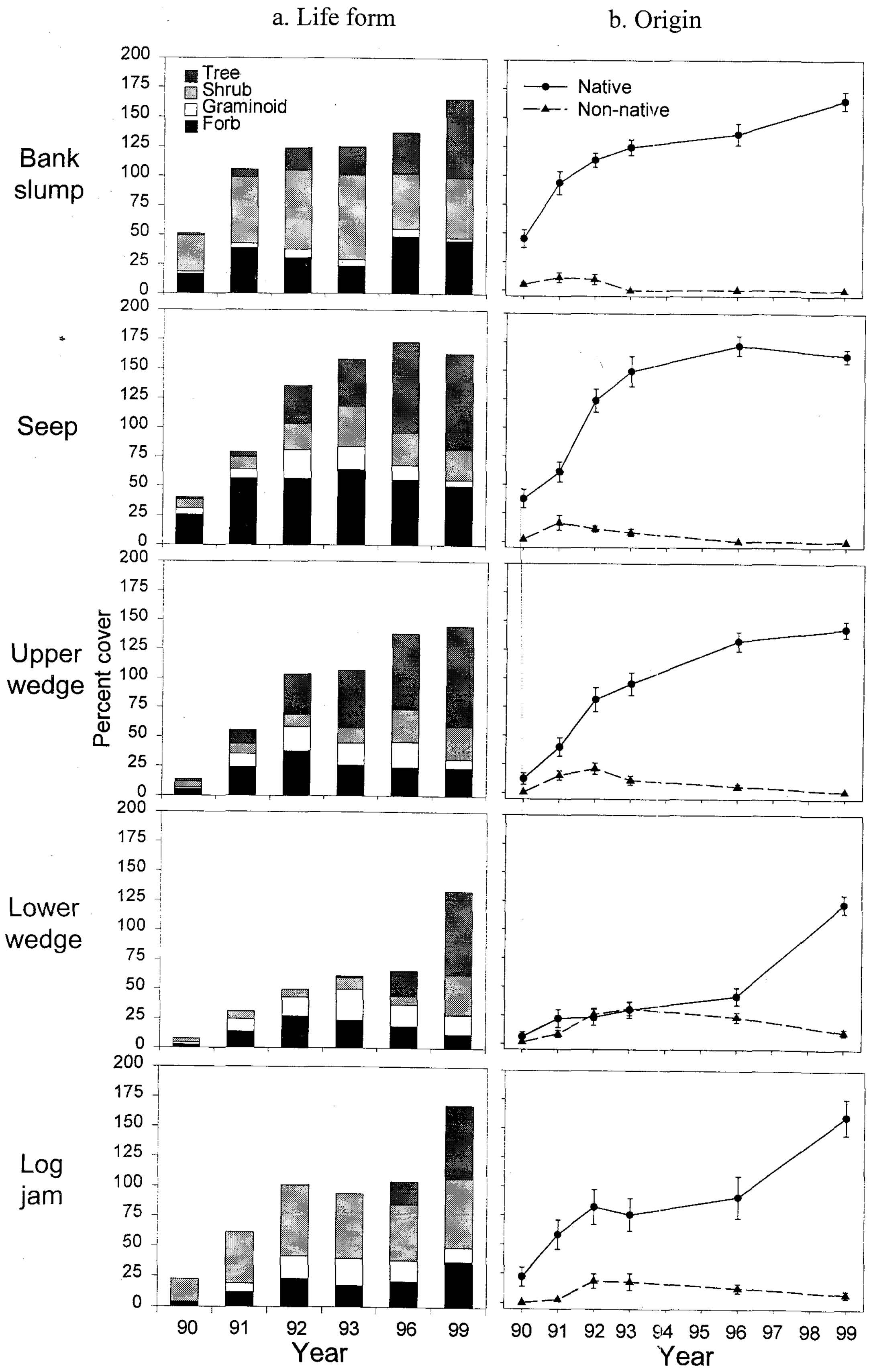

Figure 7. Percent Cover of Plants by (a) Life Form and (b) Origin in Five Areas of the Debris-Flow Deposit.

