Swanson

AN ABSTRACT OF THE THESIS OF

Jeanne Leslie Gecy for the degree of Master of Science in Botany and Plant Pathology presented on July 14, 1988.

Title: Propagule Sources, Disturbance Characteristics and the Initial Establishment of Riparian Vegetation after Debris Flows.

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Debris flows are a major cause of disturbance to riparian vegetation. Both observational and experimental studies were used to examine the initial recovery of riparian vegetation after debris flows on headwater streams in the western Cascades of Oregon. My goal was to determine the roles of seedlings and vegetative sprouts, propagule sources, and disturbance characteristics in early succession.

I sampled three debris flows at the end of the first growing season after disturbance. Vegetative regrowth dominated early succession, providing 74% of the total cover. Early successional patterns reflected the type (scour and deposit) and intensity of disturbance. Vegetative regrowth (13.7% cover, 28 shoots/m^2) and total cover (14.8%) were highest on low intensity scour.

Seedling establishment was highest on fine and gravel deposits (2.1%-3.0% cover, 38-46 seedlings/m^2). The observational results also showed that revegetation of debris flows by sources other than dispersed seed is important. These additional sources are the residual propagule bank and the disturbance-transported propagule bank.

I hypothesized that the differences in total cover, seedling establishment, and vegetative regrowth resulted from differences in how scour and deposition affected propagule availability. I used this hypothesis to develop predictions of the effects of increasing intensity of scour and deposition on these three vegetation attributes and constructed experimental debris flow treatments to test the predictions. Six treatments provided three depths of deposition (5, 10 and 19 cm), two depths of scour (2.5 and 5 cm) and a control (no substrate modification). As in the observational study, the experimental results were recorded at the end of the first growing season after disturbance. The potential contributions of all three propagule sources to revegetation were also assessed.

Total cover and vegetative regrowth decreased with increasing intensity of both types of disturbance, but seedling establishment did not differ with disturbance type or intensity. The predictions for total cover, vegetative regrowth, and seedling establishment on deposits were consistent with the experimental results, but the predictions for seedling establishment on scour were not.

Most individuals establishing on the experimental site in the first growing season came from seeds and vegetative propagules in the transported and residual propagule banks (4731 and 8538 propagules/m^2 respectively). Dispersed seed contributed 31 seeds/m^2.

Fifteen species, comprising 59.2% of the overall cover, showed significant responses to the experimental treatments. These species responded individualistically to the disturbances and their responses could not be explained solely on the basis of propagule availability. The high cover of six species (for example _Madia_ _gracilis_ and _Epilobium_ _paniculatum_) on deposits clearly resulted from differences in propagule availability between the residual and transported propagule banks. But the responses of most other species (for example _Oxalis_ _oregana_ and _trilliifolia_, _Petasites_ _frigidus_ and _Galium_ _triflorum_) were determined by propagule availability, propagule removal by scour, physiological tolerances to disturbance and morphological characteristics.

This thesis demonstrates that both seedlings and vegetative sprouts are important in early debris flow succession, that debris flow revegetation can occur from three propagule sources and that one mechanism through which early successional patterns develop is through differences in how scour and deposition affect propagule availability. This thesis also demonstrates that understanding early succession requires a consideration not only of disturbance characteristics and propagule availability, but of individualistic species responses to disturbance.

Propagule Sources, Disturbance Characteristics and the Initial Establishment of Riparian Vegetation after Debris Flows

by

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TABLE OF CONTENTS

Chapter Page

LIST OF TABLES

LIST OF FIGURES

Propagule Sources, Disturbance Characteristics and the Initial Establishment of Riparian Vegetation after Debris Flows

Chapter 1

INTRODUCTION

Riparian vegetation occupies a narrow, three-dimensional zone of interaction between terrestrial and aquatic communities (Swanson et al. 1982), consisting of species whose presence can be attributed to stream-related factors, such as annual fluctuations in streamflow and a favorable microclimate (Kauffman and Krueger 1984). Because of the favorable microclimate (moderate temperatures, high humidity and low moisture stress) and high nutrient availability (Brown 1981, Mitsch et al. 1979), riparian communities are often more productive than adjacent upland communities (Brinson et al. 1981, Swanson et al. 1982). Riparian communities can also be characterized by high species richness, strong, small-scale differentiation of species distributions, and high structural diversity (Kauffman 1988, Swanson et al. 1982).

Both generalists, species that also inhabit adjacent upland communities, such as *Acer circinatum* and *Oxalis oregana*, and species restricted to the riparian zone, such as *Boykinia elata*, *Mitella ovalis* and *Petasites frigidus*, coexist in riparian communities (Swanson et al. 1982). The generalist species may represent competitive species (sensu

Grime 1979) able to extend their range into the riparian zone because of its abundant resources and favorable microclimate (or low stress, sensu Grime 1979), while the specialist species may be stress tolerant or ruderal species (sensu Grime 1979) restricted to streamsides and possessing life history strategies adapted to tolerate the stress and disturbance imposed by annual flooding (Menges and Waller 1983, Swanson et al. 1982).

Most research on the factors influencing the composition and distribution of species within riparian communities, however, have been conducted on floodplains of large streams and rivers. These alluvial systems, characterized by progressive, lateral channel migration, often contain several zones of riparian vegetation. This zonation has been alternatively interpreted as a result of a successional gradient (Bliss and Cantlon 1957, Fonda 1974, Nanson and Beach 1977, Robertson et al. 1978) or as a result of steep environmental gradients in substrate texture, soil aeration, moisture availability, temperature and flood frequency with distance from the stream (Bell 1974, Frye and Quinn 1979, Hawk and Zobel 1974, Osterkamp and Hupp 1984, Padgett 1982).

Spatially distinct vegetation zones are less common along headwater streams. In headwater streams, both recurrent and catastrophic disturbances interact to affect the development of riparian vegetation (Grant 1986, Gregory et al. 1988). Recurrent, low intensity disturbance caused by annual fluctuations in streamflow creates small gaps, and transports both propagules and sediment (Harris 1984, Sharitz and Schneider 1986, Staniforth and Cavers 1976, Swanson et al. 1982). Catastrophic disturbance caused by debris flows, forest harvesting practices, fires and severe floods removes much above-ground vegetation, and also creates and modifies geomorphic surfaces (Swanson 1980). The interaction between annual and catastrophic disturbances can create a mosaic of geomorphic surfaces and produce a high degree of spatial and temporal heterogeneity in riparian communities (Campbell and Franklin 1979, Grant 1986, Gregory et al. 1988, Swanson et al. 1982).

Numerous factors (steep gradients in environmental factors, light availability, recurrent and catastrophic disturbances and life history characteristics) interact to control riparian species establishment and distribution along headwater streams (Campbell and Franklin 1979, Swanson et al. 1982). The establishment and regrowth responses of riparian vegetation following recurrent, low intensity disturbances, and the mechanisms through which riparian vegetation reestablishes following more severe disturbances are particularly important in headwater streams because these responses control the light, nutrient and debris inputs to the streams and affect the development of aquatic communities (Cummins 1974, Franklin et al. 1981, Swanson and Lienkamper 1978, Swanson et al. 1982, Triska et al. 1982). Recent research (Bryant 1987, Bryant and Chapin 1986, Krasny 1986, McBride and Strahan 1984, Menges and Waller 1983, Walker 1985, Walker and Chapin 1986, Walker et al. 1986, Walker et al. 1987) has described some of the ways these factors interact to influence the establishment and development of riparian vegetation after disturbance in alluvial systems. There has been little study, however, of how these factors interact in headwater streams after either recurrent or catastrophic disturbance (but see Campbell and Franklin 1979).

Debris flows are a major disturbance to riparian vegetation in humid, mountainous areas (Swanston 1978, Veblen and Ashton 1978). They typically originate in the steep, first and second-order streams that make up most of the overall channel length within a drainage (Beschta and Platts 1986, Swanson and Lienkaemper 1978). These rapid, shallow mass movements of soil, organic debris and alluvium through stream channels can be very heterogeneous in their effects, scouring all soil and stored propagules to bedrock, shearing off the top of vegetation without removing any substrate, or depositing material along their tracks (Costa 1984, Flaccus 1959). The types of material deposited and the depths of deposition and scour can differ both within and among debris flow sites (Adams and Sidle 1986). This variation in scour and deposition produces variability in understory cover and composition (Hull and Scott 1982, Miles et al. 1984, Miles and Swanson 1986, Smith et al. 1986, Veblen and Ashton 1978). The composition of the adjacent undisturbed vegetation also influences vegetation patterns and successional processes (Hull and Scott 1982, Hupp 1983a, Miles and Swanson 1986, Smith et al. 1986).

Plant successional theory concentrates on the importance of seed dispersal following disturbance (Connell 1978, Connell and Slatyer 1977). The revegetation of mass movements, in particular, may depend on seedling establishment from dispersed seed (Cline, S. and F.J. Swanson, personal communication, Flaccus 1959, Hupp 1983a). But there has been little direct study of the early successional processes operating in riparian zones after debris flows (see also McKee and Harmon 1987). Seedlings and vegetative sprouts from soil propagule banks are often more important than dispersed seed in early successional communities (Archibold 1978, Hill and Stevens 1981, Hopkins and Graham 1984, Kellman 1974, Purdie and Slatyer 1976, Young et al. 1987). Because of material deposit, debris flows produce an additional source of establishment for seedlings and vegetative sprouts through the transport and deposition of seed and vegetative fragments (Adams et al. 1987).

Community properties, such as cover, species composition and life form dominance during succession, vary depending on the disturbance characteristics (type, intensity, area affected, timing, frequency), the characteristics of the pre-existing vegetation, and chance events (Franklin 1981, Glenn-Lewin 1980, Noble and Slatyer 1980, White and Pickett 1985, Sousa 1984).

Disturbance can affect the development of community properties in several ways. Disturbance can reduce the survival of individuals or species (Franklin et al. 1985), modify microenvironmental conditions (Bazzaz 1983), and change both resource and propagule availability (Pickett et al. 1987a and b). Few studies, however, have actually examined the roles of disturbance characteristics in site revegetation.

In this thesis I combine observational studies on three debris flows with field experimentation in an examination of the roles of seedlings and vegetative sprouts, propagule sources and disturbance characteristics in early riparian succession.

Chapter two presents data and interpretations of early succession on the three debris flows. I examine the contribution of seedlings and vegetative sprouts to the initial reestablishment of cover. I then document the relationships between disturbance characteristics (the type of deposition and the intensity of scour) and total cover, seedlings and vegetative sprouts. These relationships help to show whether these disturbance characteristics are important influences on the initial successional stages.

In chapter three, I hypothesize that early successional patterns after debris flows result from differences in how scour and deposition affect propagule availability. I use this hypothesis to develop predictions of the effects of increasing intensity of scour and deposition on seedling establishment, vegetative regrowth, and community cover. I present the results of an experiment designed to test these predictions. In addition I examine the responses of individual species to disturbance and explain how these responses affect overall community patterns.

I examine the similarities and differences between my observational and experimental studies and summarize my overall thesis conclusions in the final chapter. I also propose questions for further research on the mechanisms contributing to initial revegetation of riparian communities after catastrophic disturbance and explain how continued monitoring of my experimental site may provide some answers to these questions.

Chapter 2

FACTORS AFFECTING FIRST YEAR ESTABLISHMENT OF RIPARIAN VEGETATION AFTER CATASTROPHIC DISTURBANCE BY DEBRIS FLOWS

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ABSTRACT

We sampled three debris flows in the western Oregon Cascades near the end of the first growing season following disturbance. Our goals were (a) to examine the contributions of seedlings and vegetative sprouts to initial revegetation and (b) to compare the influences of debris flow scour and deposition (disturbance characteristics) and predisturbance vegetation type, disturbance location, and topographic position (site characteristics) on early successional patterns. Vegetative regrowth dominated early succession, providing 74% of the total cover. Seventy-five percent of the species established at least partially through vegetative means. Both debris flow scour and deposition and the predisturbance vegetation type strongly influenced

community cover, seedling establishment, and vegetative regrowth. Vegetative regrowth (13.7% cover, 28 shoots/m^2) and total cover (14.8%) were highest on low intensity scour. Seedling establishment was highest on fine and gravel deposits (2.1-3.0% cover, 38-46 seedlings/m^2). Total cover (10.8%) and vegetative regrowth (9.8% cover, 21.2 shoots/m^2) were highest on the clear-cut reaches; seedling establishment was highest on the hardwood reaches (3.2% cover, 49.3 seedlings/m^2). The type of deposit and the intensity of scour were the most important influences on debris flow revegetation, however.

These results show (a) the important role of disturbance characteristics in determining revegetation patterns, (b) that both seedlings and vegetative sprouts contribute to the revegetation of debris flows, and (c) that establishment can occur from sources other than dispersed seed. These additional sources are the residual propagule bank and the disturbance-transported propagule bank. We hypothesize that early successional patterns after debris flows result from differences in the effects of scour and deposition on seedlings, vegetative sprouts and propagule sources.

INTRODUCTION

Patterns of vegetation establishment following disturbance can determine subsequent community dynamics (Grubb 1977, McCune and Allen 1985, Peet and Christensen 1980). Variation in early successional composition and cover leads to the development of multiple successional pathways on otherwise similar sites (Franklin 1981, Glenn-Lewin 1980, Humphrey 1984, Krasny 1986, McCune and Allen 1985, Noble and Slatyer 1980). The mechanisms of early succession, however, are poorly understood. Plant successional theory in general concentrates on the importance of seed dispersal following disturbance (Connell 1978, Connell and Slatyer 1977). Vegetative regrowth and seedling establishment from on-site propagule sources, however, often contribute more to initial revegetation (Archibold 1978, Hopkins and Graham 1984, Stickney 1986, Tsuyuzaki 1987, Young et al. 1987). Some disturbances, such as debris flows, produce an additional source of propagules through the transport and deposition of seed and vegetative fragments (Adams et al. 1987).