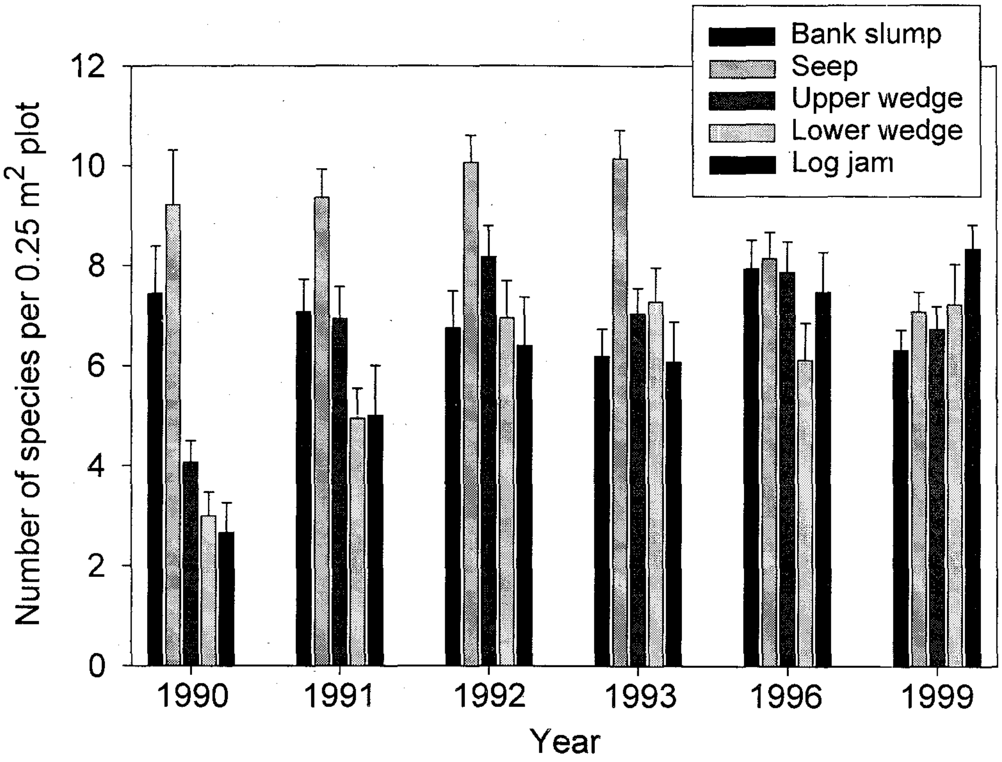

Figure 8. Mean Number of Taxa Per 0.25 m^2 Plot in Five Areas of the Debris-Flow Deposit. Error bars are standard errors.

Additional patterns emerge in the scatterplot of Axes 1 and 3. There is a high degree of overlap in the trajectories of the bank slump and seep. However, there is also stratification of deposit areas that roughly corresponds to their physical location on the site, from the bank slump and seep at the upper end of the deposit to the lower sediment wedge and log jam at the lower end, with the upper sediment wedge in between (Figure 9b). The taxa correlated with Axis 3 reflect compositional differences and similarities among deposit areas. For example, the bank slump and seep were characterized by an abundance of Mexican hedge-nettle (r = 0.71) and starwort (r = 0.62) and the occurrence of monkeyflower (r = 0.69). In contrast, the lower sediment wedge and log jam were characterized by various graminoids associated with open or disturbed areas, including roughstalk bluegrass (*Poa trivialis*) (r = -0.77), ryegrass (r = -0.50), and tall mannagrass (*Glyceria elata*) (r = -0.46). Vine maple (r = -0.52) was unique to the log jam. Several species that occurred exclusively (although infrequently) on the upper sediment wedge – Douglas fir, western hemlock, and Alaska oniongrass (*Melica subulata*) – probably factored into it its distinct location in ordination space.

DISCUSSION

Plant succession on the debris-flow deposit varied with substrate and was influenced by the composition of early colonizers and the presence of vegetative propagules. Local seed sources and competitive interactions among plants also may have played a role. The relative importance of these factors, and the degree to which they were confounded, are difficult to evaluate without explicit experimentation. What is clear is that fine-scale heterogeneity was present in both the physical environment and the plant community that developed.

Substrate Variation

Variability in the physical environment has been shown to be a major driver of revegetation patterns following mass failure, especially at a scale that incorporates areas of scour, persistent erosion, deposition, and residual vegetation (Flaccus, 1959; Hull and Scott, 1982; Miles and Swanson, 1986; Gecy and Wilson, 1990; Guariguata, 1990). But heterogeneity in revegetation also is evident at finer scales, that is, within zones of deposition, as demonstrated by this

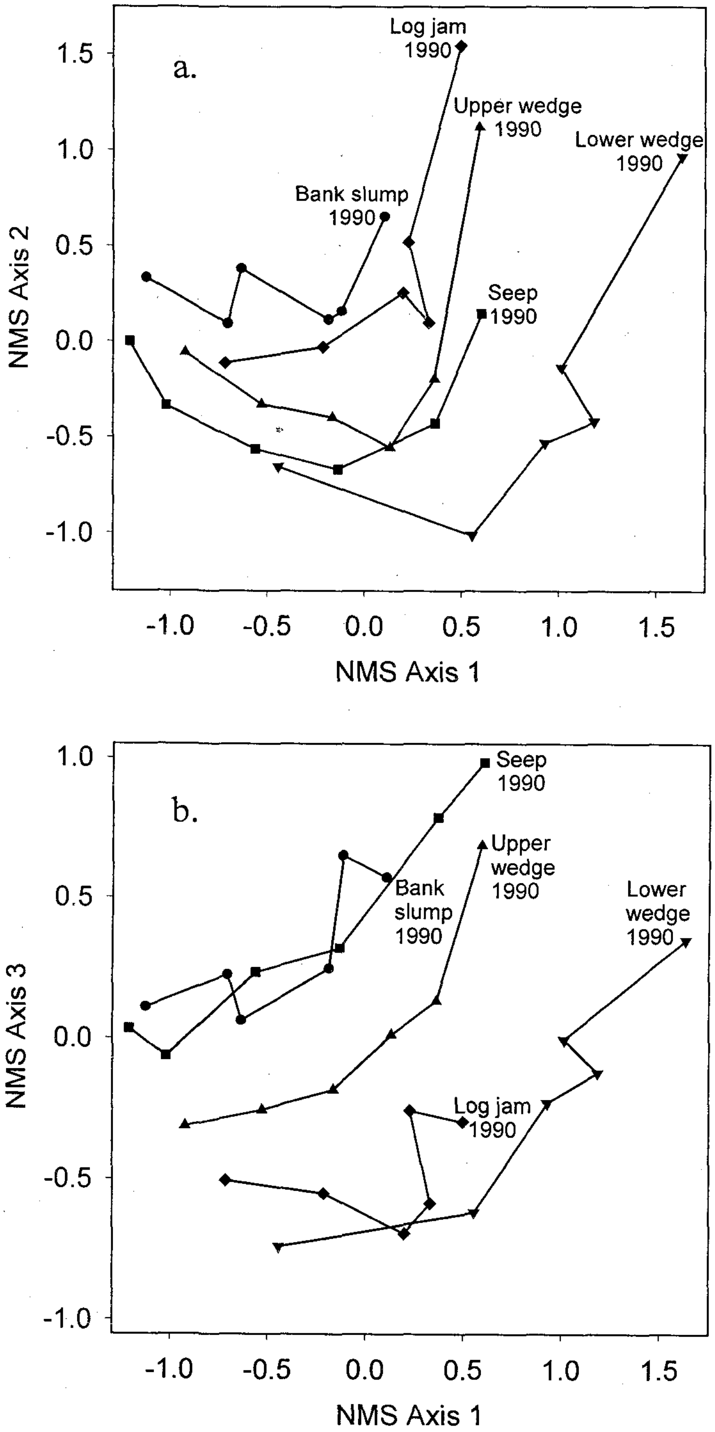

Figure 9. Ordination Diagram From Nonmetric Multidimensional Scaling (NMS) of Percent Cover in Five Areas of the Debris-Flow Deposit Over a Ten-Year Period. Variability in the data has been reduced to three dimensions, or axes, shown as scatterplots of (a) Axis 1 vs. Axis 2, and (b) Axis 1 vs. Axis 3. Points represent composite sample units of each area in each year. Lines connect the same area from one year to the next, beginning in 1990 and ending in 1999. The distance between points approximates their dissimilarity; that is, points close together are more similar in composition than points further apart.

study and others (Guariguata, 1990). This is not surprising given that depositional zones contain a mix of sediment, wood, litter, as well as seeds and vegetative propagules (Guariguata, 1990; Johnson *et al.,* 2000). The mixing of substrates probably accounts for the variability seen in the chemical properties and fertility of deposit soils (Adams and Sidle, 1987; Guariguata, 1990), factors that may ultimately influence plant establishment and growth (Dalling and Tanner, 1995).