It is often difficult to distinguish between the sources of propagules (on-site, off-site and disturbance-transported) and the means of establishment (from seed or from vegetative sprouts). Many (for example Bazzaz 1983), confuse the means of establishment with propagule sources, assuming that all seedlings originate from dispersed seed.

Yet, these distinctions are necessary to understand the processes underlying early vegetation recovery after disturbance.

The relative contributions of propagule sources, vegetative sprouts and seedlings have been well documented only after fire or clear-cutting (Archibold 1978, Abrahamson 1984, Ewel et al. 1981, Hanes and Jones 1967, Hill and Stevens 1981, James 1984, Keeley and Keeley 1981 and 1984, Lyon and Stickney 1976, Purdie and Slatyer 1976, Stocker 1981, Stickney 1986, Rowe 1981, Uhl et al. 1981 and 1982, Young et al. 1987). The role of propagule sources and means of establishment in succession after other disturbance types is less well known.

Debris flows are a major cause of disturbance to riparian vegetation in humid, mountainous areas (Swanston 1978, Veblen and Ashton 1978). A high pore water pressure that develops during storms triggers these shallow mass movements (Swanston 1978, Swanston and Swanson 1976). They can be very erosive and intense disturbances, exerting impact forces up to 4000 newtons/m^2 and scouring all soil to bedrock (Costa 1984). Since mass movements are so intense, many (Flaccus 1959, Hupp 1983a, Sousa 1984) assume that this type of disturbance removes all preexisting vegetation and stored propagules, leaving dispersal as the only source of revegetation. These studies ignore the potential contributions of both the residual and transported propagules to revegetation. Yet debris flows may only shear off the above-ground vegetation without removing any substrate or propagules (Costa 1984, Flaccus 1959) and vegetative resprouting from transported fragments within deposits can dominate early succession on mass movement sites (Adams et al. 1987).

Debris flows can deposit fine material, cobble and organic debris during a single event. The types of material deposited and the depths of deposition and scour can differ both within and among debris flow sites (Adams and Sidle 1986, Miles et al. 1984). This variation in scour and deposition produces variability in understory cover and composition (Hull and Scott 1982, Miles et al. 1984, Miles and Swanson 1986, Smith et al. 1986, Veblen and Ashton 1978). The composition of the adjacent undisturbed vegetation also influences vegetation patterns and successional processes (Hull and Scott 1982, Hupp 1983a, Miles and Swanson 1986, Smith et al. 1986).

The objectives of our study are (1) to examine the contribution of seedlings and vegetative sprouts to early succession after debris flows, (2) to document the relationship between scour and deposition (disturbance characteristics) and riparian vegetation recovery from both vegetative regrowth and seedling establishment, (3) to compare the influence of disturbance characteristics (scour and deposition) and site characteristics (vegetation type, disturbance location, and topographic position relative to the stream) on early riparian succession, and (4) to hypothesize how scour and deposition influence initial revegetation.

STUDY AREA

This study was in the Williamette National Forest in the west-central Cascade Mountains near the town of Blue River, Oregon (Figure 2-1). The climate of the area is mild, characterized by wet winters and warm, dry summers. The average annual precipitation is 2400 mm, mostly occurring as rain during the winter months. The terrain is deeply dissected with frequent occurrence of both deep-seated and shallow mass movements, particularly in the lower elevation forests (below 850 m) underlain by hydrothermally altered volcanoclastic rocks (Swanson and James 1975).

We selected three first order streams experiencing debris flows in February as study sites. Two of the sites were in the H.J. Andrews Experimental Forest, Experimental Watershed 10 (WS10) and the Mack Creek Road flow. The third site, Zeolite Creek, a previously unnamed tributary of the North Fork of Quartz Creek, was in the adjacent Blue River drainage (Figure 2-1).

WS10 faced southwest and ranged in elevation from 463 to 610 m. Before it was clearcut in 1975, a 450 year old stand of Pseudotsuga menziesii (nomenclature according to Hitchcock and Cronquist 1974) dominated the site. The canopy of the riparian community included individuals of Psuedotsuga menziesii, Tsuga heterophylla, Acer macrophylla, Thuja plicata and Alnus rubra. Common understory species included *Acer circinatum*, *Vaccinium parvifolium*, *Aralia californica*, *Gaultheria shallon* and *Berberis nervosa* (Hawk 1979). After clearcutting, *Acer circinatum* and *Epilobium angustifolium* dominated the site. The 1986 debris flow affected 220 m of stream length.

The Mack Creek Road site had a northwest exposure and ranged in elevation from 561 to 732 m. The length of the flow, 480 m, was more than double that of WS10. We identified three distinct reaches on the site, each with different land use histories. The upper reach where the debris flow originated was clearcut in 1982 (V. Puleo, personal communication). Since the stream was close to the boundary of the harvest unit, an *Acer circinatum* dominated clearcut bordered this reach on only one side. A *Tsuga heterophylla*-*Thuja plicata*/*Acer circinatum* forest bordered the other side of this reach. The middle reach was unaffected by forest management activities and a *Pseudotsuga menziesii*-*Tsuga heterophylla*-*Thuja plicata* dominated forest bordered both sides. The lower reach was disturbed by fire and logging approximately 40 years ago (F.J. Swanson, personal communication). A mixed hardwood stand of *Alnus rubra*, *Populus trichocarpa*, *Populus tremuloides*, *Pseudotsuga menziesii* and *Acer macrophyllum* dominated the lower reach.

Zeolite Creek had a northwest exposure for the majority of the length sampled, but two of the upper sampling transects were on a southwest-facing slope. The elevation at the base of the debris flow path was 550 m. The length of the stream affected by the flow exceeded the 480 m sampled. A *Pseudotsuga menziesii*-*Tsuga heterophylla* forest bordered the debris flow for most of its length. No recent forest management activities disturbed this reach (V. Puleo, personal communication). The upper 130 m of the debris flow path was clear-cut in 1976. An *Acer circinatum* dominated community bordered this reach.

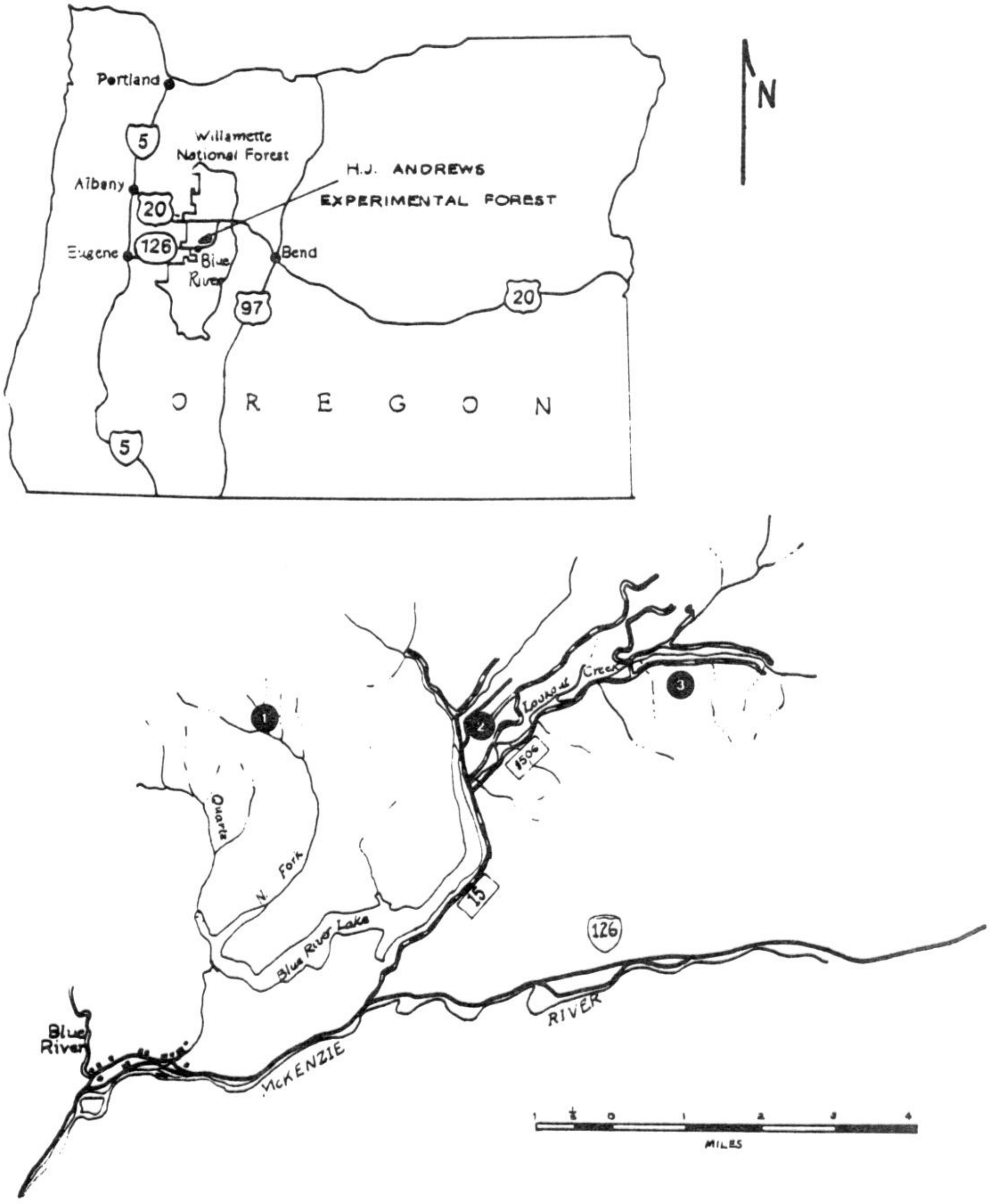

Figure 2-1. The location of the three debris flows within the Williamette National Forest. 1=Zeolite Creek, 2=WS10, 3=Mack Creek Road.

METHODS

Sampling

On each site, we placed 20 to 25 sampling transects perpendicular to the stream. We sampled the portion of the debris flow in which the disturbance removed most of the above-ground vegetation, placing transects from the lower edge of the denuded area to the point at which the main body of the flow originated. Transects were at 10-m intervals on WS10 and 20-m intervals on the other sites. The width of the disturbance zone determined the length of each transect.

We sampled vegetation in late August and early September, near the end of the first growing season to coincide with the peak cover of most riparian species (see Campbell and Franklin 1979 for the phenology of important western Cascades riparian species).

We placed Daubenmire plots (20-by-50 cm) at 2-m intervals along each transect, recording total cover, species cover and the cover and number of seedlings and vegetative sprouts. We defined total cover as the percentage ground obscured by vegetation rooted within the plot. We summed the cover of all individuals establishing by seed or by vegetative means to determine seedling and vegetative cover. Thus defined, seedling and vegetative cover could exceed the total plot cover.

We considered each shoot system to represent a single individual. If attached vegetative parts were directly observable by careful probing in the soil, we identified the individual as a vegetative sprout. We identified an individual as a seedling if it met one of the following criteria:

1. It was an annual species
2. Cotyledons were present
3. We were able to observe differences in the emergence patterns between seedlings and vegetative sprouts within a species.

If we could not determine the means of establishment of an individual, we classified it as undetermined. We transplanted seedlings of common species and all vegetative sprouts that we could not identify in the field and allowed them to grow until identification was possible. Unidentifiable seedlings that occurred in only a few plots were tallied as unknowns.

In each plot, we recorded the type of scour or depositional surface created by the debris flow and the position of the disturbed surface relative to the stream. We further subdivided scoured surfaces based on the intensity of scour and depositional surfaces according to the type of material deposited. We also noted any secondary effects of slumping, surface erosion, or redeposition of substrate. Slumping of unstable soil on steep cut banks was the only secondary effect observed during the first year of sampling. We observed eight surface types:

> Low Intensity Scour: All above-ground vegetation and litter removed with the residual mineral soil left intact
>
> Moderate Scour: All above ground vegetation and at least some of the residual mineral soil removed
>
> Intense Scour: All above- and below-ground vegetation and substrate removed to the underlying bedrock. Bedrock areas at the head of the debris flow were also in this category.
>
> Fine Deposits: All material less than or equal to 4 mm in diameter
>
> Gravel Deposits: Inorganic material between 4 and 64 mm in diameter
>
> Cobble Deposits: Inorganic material with a diameter larger than 64 mm
>
> Debris Deposits: Deposits of bark, branches, stumps, logs and downed trees or shrubs
>
> Unstable: Regardless of scour or deposition, the remaining or newly deposited soil unstable due to secondary effects.

To describe the topographic position of the disturbed surfaces relative to the stream, we divided the riparian zone into active, border and outer zones, based on distinct topographic breaks as described by Campbell and Franklin (1979). The active zone included only the area within the streambed. The border zone was all area between the active zone and the next distinct topographic break. It included both the floodplain surface and the side slopes of the channel. This subzone was variable in width and slope. The outer zone abutted the adjacent hillslope. If the deposition of material obscured all topographic breaks, we listed the zone type as undistinguishable.

We described the vegetation type within which each transect was located based on the dominant canopy species in the adjacent undisturbed forest. Three main vegetation types were (1) *Acer circinatum* dominated clear-cut, (2) mixed hardwood stand, including individuals of *Alnus rubra*, *Acer macrophylla* and *Populus trichocarpa* and (3) conifer community dominated by *Tsuga heterophylla* and either *Pseudotsuga menziesii* or *Thuja plicata*. If a clear-cut bordered a transect on at least one side we classified it as clear-cut influenced.

Statistical analysis

We used analysis of variance to examine differences in total cover, seedling establishment and vegetative regrowth according to site and disturbance characteristics. The site and disturbance characteristics were the disturbance location, the predisturbance vegetation, the topographic position relative to the stream, and the type of disturbance surface. These categorical variables were converted to indicator variables for the purposes of regression. Further exploration of significant relationships was through Least Significant Difference (LSD) analysis of means. Regression models identified site and disturbance characteristics which significantly reduced variation in early successional patterns. The data were first log-transformed, leading to stabilized variances and normal distributions of errors. We performed all analyses on the transformed data.

RESULTS

Distribution of disturbance surfaces

The three sites differed in the distribution of depositional and scour surfaces. Large differences occurred in the frequency of the three scour surfaces and in the deposits of both fine material and gravel (Table 2-1). Most of the surfaces on WS10 were of the scour type (63%), with high frequencies of both the low and moderate intensity scour surfaces. While the surfaces on Zeolite Creek were more evenly split between scour (40%) and deposition (60%) than on the other two sites, a larger proportion of its surfaces were very intensely scoured (19%). Very little scour of any intensity occurred on Mack Creek Road, where the surfaces were primarily depositional (94%).

TABLE 2-1. Relative frequencies of the disturbance surfaces on each of the three study sites.

SURFACE	WS10	MACK CR RD	ZEOLITE CR
Low intensity scour	32.9	4.1	12.7
Moderate scour	23.7	2.0	8.8
Intense scour	6.6	1.0	18.6
TOTAL SCOUR	63.2	7.1	40.2
Fine deposits	7.9	59.9	14.7
Gravel deposits	0	22.8	23.5
Rock deposits	0	2.0	7.8
Debris deposits	19.7	8.1	12.7
TOTAL DEPOSITION	27.6	92.9	58.8
Unstable surfaces	9.2	0	1.0

Total cover and the means of establishment

Total cover did not differ much among the three sites (ANOVA, P>.05), ranging between 7.2% and 10.7% (Table 2-2), but the means of establishment differed significantly (ANOVA, P<.0001 for numbers of seedlings and vegetative sprouts and P<.0005 for seedling and vegetative cover). Seedling density (Table 2-2) was greatest on the deposition-dominated Mack Creek Road (44 seedlings/m^2) but the seedling cover was highest on Zeolite Creek (2.7%). Vegetative regrowth dominated the scoured WS10 both in numbers (28 sprouts/m^2) and cover (10.2%). As surfaces were more evenly split between scour and deposition on Zeolite Creek, the contributions of seedlings and vegetative sprouts to cover were more equal (32% and 59% respectively, Table 2-3).

At the Mack Creek Road and Zeolite Creek sites, and hence, overall, most of the individuals establishing at the end of the first year were seedlings (Table 2-3). Vegetative sprouts provided most of the total cover in the first year, however. Over all three sites, 65% of the individuals establishing in the first year were seedlings, but vegetative sprouts provided 74% of the total cover.

Table 2-2. Total cover and means of establishment (mean ± standard error) within each site and for all sites combined. Cover is expressed in percent, the number of seedlings and vegetative sprouts as the number of individuals/m^2. n=number of $0.1m^2$ plots on each site, S=seedling, SPR=vegetative sprout.

	TOTAL COVER	COVER OF SPR	COVER OF S	NUMBER OF SPR	NUMBER OF S
WS10 n=99	10.7±1.7	10.2±2.0	1.1±0.3	28.0±4.2	11.0±2.3
MACK CR RD n=197	7.2±0.9	5.0±0.9	1.9±0.2	9.0±1.1	44.0±4.1
ZEOLITE CR n=102	7.7±1.3	5.0±1.3	2.7±0.7	9.0±1.4	15.0±2.0
ALL SITES n=398	8.2±0.7	6.3±0.7	1.9±0.2	14.0±1.2	28.0±2.2
ANOVA (2 d.f)	P>.05	P <.0005	P <.0005	P <.0001	P <.0001

Table 2-3. The contribution of seedlings (S), vegetative sprouts (SPR) and individuals of undetermined origin (UNDET) to total cover and abundance.

SITE	PERCENT COVER			PERCENT ABUNDANCE		
	S	SPR	UNDET	S	SPR	UNDET
WS10	9.5	89.7	0.8	27.3	70.2	2.5
MACK CR RD	26.4	69.6	4.0	81.3	16.2	2.5
ZEOLITE CR	32.0	59.2	8.8	57.1	32.6	10.3
ALL SITES	22.2	73.7	4.1	64.9	31.3	3.8

Species composition and means of establishment

Almost three-quarters of the 57 species observed on all three sites established vegetatively. Eighteen species established as both vegetative sprouts and seedlings. Twenty-three species established only as vegetative sprouts and 16 species established only as seedlings (Table 2-4).

Herbaceous species dominated initial revegetation, not only in terms of number of species and cover, but also numbers of individuals. Trees were abundant only on the deposition-dominated Mack Creek Road. On this site, six tree species accounted for 91% of the seedlings and 17% of the vegetative sprouts. On the other two sites, herbaceous species were more common. Herbaceous species accounted for 93% of the seedlings and 98% of the vegetative sprouts on WS10. Eighty-four percent of the seedlings and 94% of the vegetative sprouts on Zeolite Creek were herbaceous.

Invading species, those species typically found after disturbance and not present in undisturbed communities (sensu Dyrness 1973) established on the debris flows. Invaders included _Anaphalis_ _margaritacea_, _Cirsium_ _vulgare_, _Senecio_ _sylvaticus_ and _Epilobium_ _watsonii_. Residual species, those species commonly found in undisturbed forest or riparian communities also established. Riparian species typical of less disturbed sites included _Boykinia_ _elata_, _Carex_ sp., _Galium_ _triflorum_, _Oxalis_ _oregana_, and _Petasites_ _frigidus_ (Campbell and Franklin 1979). Forest residuals

Table 2-4. Average cover and relative frequency (freq) of vascular plant species on each of the three study sites. Both cover and relative frequency as expressed in percent. The means through which each species was observed to establish are listed in parentheses. V=vegetative means, S=by seed, WS10=Watershed 10, MCR=Mack Creek Road, ZC=Zeolite Creek.

	WS10		MCR		ZC	
	Cover	Freq	Cover	Freq	Cover	Freq
TREES						
Acer macrophyllum (V)	12.5	.02	0	0	0	0
Alnus rubra (S)	0	0	3.4	.26	1.2	.09
Populus trichocarpa (V)	0	0	25.6	.03	0	0
Prunus emarginata (S)	0	0	1.2	.08	0	0
Pseudotsuga menziesii (S)	1.0	.01	.7	.02	2.0	.02
Thuja plicata (S)	0	0	.9	.31	.2	.01
Tsuga heterophylla (S)	.2	.06	.8	.42	.7	.10
TALL SHRUBS AND LOW HERBS						
Corylus cornuta (V)	5.0	.01	0	0	0	0
Rhamnus purshiana (V)	5.0	.01	0	0	0	0
Salix sitchensis (S)	0	0	1.0	.02	0	0
HERBS AND LOW SHRUBS						
Adiantum pedatum (V)	0	0	0	0	40.0	.01
Agrostis alba (V,S)	0	0	8.6	.02	4.2	.16
Anaphalis margaritacea (V,S)	7.0	.02	.5	.02	3.0	.02
Aralia californica (V,S)	55.0	.02	0	0	11.5	.14
Asarum caudatum (V)	3.0	.01	0	0	0	0
Berberis nervosa (V)	5.0	.02	0	0	2.0	.01
Blechnum spicant (V)	25.0	.01	31.7	.02	0	0
Boykinia elata (V,S)	2.8	.07	1.0	.04	1.3	.12
Cardamine oligosperma (S)	.8	.05	.2	<.01	0	0
Carex sp. (V,S)	2.6	.09	1.6	.08	3.7	.20
Cirsium vulgare (S)	20.0	.01	1.4	.02	3.2	.04
Cirsium sp. (S)	0	0	0	0	23.4	.05
Collomia heterophylla (S)	1.0	.04	0	0	2.2	.06
Coptis laciniata (V)	4.7	.03	0	0	0	0
Dicentra formosa (V,S)	5.0	.01	.2	<.01	5.0	.05
Epilobium angustifolium (V,S)	6.1	.11	0	0	0	0
Epilobium watsonii* (V,S)	2.7	.17	2.1	.05	10.2	.05
Erodium cicutarium (S)	1.0	.01	0	0	0	0
Equisetum arvense (V)	0	0	2.0	.04	0	0
Equisetum telmateia (V)	0	0	15.8	.07	9.0	.01

Table 2-4. (Continued).

	WS10		MCR		ZC	
	Cover	Freq	Cover	Freq	Cover	Freq
Festuca arundinoidea (V,S)	0	0	0	0	4.5	.06
Galium triflorum (V,S)	1.0	.01	2.2	.01	3.3	.08
Gaultheria shallon (V)	9.4	.05	3.0	<.01	0	0
Gymnocarpium dryopteris (V)	0	0	20.0	<.01	0	0
Hieracium albiflorum (S)	1.0	.01	0	0	10.0	.01
Linnaea borealis (V)	5.0	.02	6.0	<.01	1.0	.01
Lotus purshiana (S)	0	0	2.8	.01	0	0
Luzula parviflora (V,S)	0	0	1.0	<.01	3.3	.08
Mitella ovalis (V)	2.8	.02	0	0	2.2	.04
Montia parvifolia (S)	0	0	0	0	2.0	.02
Montia sibirica (V,S)	0	0	.5	<.01	.8	.02
Osmorhiza chilensis (V)	0	0	0	0	.5	.01
Oxalis oregana (V,S)	8.3	.10	2.0	.07	3.7	.07
Petasites frigidus (V,S)	.5	.02	8.0	.15	10.5	.04
Polystichum munitum (V)	23.8	.04	7.0	<.01	10.0	.01
Pteridium aquilinum (V)	0	0	70.0	<.01	0	0
Rubus leucodermis (V,S)	5.0	.02	6.7	.02	4.6	.04
Rubus parviflorus (V)	21.8	.04	0	0	0	0
Rubus ursinus (V,S)	7.8	.37	7.1	.05	10.2	.06
Senecio sylvaticus (S)	1.0	.06	1.8	.02	1.0	.02
Thalictrum occidentale (V)	0	0	0	0	7.0	.01
Tolmiea menziesii (V,S)	.6	.04	.6	.01	.4	.02
Trientalis latifolia (V)	2.0	.02	1.1	.02	0	0
Trifolium sp. (S)	0	0	2.0	.01	0	0
Vancouveria hexandra (V)	3.1	.07	0	0	1.0	.01
Viola sempervirens (V,S)	4.0	.07	0	0	0	0
Whipplea modesta (V)	0	0	0	0	5.0	.01

*includes individuals of both Epilobium watsonii and Epilobium glandulosum: both species were present on the sites but identification between the two species required the destruction of each individual.

included Pseudotsuga menziesii, Linnaea borealis, Tolmiea menziesii, and Tsuga heterophylla (Franklin and Dyrness 1973).

Effects of scour and deposition

Significant relationships existed between the disturbance surfaces and total cover, seedling establishment and vegetative regrowth (ANOVA, $P<.0001$). Total cover was highest (LSD analysis of means, $P<.05$) on low intensity scour (14.8%, Table 2-5). Vegetative sprout cover was also high (13.7%) on low intensity scour. It was not significantly higher, however, than the vegetative cover on debris deposits (8.6%), the next largest category. The cover of seedlings was highest (LSD analysis of means, $P<.05$) on three surfaces, low intensity scour (2.1%) and fine (2.2%) and gravel deposits (3.0%).

Few individuals established on intense scour, unstable surfaces and cobble deposits. Cover was correspondingly low on these surfaces, ranging between 0 and 2.4%.

The cover of vegetative sprouts was higher than the cover of seedlings on all surfaces except the unstable surfaces. On these unstable surfaces, both seedling and vegetative cover equalled 0.4%. The relative contributions of each means of establishment to total cover changed dramatically with the type of surface, however (Table 2-5). Vegetative regrowth contributed most to total cover on the three scour surfaces contributing from 83.7 to 100% of the cover. Seedlings contributed most to the total cover on fine, gravel and cobble deposits. On these surfaces, 28.7 to 43.8% of the total cover was from seedlings.

Seedlings were more abundant than vegetative sprouts on fine, gravel and cobble deposits. Seventy-nine to ninety percent of the individuals were seedlings. Vegetative sprouts were more abundant than seedlings on scour surfaces and debris deposits, contributing from 55.3 to 100.0% of the total establishment.

Effects of vegetation type and topographic position

Significant relationships also existed between the vegetation type and total cover and the means of establishment (ANOVA, $P<.03$ for total cover, $P<.0001$ for cover and number-by-mechanism, Table 2-6). Cover was higher (LSD analysis of means, $P<.05$) on the clear-cut (10.8%) and hardwood-influenced reaches (9.2%) than on the reaches where the adjacent vegetation was dominated by conifers (4.4%). While vegetative sprout cover was greater than seedling cover in all vegetation types, the relative contributions of the two means of establishment to cover differed. Vegetative sprouts dominated clear-cut reaches, contributing to 85% of the total cover. Both cover (9.8%) and abundance (21.2 sprouts/m^2) were higher (LSD analysis of means, $P<.05$) on clear-cut reaches than on the conifer or hardwood reaches. Seedling cover was highest (LSD analysis of means, $P<.05$) on the hardwood-dominated reaches, averaging 3.3% and contributing to 38% of the total cover. Seedlings were more abundant (LSD analysis of means, $P<.05$) on both the hardwood (49.3 seedlings/m^2) and conifer-dominated reaches (34.0 seedlings/m^2) than on the clear-cut reaches (16.1 seedlings/m^2). More than 83% of individuals within these two vegetation types were seedlings.

We observed some similarity in composition between the undisturbed vegetation and the tree seedlings establishing on the disturbed reach. Alnus rubra seedlings were abundant only on the hardwood-dominated reach. Tsuga heterophylla, Thuja plicata and Pseudotsuga menziesii were most abundant on conifer-dominated reaches.