In our study, the physical setting of the debris-flow deposit was a template for the patterns we observed in plant succession. For example, there was variability in the elevation of deposit surfaces above the stream channel and in the degree of channel constraint, both of which were less in the lower wedge and log jam areas. Differences in surface soil moisture were apparent, with relatively moist soils on the seep area and seemingly more droughty soils on much of the sediment wedge and log jam. Rocks and logs, prominent on the sediment wedge and log jam, respectively, may have limited the rooting potential of colonizing plants (Adams and Sidle, 1987). The abiotic environment of the site may have been influenced by the large trees in the buffer strip (Figure 1c and Figure 2), whose shade was cast primarily on the upper two-thirds of the deposit, leaving the lower (southern) third more exposed to solar radiation. Together, these conditions presented a suite of microhabitats for plant colonization and growth, thereby contributing to fine-scale heterogeneity in the plant community.

Successional Patterns

Colonization of the debris-flow deposit occurred quickly. Indeed, more than 80 percent of the taxa had been documented by the second year. These included light-demanding pioneers as well as other taxa typically associated with later stages of succession (Henderson, 1978). More significant is that over two-thirds of those taxa were still present in 1999. This underscores the importance of initial composition of colonizers and their persistence in plant succession, as recognized by Egler (1954).

The progression from open conditions with an abundance of weedy forbs and graminoids to a stage dominated by densely growing trees and shade-tolerant understory plants is characteristic of early succession (Flaccus, 1959; Henderson, 1978). The weedy herbaceous stage is thought to last just a few years, yet on the lower sediment wedge, forbs and graminoids dominated for at least seven years, and nonnative taxa were slower to decline than elsewhere (Figure 7). Persistence of these taxa was probably related to the low density of red alder, salmonberry, and other woody plants, and the corresponding lag in development of canopy cover (i.e., shade). The fact that salmonberry was unable to attain dominance on the lower wedge was surprising, considering that its density and cover, while low, were greater than those of red alder for several years (Figure 6). This suggests that salmonberry may be affected by constraints other than competition for light, such as those imposed by droughty soils (Ruth, 1970).

Red alder and salmonberry, the two dominant species over much of the deposit, established abundantly in the first year. Salmonberry's prominence, particularly on the bank slump, was tied to rhizomes that were transported with the deposit and subsequently sprouted. Post-disturbance sprouting from root crowns and rhizomes and rapid growth of aerial stems allow salmonberry to develop a dense canopy that can shade out other plant species (Tappeiner *et al.,* 1991). Salmonberry sprouts can grow 0.5 m in a few months and up to 2 or 3 m within a few years (Ruth, 1956). Furthermore, the rhizomes can spread rapidly (1 to 2.5 $m/m^2/yr$), especially in the absence of overhead competition (Tappeiner *et al.,* 1991). Each of these traits provide salmonberry with successful strategies for colonizing disturbed environments. On the debris flow site, vegetative reproduction of salmonberry, as well as that of sword fern and possibly other taxa, led to a rapid increase in cover on the bank slump and may explain why dissimilarity (i.e., change) over time was less there than other areas. The role of sprouting vegetation has been recognized in other studies of succession after mass failure (Flaccus, 1959; Gecy and Wilson, 1990; Guariguata, 1990), but it remains uncertain whether it hastens a return to predisturbance community types. Salmonberry also reproduced from seed, although we could not assess the seedlings' role in succession as we did not track individual plants through time. Like the rhizomes, salmonberry seeds may have been transported with the debris flow, as they can be plentiful in the soil seed bank (Ruth, 1970).