The topographic position of the disturbed surface relative to the stream significantly affected only the cover of seedlings (ANOVA, $P<.04$). Seedling cover was lowest (LSD analysis of means, $P<.05$) where zones were undistinguishable (1.7%). Seedling cover was highest in the active zone (3.3%) where moisture was available throughout the growing season.

TABLE 2-5. Total cover and means of establishment (mean ± standard error) on each of the disturbance surfaces. The relative contributions of seedlings (S) and vegetative sprouts (SPR) to cover and abundance is listed in parentheses. Cover is expressed in percent, the numbers of seedlings and vegetative sprouts as the number of individuals/m^2. n=number of 0.1m^2 plots sampled on each surface type.

SURFACE	TOTAL COVER	COVER SPR	COVER S	NUMBER SPR	NUMBER S
Low intensity scour n=32	14.8±3.4	13.7±4.3 (86.6)	2.1±0.7 (13.4)	27.8±5.5 (55.3)	2.5±5.6 (44.7)
Moderate scour n=49	8.2±1.4	6.6±1.4 (83.7)	1.3±0.3 (15.3)	26.1±5.6 (66.5)	13.1±3.1 (33.5)
Intense scour n=33	0.1±0.1	0.1±0.1 (100.0)	0 (0)	3.0±0.3 (100.0)	0 (0)
Fine deposits n=142	9.9±1.5	7.3±1.5 (71.3)	3.0±0.6 (28.7)	12.3±1.8 (21.0)	46.2±5.2 (79.0)
Gravel deposits n=69	6.4±1.0	3.8±1.0 (63.5)	2.2±0.3 (36.5)	7.1+_1.6 (16.2)	36.8±4.6 (83.8)
Cobble deposits n=13	2.4±1.5	0.5±.4 (56.2)	0.4±0.3 (43.8)	1.5±1.0 (9.8)	13.8±6.5 (90.2)
Debris deposits n=51	9.8±2.0	8.6±1.9 (89.7)	1.0±0.3 (10.3)	18.8±4.8 (63.1)	11.0±3.0 (36.9)
Unstable n=9	0.4±0.2	0.2±0.2 (50.0)	0.2±0.1 (50.0)	2.2±1.5 (40.0)	3.3±1.7 (60.0)
ANOVA (7 d.f.)	P <.0001	P <.0001	P <.0001	P <.0001	P<.0001

TABLE 2-6. Total cover and means of establishment (mean ± standard error) for each of the vegetation types. The relative contributions of seedlings (S) and vegetative sprouts (SPR) to cover and abundance is listed in parentheses. Cover is expressed in percent, the numbers of seedlings and vegetative sprouts as the number of individuals/m^2. n=number of 0.1m^2 plots within each vegetation type.

	TOTAL COVER	COVER SPR	COVER S	NUMBER SPR	NUMBER S
Clear-cut n=181	10.8±1.3	9.8±1.4 (85.1)	1.7±0.4 (14.9)	21.2±2.6 (56.8)	16.1±1.9 (43.2)
Hardwood dominated n=61	9.2±2.1	5.3±1.9 (61.5)	3.3±0.6 (38.5)	9.0±2.3 (15.5)	49.3±8.6 (84.5)
Conifer dominated n=156	4.8_0.6	2.7±0.5 (68.3)	1.6±0.2 (36.7)	6.6±0.9 (16.3)	34.0±3.9 (83.7)
ANOVA (2 d.f.)	P <.03	P <.0001	P <.0001	P <.0001	P <.0001

Identification of ecologically important site and disturbance characteristics

The regression models for total cover, seedlings and vegetative sprouts differed (multiple regression ANOVA, P<.05, Table 2-7). The models for both total and seedling cover included the indicator variables for surface type, predisturbance vegetation, disturbance location, and topographic position relative to the stream. Surface type was the only characteristic that significantly reduced the variation in the cover of vegetative sprouts. All significant models included surface type as an important characteristic affecting reestablishment. More than half of these models included surface type as the only characteristic that explained any of the variability in early succession. None of the 16 models explained more than 39% of the variation in either total cover or the means of establishment.

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Table 2-7. Disturbance and site characteristics included in the regression models for each of the vegetation attributes, and the percent variation explained by the models, as determined by R^2, the regression coefficient of determination. S=surface type, VT=adjacent undisturbed vegetation type, Z=riparian subzone, L=location or site of disturbance, WS10=Watershed 10, MCR=Mack Creek Road, SPR=vegetative sprout.

VEGETATION ATTRIBUTES	SITE	CHARACTERISTICS IN MODEL	% VARIATION EXPLAINED (R^2)
Total cover	All	S,VT,Z or L	24
	WS10	S	38
	Zeolite	S	39
	MCR	none	–
SPR Cover	All	S	16
	WS10	S	28
	Zeolite	S	32
	MCR	none	-
Number of SPR	All	S	18
	WS10	S	17
	Zeolite	S,VT,Z	34
	MCR	none	-
Seedling cover	All	S,VT,Z,L	26
	WS10	S	17
	Zeolite	S,Z	32
	MCR	S,VT,Z	39
Number of seedlings	All	S,VT,Z,L	36
	WS10	none	-
	Zeolite	S	33
	MCR	S,Z	33

DISCUSSION

Surface type

All disturbance and site characteristics measured in this study--the type and intensity of scour or depositional surface created by the debris flows, the position of the surfaces relative to the stream, the vegetation type within which the disturbance occurred, and the disturbance location--significantly affected one or more of the vegetation attributes measured--total cover, vegetative regrowth and seedling establishment. Surface type was consistently the most important disturbance characteristic affecting revegetation patterns. Surface type affected all three vegetation attributes. It was also the only characteristic included in all significant regression models (Table 2-7). Therefore, most of the following discussion will concentrate on the influence of the debris flow-generated surfaces on early successional patterns.

Means of establishment and propagule sources

Chronosequence studies (Hull and Scott 1982, Miles and Swanson 1986, Smith et al. 1986, Veblen and Ashton 1978) show that the relationships between disturbance surfaces and vegetation patterns that develop in early succession are maintained throughout succession. Hull and Scott (1982) and Veblen and Ashton (1978) suggest that this results from differential creation of microsites for seedling establishment by scour and deposition. Many investigators (Flaccus 1959, Hupp 1983a, Sousa 1984) hypothesize that microsite availability for seedling establishment is crucial following rapid mass movement events. These intense disturbances are assumed (Flaccus 1959, Hupp 1983a, Sousa 1984) to remove all preexisting vegetation, including the stored propagules, making dispersal the only source of revegetation. Most of the evidence for the importance of establishment from dispersed seed onto debris flow sites comes from invasion of disturbed sites by individuals possessing means for long distance dispersal (Hupp 1983a), the dominance of species not normally found in undisturbed communities (S. Cline and F.J. Swanson, personal communication), compositional similarity between tree seedlings on the disturbed site and the adjacent undisturbed forest canopy (Hull and scott 1982), poorly developed shrub and herb layers (S. Cline and F.J. Swanson, personal communication, Flaccus 1959, Miles and Swanson 1986) and observations that disturbance characteristics did not seem to favor survival of individuals or stored propagules, but did not appear to limit dispersal (Hupp 1983a). The results of this study, however, show that seedlings are initially unimportant in debris flow revegetation and suggest that establishment of seedlings and vegetative sprouts occurred from all possible propagule sources: dispersal, the residual propagule bank and the disturbance-transported propagule bank.

The vegetative regrowth of individuals either surviving in the residual soil or regenerating from transported fragments dominated the first year of succession. Seventy-five percent of the species established at least partially through vegetative-based mechanisms (Table 2-4), providing seventy-four percent of the total cover (Table 2-3). Vegetative regrowth was greatly reduced only on the most intensely disturbed or unstable surfaces, and on these surfaces, seedling establishment was also very low.

Vegetative regrowth was high on the low and moderate intensity scour surfaces. The only source of vegetative propagules on these surfaces was the residual soil, indicating that the debris flows did not remove all predisturbance vegetation. Vegetative sprouts probably originated from both the residual and transported propagule banks on the deposits, as vegetative regrowth from transported fragments provides a significant contribution to the revegetation of mass movement sites (Adams et al. 1987) and residual species can emerge through deposits of up to a meter (Tsuyuzaki 1987, Williams 1979). While deposits greater than one meter can occur on debris flow sites, deposition depths on our sites often were less than a meter (R.D. Harr, personal communication, J.L. Gecy, personal observation).

Seedlings were abundant on fine and gravel deposits, but establishment most likely occurred from more than one source. Herbaceous species dominated early succession and the seed dispersal distances of most herbaceous species are only a few meters (Wood and del Moral 1987, Harper 1977, Levin and Kerster 1974, Hill and Stevens 1981, Silvertown 1982). Even the seed of wind-dispersed species declines exponentially from its source, with most seed deposited very close to the parent plant (McEvoy and Cox 1987). In addition, we found that seedlings established from all three propagule sources on a simulated debris flow (chapter 3), with the contribution of dispersed seed to revegetation much lower (31 seeds/m^2) than the contributions of the disturbance-transported and residual propagule banks (4484-7793 seeds/m^2).

Both species typically found in undisturbed riparian and old-growth communities and species typically found on disturbed sites (invaders sensu Dyrness 1973) established on our debris flow sites. The invading species could have established from any of the three propagule sources. Recruitment of the invaders Senecio sylvaticus, Epilobium angustifolium and Epilobium watsonii as seedlings from persistent propagule banks occurs following other types of catastrophic disturbance (Archibold 1978, chapter 3, Kellman 1974, Roberts 1981) and the invaders Epilobium angustifolium, Epilobium watsonii, Anaphalis margaritacea and Rubus ursinus established through both vegetative means and seed on our sites. Even though these species possess means for long distance seed dispersal, their presence on disturbed sites does not necessarily indicate that they established from dispersed seed.

Some wind-dispersed or bird-disseminated seed, however, probably dispersed from adjacent vegetation onto these narrow (6 to 28 m wide) debris flow sites. This narrow patch geometry probably also allowed the dispersal of tree seed from the adjacent undisturbed canopy onto the debris flows, as we observed similarities between the adjacent canopy and the tree seedlings on our sites. Hull and Scott (1982) suggest that such compositional similarity provides evidence for the importance of seed dispersal in debris flow revegetation. Our data show that although dispersal might contribute strongly to tree seedling establishment, dispersal is not important in overall site revegetation.

Some studies (Flaccus 1959, Miles and Swanson 1986) find species-poor shrub and herb layers after mass movements. These studies attribute this low species richness to the combination of two factors: the removal of all buried propagules and the rapid dominance of a few fast-growing tree species which out-compete all other species. In contrast, species richness was high on our study sites and herbaceous species dominated the cover and the species composition. We believe that the high species richness observed on our sites occurred because species arising from vegetative parts, buried seed and dispersed seed all contributed to early revegetation. If dispersed seed were the only contribution to revegetation, species richness would be lower. The poor development of the herb and shrub layers observed by others (Flaccus 1959, Miles and Swanson 1986) may have been caused by the removal of the residual propagule bank by the disturbance. Differential herbivory (observed on landslide sites in the Queen Charlotte Islands in British Columbia by Smith et al. [1986]) or other limiting factors could also account for the low species richness on those sites.

It has been suggested (Hupp 1983a, Sousa 1984) that rapid mass movement events, such as debris flows, are unique disturbances because of their dramatic ability to eliminate all predisturbance vegetation. The results of this study, however, show that even though debris flows remove above-ground vegetation and redistribute both stored propagules and substrate, the predisturbance vegetation is not necessarily eliminated. Dispersal was not necessary for the revegetation of the three debris flows we studied. It probably was necessary for tree establishment, however, as resprouting is limited in most Pacific Northwest tree species and seed of most tree species is conspicuously absent from seed banks (Silvertown 1982, Pratt et al. 1982, Thompson 1978).

Roles of vegetation type, topographic position and disturbance location

The role of the vegetation type in early debris flow succession was complex on the three sites we studied. The land management history on our sites determined the composition of both the predisturbance vegetation and the adjacent undisturbed vegetation. Adjacent vegetation can be a major source of seed dispersed into a disturbed area and can control the light regime of a disturbed site (Hull and Scott 1982, Hupp 1983a, Kellman 1974, Swanson et al. 1982). Community recovery is also influenced by the availability of on-site propagules (Pickett and White 1985, Sousa 1980), which is largely determined by the composition of the predisturbance vegetation.

We suggest that the ability of the preexisting community to recover from disturbance had a stronger effect on the initial revegetation of our sites than the seed dispersal ability or the shading effects of the adjacent vegetation. Although we observed some compositional similarity between the tree seedlings establishing on the debris flows and the dominant tree species in the adjacent canopy, the cover of these individuals was low and did not contribute much to the total cover. In addition, although seed germination is often stimulated by increased light

(Bazzaz 1983, Thompson et al. 1977), seedling establishment was lowest on the more open clear-cut reaches. In contrast, vegetative regrowth was very high on the clear-cut reaches and much lower on the less recently disturbed conifer reaches.

These results were unexpected, as many studies (Kellman 1974, Pratt et al. 1982, Thompson 1978) suggest that the importance of buried seed to site revegetation decreases, and the importance of vegetative sprouts increases with time since last disturbance. This suggested change in the relative contributions of buried seeds and vegetative buds results from decreases in both the viability of buried seed and the input of new seed to the on-site propagule bank (Kellman 1974, Young et al. 1987), as species characteristic of less disturbed sites allocate fewer resources to seed production, reproducing mainly through vegetative spread (Pratt et al. 1982). Based on these studies, we expected vegetative regrowth to dominate the less recently disturbed conifer reaches and seedling establishment to dominate the clear-cut reaches, the reverse of the observed pattern. We propose two explanations for these unexpected results.

The first explanation is that the relative contribution of vegetative sprouts to site revegetation does not always increase through time as documented by Granstrom (1982), Moore and Wein (1977) and Young et al.

(1987) on other sites. The depth of perennating structures in the soil can affect the ability of species to establish as seedlings or vegetative sprouts following disturbance (Pratt et al. 1984). Yet, the distribution of seed in the soil tends to deepen through time, and vegetative perennating structures may migrate upwards in the soil profile as the time since the last disturbance increases (Rowe 1983). Thus, scour by debris flows may have removed more resprouting species on the less disturbed conifer reaches than on the more recently disturbed clear-cut and hardwood reaches.

Differences in life history strategies between early and late successional communities could also explain why vegetative resprouting was higher on the clear-cut reaches than on the conifer reaches. Early successional communities often are composed of species with faster rhizome growth and a potentially greater ability to respond to disturbance than species characteristic of less-disturbed sites (Leps et al. 1982, Sobey and Barkhouse 1977). In addition, species that maintain themselves vegetatively in the absence of disturbance in a late successional community may not necessarily be able to resprout following disturbance (Rowe 1983).

Since others document relatively abundant vegetative regrowth in clear-cut communities following other disturbances (Franklin et al. 1985, Halpern 1987, Smith et al. 1987, Stickney 1986), further research on the underlying mechanisms causing this relationship is needed.

The topographic position of the disturbed surfaces relative to the stream had no significant influence on either total cover or vegetative regrowth. This was surprising as Campbell and Franklin (1979) identified strong relationships between riparian community structure and the riparian subzone. Studies of the environmental factors controlling undisturbed riparian communities show that species distribution is at least in part influenced by a moisture gradient extending from the stream (Fonda 1974, Harris 1984, McBride and Strahan 1984, Padgett 1982). Several possible explanations exist for this general lack of significance: (1) the riparian subzone influenced only seedling establishment which was initially unimportant in terms of cover, whereas the vegetative sprouts responded more to the type of disturbance surface created and the microtopographic relief within each subzone than to the distance from the stream; (2) gradient patterns do not develop until later in succession (Wood and del Moral, 1987); and (3) the riparian subzone consists of two gradients--decreasing moisture and decreasing disturbance intensity with distance from the stream--that have counterbalancing effects on the reestablishment of cover.

In spite of the convergence of cover among sites, disturbance location was a significant factor in three of the five regression models built to describe early successional patterns. The distribution of surfaces and the vegetation types varied among the three debris flows we studied. Since both the disturbance surfaces and vegetation types strongly affected revegetation, the importance of seedlings and vegetative sprouts differed among these sites. Seedling establishment was highest on the deposition-dominated Mack Creek Road, particularly within the hardwood and clear-cut reaches. Vegetative regrowth dominated the scoured and clear-cut WS10. The contributions of the two means of establishment to revegetation of Zeolite Creek were more equal. The disturbance surfaces were more evenly distributed on this debris flow which also passed through both conifer reaches (with high seedling establishment) and clear-cut reaches (with high vegetative regrowth).

Mechanisms of disturbance

Disturbance can influence the development of community properties, such as cover, in several ways. Disturbance can reduce the survival of individuals or species (Franklin et al. 1985), modify microenvironmental conditions (Bazzaz 1983), and change both resource and propagule availability (Pickett et al. 1987a and b). The results of this study suggest that debris flows affect early successional cover patterns mainly by altering the relative contributions of seedlings and vegetative sprouts to revegetation. Total cover and vegetative regrowth were high on low and moderate intensity scour, while seedling establishment was highest on fine and gravel deposits and low intensity scour. We hypothesize that these differences resulted from differences in the effects of scour and deposition on the relative contributions of the three propagule sources (the residual propagule bank, the disturbance-transported propagule bank, and dispersed seed) to revegetation.

We interpret the high cover and abundance of seedlings on gravel and fine deposits as a result of seedling establishment from all three propagule sources. Establishment from the residual propagule bank was probably low, however, as many species are unable to emerge as seedlings from depths greater than five cm (Dawson and Bruns 1962, Hakansson and Wallgren 1972, Harty and McDonald 1972, Maun and LaPierre 1986, Wesson and Wareing 1969, Wiese and Davis 1967). Vegetative emergence through shallow deposits (less than five cm) can be high, but increasing depths of deposition progressively reduce the number of emergent shoots (Antos and Zobel 1985 and 1987, Griggs 1919, Mueller 1941). As the cover of vegetative sprouts decreased, seed germination was probably stimulated. The lower vegetative cover on the deposits exposed seeds to the high light intensities and increased temperature fluctuations necessary for gemination (Bazzaz

1983, Thompson et al. 1977). In addition, where deposits reduced vegetative emergence, there was less competition from vegetative sprouts during the establishment phase.

A concentration of stored seed in the upper few cm of soil with sharp decreases in density below this depth is characteristic of many forest and lakeshore communities (Harper 1977, Moore and Wein 1977, Nicholson and Keddy 1983, Pratt et al. 1982, Strickler and Edgertown 1976). Therefore, removal of seed can be rapid with increased depth of scour. The vertical distributions of bud banks are unknown, but most studies of the depth distributions of individual species vegetative parts have shown that they extend over a greater range of depths than seed banks (Antos and Zobel 1984, Bradley 1984, Flinn and Pringle 1981, Flinn and Wein 1977, McLean 1969, Sobey and Barkhouse 1977, Williams, 1979). The removal of stored buds should be more gradual with increased scour than the removal of stored seeds. Intense scour could remove 100% of the seed bank if the depth of scour exceeded the maximum depth of seeds in the soil. Unless scour removed all soil to bedrock, it would probably not completely eliminate the bud bank (Williams 1979, Watt 1944). We suggest that the high seedling cover on low intensity scour occurred because this low depth of scour did not remove much buried seed, but that increasing scour removed most on-site seed. This removal of buried seed resulted in the low seedling cover on the moderate and high intensity scour surfaces. While even low intensity scour probably removed some vegetative perennating structures, these results suggest that abundant vegetative regrowth occurred from deeply buried buds on the low and moderate intensity scour surfaces.

Need for experimentation

Descriptive studies can identify significant disturbance characteristics and suggest relationships between disturbance characteristics and successional patterns. In this study, we documented the importance of vegetative regrowth in early debris flow succession and showed that dispersed seed was not necessary for revegetation. Rather, establishment of new individuals probably occurred from three propagule sources: dispersed seed, the residual propagule bank and the disturbance-transported propagule bank. We identified surface type as the most important characteristic affecting debris flow revegetation, and suggested that differences in successional patterns on the disturbance surfaces resulted from differences in the effects of scour and deposition on seedlings, vegetative sprouts and propagule sources. But descriptive studies can provide only circumstantial evidence about the underlying causes of these relationships (Connell and Slatyer 1977, Wood and del Moral 1987, Finegan 1984, McConnoughay and Bazzaz 1987). Whereas the disturbance characteristics measured here significantly influenced early successional patterns, they do not explain more than 39% of the variation in either the reestablishment of cover or the means of establishment. Important additional effects on the observed patterns are likely to include the depth of deposition, the physical and chemical properties of the substrate, spatial variation in either the residual or transported propagule banks and species-specific responses to either burial or removal of plant biomass. Field experiments, in which disturbance characteristics are isolated and other sources of variation controlled, are necessary in order to link the significant disturbance characteristics identified in descriptive studies to early successional patterns.

Acknowledgements

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Chapter 3

RIPARIAN VEGETATION RECOVERY AFTER EXPERIMENTAL DEBRIS FLOW TREATMENTS

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ABSTRACT

We applied experimental debris flow treatments in a western Cascades riparian zone to test predictions of the effects of increasing intensity of scour and deposition on early successional patterns. We based these predictions on the hypothesis that early successional patterns after debris flows result from differences in how scour and deposition affect propagule availability. There were six experimental treatments: three depths of deposition (5, 10 and 19 cm), two depths of scour (2.5 and 5 cm) and a control (no substrate modification). Above-ground vegetation was removed in all treatments. We recorded total cover, species cover and the cover and number of seedlings and vegetative sprouts at the end of the first growing season. Total cover and vegetative regrowth decreased with increasing intensity of both types of

disturbance. Seedling establishment did not differ with disturbance type or intensity. The relative contributions of seedlings to site revegetation increased as disturbance intensity increased. These results were consistent with most of our predictions, but were not consistent with our predicted responses of seedlings to scour.

Most individuals establishing on our experimental site in the first growing season came from on-site sources, including seeds and vegetative propagules in both residual and transported soil.

Fifteen species, contributing 59.2% of the overall cover, showed significant and individualistic responses to the experimental treatments. The high cover of six species (for example _Madia_ _gracilis_ and _Epilobium_ _paniculatum_) on deposits clearly resulted from differences in propagule availability between the residual and transported propagule banks. The responses of most other species (for example _Oxalis_ _oregana_ and _trilliifolia_, _Petasites_ _frigidus_ and _Galium_ _triflorum_) were determined by propagule availability, propagule removal by scour, physiological tolerances to disturbance and morphological characteristics.

Despite the clear patterns in community cover, seedling establishment and vegetative regrowth with increasing disturbance intensity, understanding early succession requires a consideration of both propagule availability and individualistic species responses to disturbance.

INTRODUCTION

Successional theory emphasizes the importance of dispersal and seedling establishment following disturbance. But seedlings and vegetative sprouts from soil propagule banks are often more important than dispersed seed in early successional communities (Archibold 1978, Hill and Stevens 1981, Hopkins and Graham 1984, Kellman 1974, Purdie and Slatyer 1976, Young et al. 1987). Vegetative regrowth often dominates the reestablishment of cover (Franklin et al. 1985, Gecy and Wilson 1988, Keeley and Keeley 1984, Tsuyuzaki 1987, Young et al. 1987), contributes to community resilience (Abrahamson 1984, Halpern 1987) and controls early community composition (James 1984). Seedlings contribute less to initial cover, but add to the diversity of some early successional communities and affect later successional patterns (Hanes and Jones 1967).

The establishment rates of both seedlings and vegetative sprouts depend on propagule availability (Pickett et al. 1987a and b, Young et al. 1987) and disturbance characteristics (Grime 1979, Pickett et al. 1987a and b, Runkle 1985, Sousa 1984). Communities with similar above-ground compositions can differ in the proportions, densities and depths of seeds and buds within their propagule banks (Rowe, 1983). Differences in propagule banks at the time of disturbance can lead to different successional patterns among previously similar communities (Young et al. 1987). Often, dispersed seed is important only in communities with depauperate propagule banks at the time of disturbance (Johnson 1975, Young et al., 1987) or where very intense or severe disturbances deplete the propagule banks (Grime 1979, Malanson 1984, Sousa 1984).

Different types and intensities of disturbance may act selectively on the propagule bank, determining which seeds and buds are exposed to conditions suitable for germination (Bazzaz 1983, Moore and Wein 1977, Pratt et al. 1982, Roberts 1981) and which are able to survive the disturbance (Moore and Wein 1977). Experimental studies show that the effects of disturbance on propagule banks also depend on the depth at which propagules are buried in the soil (Cheplik and Quinn 1987, Sabiiti and Wein 1987). The effects of propagule depths on revegetation have been examined in field studies only after a single disturbance type, fire (for example, Flinn and Wein 1981, Ohman and Grigal 1981). Since fire intensity determines the depth of lethal heat penetration into the soil, species with perennating structures characteristically found in the litter or upper few cm of soil do not survive moderate to high intensity fires (Ohman and Grigal 1981), while species with perennating structures buried deeper than 5 cm often dominate early succession (Flinn and Wein 1981). This interaction between propagule depths and disturbance characteristics should also be important following other disturbances, such as debris flows, in which the depth of substrate modification is an important variable affecting successional patterns (Gecy and Wilson 1988, Miles and Swanson 1986, Smith et al. 1986, Veblen and Ashton 1978).

Debris flows are a major cause of disturbance to riparian vegetation in humid mountainous areas (Swanston 1978, Veblen and Ashton 1978). These rapid, shallow mass movements of soil, organic debris and alluvium through stream channels remove most above-ground vegetation in their paths, but can be very heterogeneous in their effects on the underlying substrates. Debris flows can scour all soil and stored propagules to bedrock, shear off the top of vegetation without removing any substrate or deposit material along their tracks (Costa 1984, Flaccus 1959). Because of the material deposit, three sources of propagules may contribute to the revegetation of debris flows and other mass movements (Adams et al. 1987): dispersed seed, the residual propagule bank and the disturbance-transported propagule bank.

Depths of scour and deposition can vary both within and among debris flow sites (Adams and Sidle 1986, Miles et al. 1984). This variation in scour and deposition produces variability in cover and composition throughout succession (Gecy and Wilson 1988, Miles and Swanson 1986, Smith et al. 1986, Veblen and Ashton 1978).

Objectives

In this experimental study, we hypothesize that early successional patterns after debris flows result from differences in how scour and deposition affect propagule availability. We use this hypothesis to develop testable predictions (Table 3-1) of the effects of increasing intensity (as measured by depth) of the two disturbance types associated with debris flows (scour and deposition) on seedling establishment, vegetative regrowth, and community cover. We test this hypotheses and its derived predictions in an experiment designed to simulate both the canopy removal and the scour and depositional effects of a debris flow. We also recognize that species differ in their germination and sprouting requirements, physiological tolerances, and morphological and life history characteristics and that these differences can lead to differences in how species respond to disturbance (Pickett et al. 1987a). Since species-specific responses to disturbance could have important influences on our experimental results (Bradley 1984, Pickett et al. 1987a and b, Sousa 1980), we also examine the responses of individual species to disturbance and how these responses affect overall community patterns.

Below we present the five predictions derived from our central hypothesis, and the justification for each prediction. These predictions are summarized in Table 3-1.