Red alder germinated from seed, the source of which was likely the mature trees in the adjacent buffer strip rather than more distant sources or the seed bank. Viability of red alder seed in the soil seed bank is estimated to be low (Haeussler and Tappeiner, 1993). The spatial distribution of alder seedlings – concentrated on the upper sediment wedge, seep, and bank slump – roughly coincided with the location of potential seed trees in the buffer strip (Figure 2). Highly localized associations between parent trees and seedlings are recognized in other species, but alder seed is very light and can be carried by wind for long distances (Harrington, 1990). Thus, it seems unusual that alder density would be so distinctly different between the upper and lower portions of the deposit. An alternative explanation for alder's absence on the lower wedge and log jam is that moisture stress or temperature extremes reduced germination or survival (Haeussler *et al.,* 1995). In addition, alder seed may have been present in these areas but could have been washed away by high stream flows. This seems plausible since debris-flow deposits typically get reworked as the stream cuts a new channel through the material (Benda, 1990). In addition, flooding can delay colonization of new substrates (Walker *et al.,* 1986).

The dispersal and reproductive mechanisms of other taxa were less clear. Aside from the sprouting we observed in salmonberry, stink currant, vine maple, and sword fern, it was our impression that all other taxa grew from seed, based on the diminutive stature of most plants in the first year. We cannot be certain of this, however, as even small parts of stoloniferous or rhizomatous plants such as youth-on-age, Mexican hedge-nettle and Oregon oxalis (*Oxalis oregana*) can form new plants. Biennials and annuals that reproduce primarily or exclusively from seed, including thistle (*Cirsium* sp.), foxglove, and groundsel, probably existed in the seed bank (van Baalen, 1982; Doucet and Cavers, 1996; Halpern *et al.,* 1997), given their presence the first growing season after disturbance. Gecy and Wilson (1990) found that plants of seed origin accounted for 67 percent of individuals in the first year after debris flows in the Cascade Range of Oregon, but that vegetative sprouts accounted for a higher percentage of cover.

The increasing dominance of red alder and the assumed competitive interactions related to it defined the middle and later years of succession in this study. This is illustrated by the convergence in successional trajectories among the five deposit areas in the ordination of taxa cover (Figure 9a). Red alder's dominance on the deposit is not surprising, given its adaptations to disturbed riparian environments. It can germinate prolifically on newly deposited or exposed substrates, and its early height growth on favorable sites can exceed 1 m/yr (Harrington, 1990). Alder also fixes nitrogen in nitrogen-limited locations such as gravel bars (Binkely *et al.,* 1992), and can tolerate poorly drained soils as well as brief inundation (Harrington, 1990). On the debris-flow deposit, rapid height growth allowed alder to outcompete all other taxa, including salmonberry, even where sprouting rhizomes gave that species a distinct early advantage. For instance, young alder trees were able to penetrate a salmonberry canopy that had reached 65 percent cover on the bank slump (Figure 6b). Dense shade produced by alder (and salmonberry) on the upper sediment wedge and seep likely led to the decline or elimination of shade-intolerant taxa, including most of the nonnative herbs (Figure 7b) as well as the

Douglas fir seedlings. Even western hemlock, one of the most shade-tolerant conifers in these forests (Packee, 1990), succumbed under the alder. It is possible that other factors such as limited soil moisture or herbivory factored into the demise of these plants. Not all taxa declined in the shade of alder, however; numerous shade-tolerant native herbs persisted or even thrived, especially in the seep area.

SUMMARY

Debris flows are an integral part of the disturbance regime in riparian areas of Oregon's Coast Range. Their impact on the physical and biotic environment can have lasting consequences for aquatic and terrestrial habitats, forest structure, and plant community dynamics. Newly deposited substrates and the high-light environment introduced by debris flows create opportunities for colonization by a variety of native and non-native plant species. We found that composition of the initial colonizers and their persistence through time were key factors in plant community development. The dominance attained by some of these colonizers, particularly red alder and salmonberry, led to convergence in the plant communities among different areas of the debris-flow deposit. Dominance of these two species is common in riparian environments of the Coast Range, and this study provides some insights into their early dynamics. However, there were also fine-scale patterns in the vegetation that persisted through ten years, suggesting that succession on these deposits can be variable. The opportunity to tease apart community patterns at fine spatial and temporal scales was possible through repeated sampling in permanent plots. Coupling research of this nature with chronosequence studies would further enhance our understanding of plant succession after debris flow.

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