Central Hypothesis: Early successional patterns after debris flows result from differences in how scour and deposition affect propagule availability.

Prediction 1: The removal of propagules by scour will decrease total cover, vegetative regrowth and seedling establishment.

Prediction 2: The relative contributions of seedlings to total cover will decrease with scour because a greater proportion of seeds than vegetative buds will be removed.

We expected high cover and abundance of both seedlings and vegetative sprouts where we removed all above-ground vegetation, but did not remove any propagules through scour. The removal of above-ground shoots usually stimulates dormant bud germination (Leakey 1981). Gap creation stimulates seed germination for many species and leads to favorable conditions for their establishment (Canham and Marks 1985, Sousa 1984, Thompson et al. 1977). Increasing depth of scour leads to increased removal of both seeds and vegetative buds, reducing the number of propagules available for revegetation.

A concentration of buried seed in the upper few cm of soil with sharp decreases in density below this depth is characteristic of many communities (Harper 1977, Moore and Wein 1977, Nicholson and Keddy 1983, Pratt et al. 1982, Strickler and Edgertown 1976). Therefore, a large proportion of buried seed can be removed by even low depths of scour. The vertical distributions of bud banks are unknown, but most studies of the depth distributions of individual species' vegetative parts have shown that they extend over a greater range of depths than seed banks (Antos and Zobel 1984, Bradley 1984, Flinn and Pringle 1981, Flinn and Wein 1977, McLean 1969, Sobey and Barkhouse 1977, Williams, 1979). The removal of stored buds should be more gradual with increased scour than the removal of stored seeds. Intense scour could remove 100% of the seed bank if the depth of scour exceeded the maximum depth of seeds in the soil. Unless scour removed all soil to bedrock, it would probably not completely eliminate the bud bank (Williams 1979, Watt 1944).

<u>Prediction</u> <u>3</u>: There will be no difference in seedling establishment among the depositional treatments because the availability of seed will not differ among these treatments.

<u>Prediction</u> <u>4</u>: Deposition will decrease vegetative regrowth by reducing the number of vegetative buds able to produce emergent shoots.

<u>Prediction</u> <u>5</u>: The relative contributions of seedlings to total cover will increase with deposition because

deposition reduces the number of vegetative buds able to produce emergent shoots, but does not affect the number of seeds available for revegetation.

Seedling establishment and vegetative regrowth from the transported propagule bank would not change with increasing depth of deposition because seeds and vegetative fragments are homogeneously distributed within the deposits. Many species are unable to emerge as seedlings from depths greater than two to five cm (Dawson and Bruns 1962, Hakansson and Wallgren 1972, Harty and McDonald 1972, Maun and LaPierre 1986, Wesson and Wareing 1969, Wiese and Davis 1967), so establishment from the residual seed bank would be unlikely even on shallow deposits (less than 5 cm). In contrast, vegetative emergence through shallow deposits can be high (Antos and Zobel 1985 and 1987, Griggs 1919, Mueller 1941). Increasing depths of deposition progressively reduce the number of emergent shoots (Antos and Zobel 1985 and 1987, Griggs 1919, Mueller 1941). Therefore, with increasing deposition, the availability of transported propagules (both seeds and buds) and buried seed remains uniform, but the ability of vegetative buds from the residual propagule bank to produce emergent shoots is reduced.

Observations on nearby sites (Gecy and Wilson 1988) led us to believe that dispersed seed would not contribute much to establishment in comparison to the other propagule sources (see also Young et al. 1987). Thus, dispersal is not included in the prediction rationale. Measurements of dispersed seed at the experimental site indicated that, in fact, dispersal contributed little to revegetation.

Table 3-1. Predicted responses to increasing depths of deposition or scour. Spr=vegetative sprout, S=seedling, Rel Contrib= relative contributions to both total cover and abundance.

	CONTROL	INCREASING SCOUR	INCREASING DEPOSITION
Total Cover	Highest	Decrease	Decrease
Cover Spr	Highest	Decrease	Decrease
Number Spr	Highest	Decrease	Decrease
Cover S	Highest	Decrease	No change
Number S	Highest	Decrease	No change
Rel contrib Spr	Equal	Increase	Decrease
Rel contrib S	Equal	Decrease	Increase

STUDY AREA

The experimental site was in the riparian zone of second-order stream in the H.J. Andrews Experimental Forest near the town of Blue River, Oregon. The elevation of this west-central Cascade Mountain site was 450 m. The climate of the area is mild, characterized by wet winters and warm, dry summers. The average annual precipitation is 2400 mm, mostly occurring as rain during the winter months. The terrain is deeply dissected with frequent occurrence of both deep-seated and shallow mass movements, particularly in the lower elevation forests (below 850 m) underlain by hydrothermally altered volcanoclastic rocks (Swanson and James 1975).

Alnus rubra dominated the canopy, but *Acer macrophyllum*, *Pseudotsuga menziesii*, *Thuja plicata* and *Tsuga heterophylla* were also present. We listed all understory species on the 375 m^2 site before manipulation based on relevés made in October, 1986 and March, 1987. This understory was floristically rich, containing more than 40 herbaceous and low shrub species (Table 6-1). Some additional preexisting species were probably missed because of the late fall and early spring sampling dates.

METHODS

Experimental Design

There were six experimental treatments, including three depths of deposition, two depths of scour and a control. The treatments were: control (no substrate modification through deposition or scour), 2.5 and 5 cm scour, and 5, 10 and 19 cm deposits. In each treatment, all above-ground vegetation and litter were removed before manipulation of the substrate (Figure 3-1).

We chose these depths of deposition based on the responses of intact individuals to burial reported by Antos and Zobel (1985 and 1987), Griggs (1918 and 1919) and Mueller (1941). These studies indicate that the emergence of intact individuals can be high through 5 cm deposits, but reduced by deposits between 5 and 15 cm. Few species are able to emerge through deposits greater than 15 cm.

We based the scour depths on the average depth distributions of seed banks and vegetative perennating structures. Seed bank studies in forest communities show that few seeds occur below a depth of 5 cm (Harper 1977, Moore and Wein 1977, Pratt et al. 1982, Strickler and Edgertown 1976). The vertical distributions of bud banks are unknown, but most studies of the depth distributions of individual species vegetative parts have shown that they extend over a greater range of depths than seed banks

(Antos and Zobel 1984, Bradley 1984, Flinn and Pringle 1981, Flinn and Wein 1977, McLean 1969, Sobey and Barkhouse 1977, Williams, 1979). We chose 2.5 cm scour to remove approximately one half of the vertical profile of the seed bank and an unknown proportion of the bud bank. We chose 5 cm scour to remove most of the seed bank and a large proportion of the bud bank.

The experimental design was stratified random to achieve interspersion of treatments (Hurlbert 1984, Figures 3-2 and 3-3). Since the site was too heterogeneous to form uniform blocks (Steel and Torrie 1980), we used covariance analysis to account for the effects of topographic position on revegetation. Topographic position can influence both the distribution of the preexisting vegetation (Campbell and Franklin 1979) and the ability of seedlings to establish following disturbance (Gecy and Wilson 1988). We recognized three topographic positions: stream-edge, boulder berm and floodplain surface. The stream bordered the stream-edge plots on at least one side. The floodplain plots were not in direct contact with the stream during the growing season. The boulder berm plots were located on one of three large boulder deposits present on the site.

The treatments were each replicated ten times in one-by-one meter plots. We used Stein's two-stage sampling (Steel and Torrie 1980) at a significance level of 0.05 and a precision of 20% to determine the treatment surface area necessary to assess total plot cover ($60m^2$). A $0.4m^2$ subplot (40-by-100 cm) was found to be adequate for detecting differences in the cover and abundance of seedlings and vegetative sprouts based on an analysis of preliminary data.

We removed all above-ground vegetation and litter from the site in mid-March. Removal of trees and shrubs occurred with minimal disturbance to the soil and without heavy machinery. We removed all other above-ground vegetation by hand-clipping and raked the site to remove the litter. This raking could have removed some early spring dispersed seed (e.g. *Salix* sp.) and any seed dispersed onto the site over the winter from the predisturbance canopy dominant *Alnus rubra* or shaken from the alder trees as they were removed. Treatment application occurred from March 25, 1987 to April 3, 1987 which is within the period of naturally-occurring debris flows in the western Cascades.

We made simulated debris flow deposits for the depositional treatments using material from four sites in the H.J. Andrews Experimental Forest: a one year-old debris flow, riparian soil from an alder-dominated stream, riparian soil from a clear-cut stream and an upland clear cut. We added the upland clear cut soil because many debris flows originate as debris avalanches from clear-cut hillslopes (Swanson and Lienkamper 1978, Swanston 1978).

We mixed soil from all four sites in a portable cement mixer. The churning of the cement mixer simulated the churning action of a debris flow along its track and the mixing of soil from different vegetation types (J.E. Costa, personal communication).

Figure 3-1. Overview of experimental site during treatment application showing the uniform removal of above-ground vegetation and litter. March 26, 1987.

Figure 3-2. Interspersion of scour and depositional treatments within a portion of the experimental site. Plots surrounded by flagging are 5 cm scour plots (orange), 2.5 cm scour (white and blue), and controls (yellow). Three depositional treatments are visible in the right foreground. A 5 cm deposit borders the stream. Directly behind this plot is a 10 cm deposit (to the left) and a 19 cm deposit (to the right). April 3, 1987.

Figure 3-3. Cover reestablishment at the end of the first growing season. The same treatments visible in Figure 3-2 are visible here. August 25, 1987.

Figure 3-2.

Figure 3-3.

Sampling

We marked and identified each individual in the 0.4m^2 subplot as a seedling or vegetative sprout as it emerged. We defined an individual as a shoot system originating from a single node. If we could directly observe attached vegetative parts by careful probing in the soil, we marked an individual as a vegetative sprout. We marked an individual as a seedling if it met one of the following three criteria:

1. It was an annual species
2. Cotyledons were present
3. We were able to observe species-specific differences in emergence patterns between seedlings and vegetative sprouts. For example, young <u>Oxalis</u> seedlings were erect with straight stems, but vegetative shoots were curved during the first month following emergence.

If we could not identify the means of establishment of an individual, we listed it as being of unknown origin.

We assessed total cover in the 1m^2 plots and mortality of marked individuals in the 0.4 m^2 subplots monthly.

The experiment ended the third week of August at the end of most of the growing season, but before senescence occurred. This date coincided with the peak cover of most riparian species (see Campbell and Franklin [1979] for the phenology of important western Cascades riparian species).

The total plot cover and subplot mortality were assessed as in the previous months. In addition, we recorded the cover, number, origin and species of each individual. Nomenclature was according to Hitchcock and Cronquist (1973). We defined total cover as the per cent ground obscured by vegetation, and species cover as the per cent ground obscured by individuals of that species. We summed the cover of all individuals establishing by seed or by vegetative means to determine seedling and vegetative cover. Thus defined, seedling cover, vegetative cover and the sum of the species cover values could exceed the total plot cover.

Assessment of Propagule Sources

We randomly collected twenty replicate soil samples from our experimental site. Each of these residual soil samples had a surface area of 0.027 m^2 and extended to a depth of 5 cm. We also randomly collected twenty samples of the transported soil. These samples each had a volume of 0.0014 m^3, equivalent to the volume of the individual residual soil samples. We mixed all samples with vermiculite and spread this mixture over 2 cm of sterile potting soil in flats. Paper toweling lined the flats to prevent seed loss through the drainage holes. We placed the flats in the Oregon State University greenhouse. The flats were watered daily. The temperature fluctuated between 22° C during the day and 13° C at night.

Contamination was assessed with ten control flats filled only with sterile potting soil and placed randomly among the propagule bank samples. We also checked the soil samples every two days for any foreign seed lying on the surface. These controls ensured that all seedlings actually emerged from the soil samples.

We counted each individual that emerged from the propagule bank samples between March 26, 1987 and July 11, 1987. We identified each emergent as a seedling or vegetative sprout and listed its taxon.

We monitored dispersal using seed traps filled with sterile potting soil. Each seed trap had a surface area of 0.17 m^2. There were nine replicate flats placed randomly on the site at the start of the experiment. We returned the flats to the Oregon State University greenhouse three times during the experiment for germination of the dispersed seed. We counted and identified germinants to species.

Statistical analysis

We used analysis of covariance (ANCOVA) to determine differences in revegetation patterns among the six experimental treatments. The vegetation attributes we examined as dependent variables were total cover, seedling establishment, vegetative regrowth and species cover. The covariate was a categorical variable that accounted for the effects of topographic position on revegetation. This categorical variable was converted to an indicator variable for the covariance analysis. Separation of means was either through Least Significant Difference (LSD) analysis or Least Significant Increase (LSI) analysis. Since the covariate was always significant, we used adjusted means in these analyses. The cover data were first log-transformed to stabilize variances and to obtain normal distributions of errors. The numbers of individuals were square-root transformed. The relative contribution of seedlings to total cover and abundance did not require transformation. We used percent similarity (PS, Gauch 1982) to compare the compositional similarity between the two propagule banks.

RESULTS

Intensity effects on total cover, seedlings and vegetative sprouts

Increasing intensity of both types of disturbance had a significant effect on total cover and the cover and abundance of vegetative sprouts (ANCOVA $P<.005$ and $P<.001$, Table 3-2, Figures 3-1 to 3-4). Total cover was highest on the controls (69.2%), 2.5 cm scour (58.9%) and 5 cm deposits (LSI analysis of means, $P<.05$), decreasing with increasing scour to 5 cm (34.2%) and with increasing deposition to 10 and 19 cm (47.6% and 42.0% respectively). The cover of vegetative sprouts was also highest on the controls (84.5%) and 5 cm deposits (57.6%). Vegetative cover decreased dramatically with scour (42.5% on 2.5 cm scour, 23.7% on 5 cm scour) and with deposition greater than 5 cm (35.8% on 10 cm deposits, 27.4% on 19 cm deposits).

The number of vegetative sprouts was highest on the controls (141.0/m^2) and 2.5 cm scour (128.8/m^2), but decreased to 46.5 shoots/m^2 on 5 cm scour. Vegetative sprout abundance also decreased with increased deposits of 5 cm (75.5/m^2) and 10 cm (41.8/m^2).

There was no significant difference in seedling establishment among any of the treatments regardless of the type or intensity of disturbance (ANCOVA, $P>.05$). Even though the cover and number of seedlings did not differ significantly with scour, seedling cover on the control (12.7%) was less than that on 2.5 cm scour (27.6%). In addition, the number of seedlings nearly doubled from 167.8/m^2 on the control to 303.5/m^2 and 312.8/m^2 on the two scour treatments. Seedling establishment was less variable on the deposits. On these treatments, seedling cover ranged between 10.5% and 22.3% and seedling abundance between 195.5/m^2 and 254.2/m^2.

The experimental treatments had a significant effect on the relative contributions of seedlings to revegetation (ANCOVA, $P<.03$ for relative cover and $P<.0001$ for relative abundance). The relative contribution of seedlings to both total cover and abundance increased significantly with increasing intensity of scour and with deposition greater than 5 cm (Figures 3-1 and 2). Seedling relative cover increased from less than 20% on the controls to almost 50% on 5 cm scour and 19 cm deposits. The relative contributions of seedlings to overall abundance also increased from 54% on the control to more than 80% on the two high intensity treatments.

There were no significant differences in mortality associated with any of the experimental treatments (ANCOVA, $P>.05$, Table 3-3). The observed patterns of establishment reflected the patterns of emergence. Seedling mortality ranged between 17% of the total seedling emergence on 19 cm deposits to 37.9% on the controls and 5 cm deposits.

Table 3-2. Mean cover (%) and abundance (number/m^2) on each of the experimental surfaces after adjustment for the covariate of topographic position. Total cover is defined as the per cent ground obscured by vegetation. The cover of all individuals establishing by seed or vegetatively was summed to determine seedling and vegetative cover. Thus defined, seedling or vegetative cover could exceed the total plot cover. S=seedling, SPR=vegetative sprout, ANCOVA=analysis of covariance, S_D=average standard deviation of the differences between the adjusted means (Snedecor and Cochran 1967).

TREATMENT	TOTAL COVER	COVER SPR	COVER S	NUMBER SPR	NUMBER S
Control	69.2	84.5	12.7	141.0	167.8
2.5 cm scour	58.9	42.5	27.6	128.8	303.5
5.0 cm scour	34.2	23.7	14.4	46.5	312.8
5.0 cm deposits	56.3	57.6	10.5	75.5	195.5
10.0 cm deposits	47.6	35.8	15.5	41.8	162.5
19.0 cm deposits	42.0	27.4	22.3	45.0	254.2
S_D	7.8	13.6	7.2	34.2	83.4
ANCOVA (5,52 d.f.)	$P <.005$	$P <.001$	$P>.05$	$P <.005$	$P>.05$

Figure 3-4. Changes in total, vegetative and seedling cover with increasing disturbance intensity (as measured by depth of disturbance). The x-axis represents % cover after adjustment for the covariate of topographic position. The y-axis represents depth of disturbance from the control, the 0 on the y-axis. Positive values on the y-axis represent deposit depths. Negative values represent scour depths. Total cover=% ground obscured by vegetation, Cover S=sum of the cover values for all seedlings, Cover SPR=sum of cover of all individuals establishing as vegetative sprouts. Thus defined, seedling or vegetative sprout cover could exceed total plot cover.

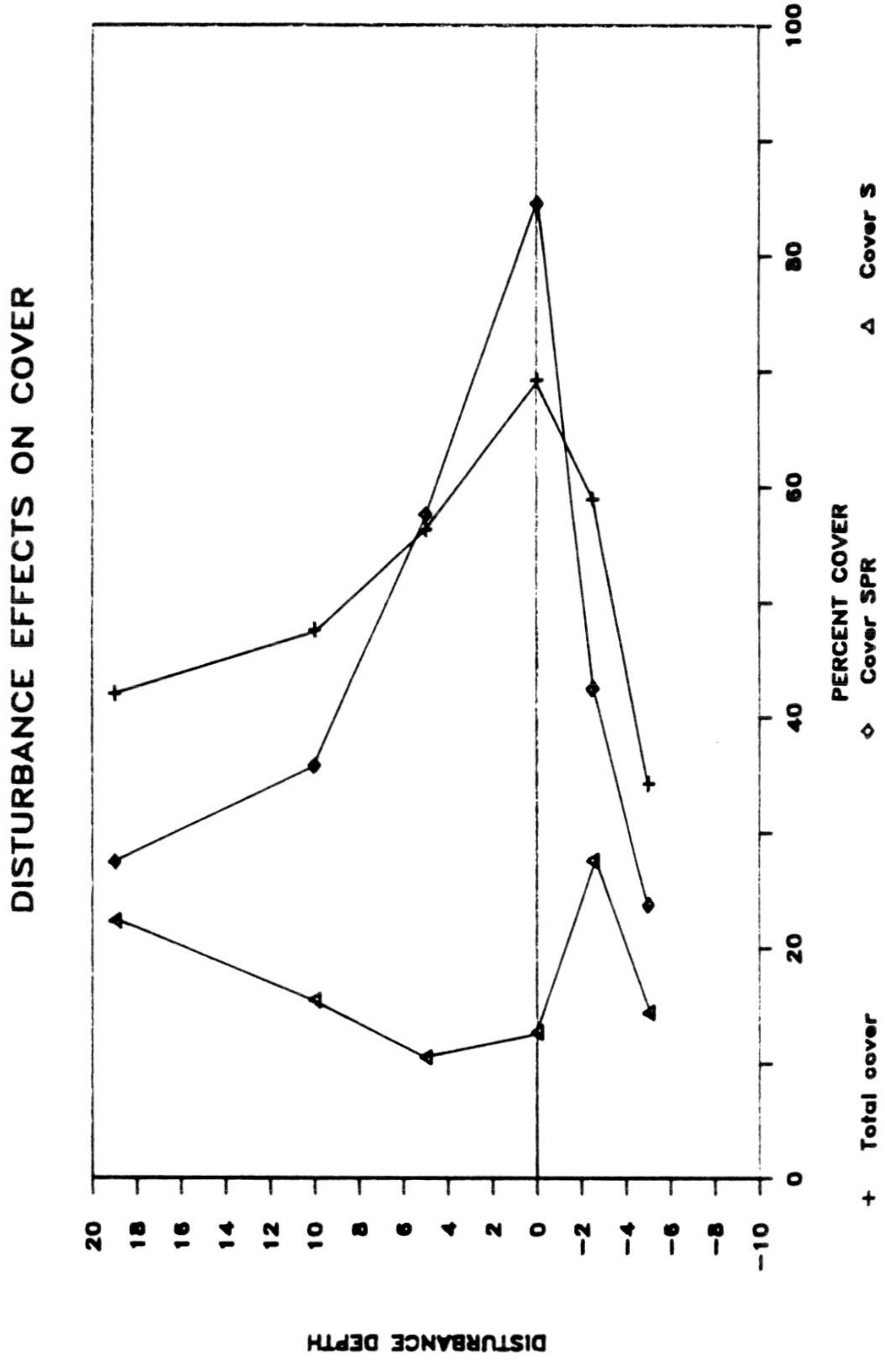
DISTURBANCE EFFECTS ON COVER
PERCENT COVER
0
20
40
60
80
100
DISTURBANCE DEPTH
20
18
16
14
12
10
8
6
4
2
0
-2
-4
-6
-8
-10
+ Total cover
◇ Cover SPR
△ Cover S

Figure 3-4.

Figure 3-5. Changes in abundance of seedlings (S) and vegetative sprouts (SPR) with increasing disturbance intensity (depth). All values are expressed as the number of individuals /m^2 after adjustment for the covariate of topographic position. The x-axis represents the number of individuals. The y-axis represents depth of disturbance from the control, the 0 on the y-axis. Positive values on the y-axis represent deposit depths. Negative values represent scour depths. SPR=vegetative sprout, S=seedling.

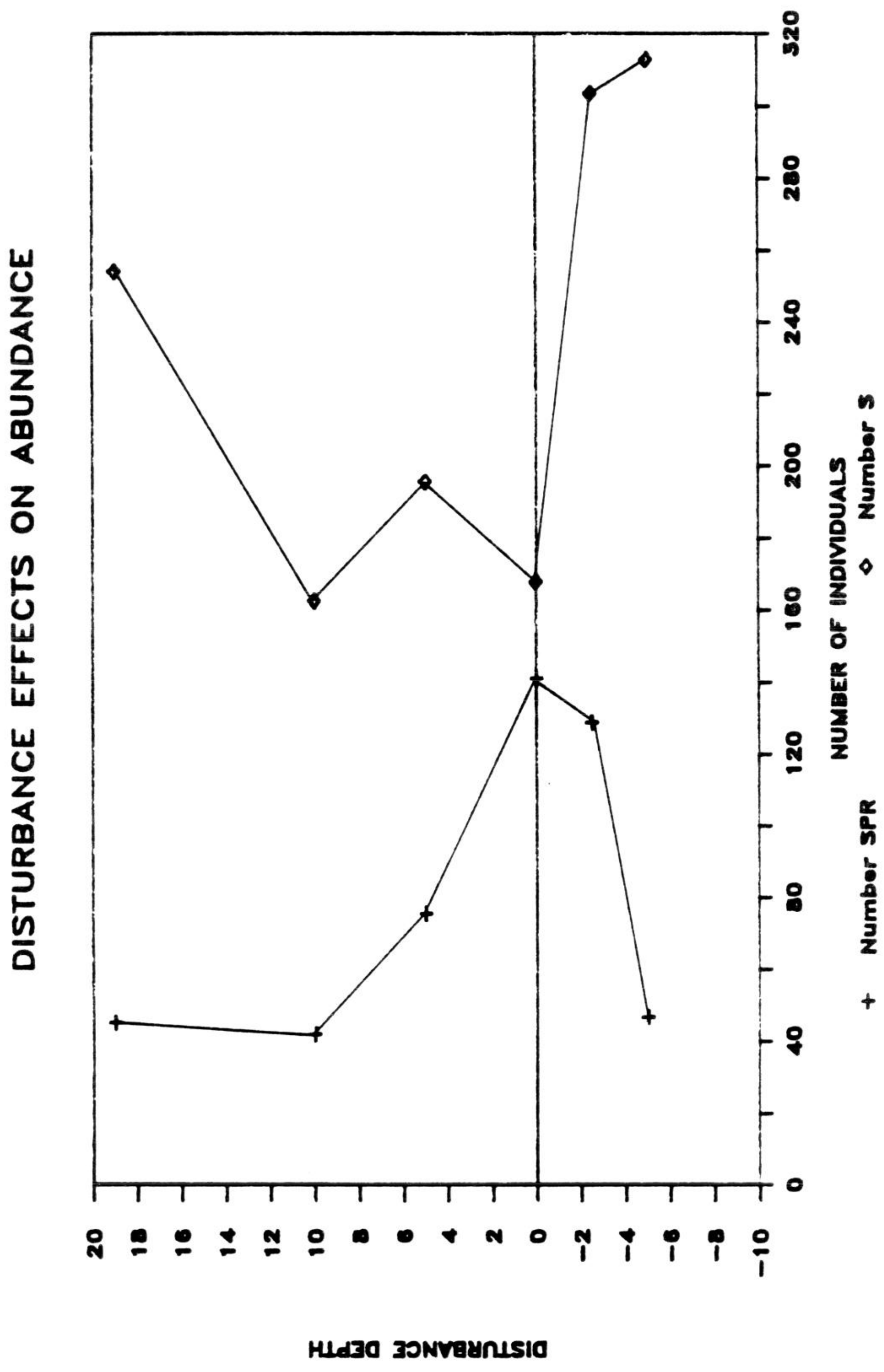
DISTURBANCE EFFECTS ON ABUNDANCE
DISTURBANCE DEPTH
20
18
16
14
12
10
8
6
4
2
0
-2
-4
-6
-8
-10
NUMBER OF INDIVIDUALS
0
40
80
120
160
200
240
280
320
+ Number SPR
◇ Number S

Figure 3-5.

Table 3-3. Mean mortality of seedlings (S) and vegetative sprouts (SPR) on each of the six experimental surfaces. The numbers of seedlings and vegetative sprouts are expressed as the average number of individuals emerging by that mechanism that died during the five month experiment/m^2 after adjustment for the covariate of topographic position. The per cent values express the per cent mortality in relation to total emergence. ANCOVA=analysis of covariance, S_D=average standard deviation of the differences between the adjusted means (Snedecor and Cochran 1967).

TREATMENT	NUMBER SPR	PER CENT SPR	NUMBER S	PER CENT S
Control	13.0	14.8	49.5	37.7
2.5 cm Scour	14.5	8.1	56.8	27.5
5.0 cm Scour	6.5	12.1	58.0	21.2
5.0 cm Deposits	13.5	16.8	50.2	37.5
10.0 cm Deposits	10.2	21.8	63.8	32.6
19.0 cm Deposits	5.2	9.9	49.2	17.1
S_D	6.7	7.7	17.1	9.0
ANCOVA (df 5,52)	$P>.05$	$P>.05$	$P>.05$	$P>.05$

Mortality of vegetative sprouts ranged between 8.1% on the 2.5 cm scour and 21.8% on the 10 cm deposits.

Species responses

Although 70 species established on our experimental site, 4-7 species accounted for 65.7 to 89.9% of the cover on each of the treatments (Table 3-4). Petasites frigidus and Stachys cooleyae dominated cover on all treatments. Petasites increased its dominance on the control and depositional treatments, contributing between 34.9% and 50.4% of the total plot cover. Epilobium watsonii, Oxalis oregana and trilliifolia were also important species on at least half of the treatments. Although Boykinia elata dominated cover only on 5 cm scour, it was the most abundant seedling species, comprising between 22 and 35% of all seedlings establishing on our site.

Only 40 of the 70 species on our site had frequencies large enough for statistical analysis. Fifteen of these 40 species, contributing 59.2% of the overall cover, showed a significant response to the treatments (ANCOVA, $P<.05$, Table 3-5). More than half of the dominant species (53.8%), but only 29.6% of the rarer species, showed significant differences in cover on the treatments.

The 15 species significantly affected by the treatments showed different types of responses. The cover of Galium triflorum was highest on the controls, where there was no substrate modification (3.4%, LSD analysis of means, P<.05). Two species had higher cover on the depositional and control treatments than on scour. Petasites frigidus had its highest cover on the controls and deposits, with higher cover on these treatments (18.8-31.3%) than on scour (5.9-12.6%). Polystichum munitum had highest cover on the controls (4.4%) and 5 cm deposits (7.6%). Eight species had their highest cover only on the deposits, including the dominants Collomia heterophylla and Conyza canadensis and 6 of the 7 rarer species responding to the treatments: Cardamine oblongifolia, Epilobium paniculatum, Gnaphalium microcephalum, Holcus lanatus, Madia gracilis and Stellaria crispa. The maximum cover of these species was low, ranging between 0.2% (Cardamine oblongifolia) and 3.1%. (Conyza canadensis).

Only four species had their highest cover on the scour treatments (LSD analysis of means, P<.05). The two species of Oxalis had higher cover on the controls (18.2%) and 2.5 cm scour (12.1%) than on the deeper deposits (0%). The cover of these species was also low on 5 cm scour (1.9%). The cover of Cirsium vulgare (5.9%) was higher on 2.5 cm scour than on the deposits. Alnus rubra was the only non-dominant species to show a significant increase in cover with scour, with highest cover on 2.5 cm scour (1.2%).

Six dominant species--Aruncus sylvester, Epilobium watsonii, Carex deweyana, Boykinia elata, Senecio

Table 3-4. Dominant species on each of the experimental treatments and the average proportion of the total plot cover provided by each species. All species with at least 5% relative cover on a treatment are listed. A dash (-) indicates the species was present on the treatment but did not contribute to at least 5% of the total plot cover. 0 indicates the species did not occur on the treatment.

SPECIES	CONTROL	SCOUR		DEPOSIT		
		2.5cm	5cm	5cm	10cm	19cm
Aruncus sylvester	5.4	-	6.2	-	-	-
Boykinia elata	-	-	9.1	-	-	-
Carex deweyana	-	-	10.0	-	-	-
Cirsium vulgare	-	8.8	-	-	-	-
Collomia heterophylla	-	0	5.5	-	5.2	-
Conyza canadensis	0	-	-	-	-	6.0
Epilobium watsonii	-	13.1	11.6	-	6.7	6.6
Oxalis oregana and trillifolia	20.3	17.8	6.2	8.9	-	-
Petasites frigidus	34.9	18.6	19.1	42.0	50.4	36.7
Polystichum munitum	-	0	-	11.5	0	0
Senecio sylvaticus	-	5.3	-	-	-	-
Stachys cooleyae	5.1	9.9	8.4	8.4	9.0	9.4
Proportional cover of dominants	65.7	89.0	80.3	75.9	71.3	58.7

Table 3-5. Mean cover (%) of vascular plant species on each of the experimental treatments after adjustment for the covariate of topographic position. All species occurring on at least 5 plots are listed. A 0 cover value indicates the species did not occur on the treatment. Significance values for the analysis of covariance (ANCOVA) of species responses to the treatments are given. The means through which each species was observed to establish are listed in parentheses after the species name (V=vegetative means, S=by seed or spore). S_D=average standard deviation of the differences between the adjusted means (Snedecor and Cochran 1967). *=P<.05, **=P<.01, ***=P<.001, NS=not significant.

SPECIES	CONTROL	SCOUR		DEPOSIT				
		2.5cm	5cm	5cm	10cm	19cm	SD	ANCOVA
TREES								
Alnus rubra (S)	0.4	1.2	0.3	0.1	0.1	0.1	0.3	*
Prunus emarginata (S)	0.2	0.3	0.4	0.4	0.4	0.3	0.1	NS
LOW SHRUBS AND HERBS								
Adiantum pedatum (S,V)	2.0	0.6	0.3	0.9	0.5	0.0	1.3	NS
Agrostis exarata (S,V)	0.6	0.9	0.5	1.6	1.4	2.1	0.8	NS
Anaphalis margaritacea (S)	0.5	0.6	0.2	0.3	0.8	0.8	0.7	NS
Aruncus sylvester (S,V)	4.8	2.8	1.9	2.1	<.1	0.6	2.3	NS
Boykinia elata (S,V)	1.0	3.1	2.8	1.5	1.0	2.0	1.0	NS
Cardamine oligosperma (S)	0.0	0.0	0.0	0.0	0.1	0.2	0.1	*
Carex deweyana (S,V)	1.4	1.7	3.1	1.0	1.0	0.9	1.2	NS
Cirsium sp. (S)	0.0	<.1	0.1	1.0	0.0	0.3	0.6	NS
Cirsium vulgare (S)	2.0	6.0	<.1	0.3	0.8	1.3	2.1	**
Collomia heterophylla (S)	<.1	0.0	1.7	1.8	2.7	1.7	1.1	***
Conyza canadensis (S)	0.0	<.1	0.2	0.7	1.0	3.1	0.7	***
Deschampsia elongata (S)	<.1	0.1	0.1	0.2	0.2	0.2	0.1	NS
Epilobium paniculatum (S)	0.0	0.0	0.0	<.1	0.2	0.9	0.2	***
Epilobium watsonii (S,V)	1.1	8.9	3.6	1.5	3.5	3.4	3.4	NS
Equisetum sp. (S,V)	<.1	0.0	0.0	0.3	0.2	0.6	0.3	NS
Festuca arundinoidea (S,V)	0.0	0.0	0.0	0.2	0.2	<.1	0.1	NS
Galium triflorum (S,V)	3.4	0.6	0.5	0.2	0.1	0.1	1.1	***
Gnaphalium microcephalum (S)	0.0	0.0	0.0	0.1	0.0	0.5	0.2	**
Holcus lanatus (S,V)	0.0	0.0	0.0	0.1	1.3	0.7	0.5	*
Hypericum perforatum (S)	1.1	0.7	0.8	0.1	0.1	0.1	0.7	NS
Juncus effusus (S,V)	0.1	0.2	0.6	0.1	<.1	0.4	0.2	NS
Juncus ensifolius (S,V)	<.1	0.3	0.4	<.1	0.1	0.1	0.1	NS
Lactuca murialis (S)	0.7	0.2	0.0	0.0	0.4	0.1	0.4	NS
Lotus purshiana (S)	0.2	0.6	0.0	1.3	0.3	1.5	0.6	NS
Luzula parviflora (S,V)	0.7	0.7	0.9	0.3	<.1	0.1	0.6	NS

Table 3-5. (Continued).

SPECIES	CONTROL	SCOUR		DEPOSIT				
		2.5cm	5cm	5cm	10cm	19cm	SD	ANCOVA
Madia gracilis (S)	0.0	0.0	0.0	0.5	0.7	2.4	0.8	*
Mitella ovalis (S,V)	0.4	0.3	0.2	0.1	<.1	0.1	0.2	NS
Montia sibirica (S,V)	0.9	0.0	0.0	0.2	0.1	<.1	0.4	NS
Oxalis oregana and trillifolia (S,V)	18.2	12.1	1.9	6.0	0.5	<.1	6.6	*
Petasites frigidus (V)	31.3	12.6	5.9	28.2	26.4	18.8	8.9	*
Polystichum munitum (V)	4.4	0.0	<.1	7.7	0.0	0.0	3.2	*
Rubus ursinus (S,V)	3.2	2.1	1.3	1.8	0.6	0.4	1.6	NS
Senecio sylvaticus (S)	1.1	3.6	0.2	0.2	2.0	1.3	1.5	NS
Stachys cooleyae (S,V)	4.6	6.7	2.6	5.6	4.7	4.8	4.6	NS
Stellaria crispa (S)	0.0	<.1	0.0	<.1	0.3	0.1	0.1	***
Tolmiea menziesii (S,V)	4.2	0.9	0.4	0.7	0.6	0.9	1.8	NS
Trientalis latifolia (V)	1.2	0.0	0.0	<.1	0.1	0.2	0.6	NS
Cover controlled by responding species	66.6	47.9	34.0	68.1	65.3	58.4	59.2	

sylvaticus and Stachys cooleyae--did not show any significant response to the treatments (ANCOVA, P>.05). However, there was a tendency for increased cover of several of the dominant seedling species with scour. The cover of Boykinia elata was high on both 2.5 and 5 cm scour (2.8-3.1%). Epilobium watsonii and Senecio sylvaticus had their highest cover on 2.5 cm scour (8.9% and 3.6% respectively). The cover of Carex deweyana was highest on 5 cm scour (3.1%).

Propagule sources

The potential contributions of the transported and residual propagule banks to revegetation were much greater than that of dispersed seed (Table 3-6). The residual bank contained 8538 propagules/m^2, the transported bank 4731 propagules/m^2. Ninety-one percent of the residual propagule bank and 95% of the transported propagule bank were seeds. In contrast, dispersal contributed only 31 seeds/m^2 to site revegetation.

Overall, the composition of the two propagule banks was similar, with 64.5% compositional similarity between the seeds in the two propagule banks. Boykinia elata dominated the seeds in both propagule banks (Table 3-7). Forty percent of the seeds in the residual propagule bank and 58% of the seeds in the transported propagule bank were Boykinia elata. Epilobium watsonii made up 7% of the seed in both propagule banks. Carex deweyana was also an important shared seed species. Cirsium vulgare was present as seeds in both propagule banks, but was not abundant in either.

The similarity in vegetative buds between the two propagule banks was lower (32.0%) than the similarity in seeds. Five species (Petasites frigidus, Oxalis oregana, Oxalis trilliifolia, Rubus ursinus and Stachys cooleyae) accounted for 63% of the vegetative buds in the residual propagule bank. Rubus ursinus dominated the buds in the transported propagule bank (23%).

In spite of the compositional similarity between the two propagule banks, 23 species occurred in only one propagule bank and several other species were much more abundant in one of the propagule banks than in the other. For example, Epilobium paniculatum, Gnaphalium microcephalum, Madia gracilis and Stellaria crispa occurred only in the transported propagule bank. Species occurring only in the residual propagule bank included Polystichum munitum and Viola sempervirens. Petasites frigidus, Stachys cooleyae, Cardamine oblongifolia, Oxalis oregana and trillifolium, Alnus rubra and Galium triflorum were from 5 to 12 times more abundant in the residual soil than in the transported soil. Collomia heterophylla and Conyza canadensis were from 2 to 5 times more abundant in the transported soil than in the residual soil.

Six species dispersed seed into the site (Table 3-8). More than half of the dispersed seed was from one species, *Prunus emarginata*. All species present in the seed traps, except *Vicia*, also occurred in at least one of the two propagule banks.

The dominant predisturbance canopy species, *Alnus rubra*, also bordered the 375 m^2 experimental site. No *Alnus rubra* seed was dispersed into the site during the first growing season, but *Alnus rubra* seed was present in the residual propagule bank.

Table 3-6. Potential contributions of the three propagule sources to the revegetation of the experimental site.

	Residual propagule bank	Transported propagule bank	Dispersed seed
# Seeds/m^2	7793	4484	31
# Buds/m^2	545	247	0
Total/m^2	8538	4731	31

Table 3-7. Average number of seeds and buds of each species in the transported and residual propagule banks.

SPECIES	RESIDUAL PROPAGULE BANK		TRANSPORTED PROPAGULE BANK	
	# seeds/m^2	# buds/m^2	# seeds/m^2	# buds/m^2
TREES				
Acer macrophyllum	0.7	0.0	0.0	0.0
Alnus rubra	131.9	0.0	28.0	0.0
Prunus emarginata	6.1	0.0	0.0	0.0
LOW SHRUBS AND HERBS				
Agrostis exarata	51.4	0.0	140.7	25.0
Anaphalis margaritacea	181.8	0.0	77.7	0.0
Angelica arguta	0.0	0.0	0.0	5.6
Aralia californica	2.3	0.7	18.4	0.0
Aruncus sylvester	95.9	0.0	37.2	0.0
Boykinia elata	3065.1	5.2	1312.5	2.8
Cardamine oligosperma	425.7	0.0	36.8	0.0
Carex deweyana	313.4	0.0	446.6	10.1
Circaea alpina	3.1	23.4	0.0	12.9
Cirsium vulgare	22.2	0.0	15.0	0.0
Collomia heterophylla	19.2	0.0	94.0	0.0
Conyza canadensis	14.6	0.0	31.3	0.0
Deschampsia elongata	12.3	0.0	49.3	0.0
Epilobium angustifolium	2.3	0.0	2.9	5.6
Epilobium glabberrimum	2.3	0.0	2.3	0.0
Epilobium paniculatum	0.0	0.0	4.6	0.0
Epilobium watsonii	548.4	0.0	276.2	0.0
Equisetum arvense	0.0	0.0	0.0	4.3
Festuca arundinoidea	0.0	0.0	0.0	0.7
Festuca subulata	3.8	12.5	0.0	0.0
Fragaria vesca	0.0	0.0	0.0	1.7
Galium triflorum	63.6	1.0	13.0	0.0
Gnaphalium microcephalum	0.0	0.0	17.5	0.0
Hieracium albiflorum	5.4	0.0	3.3	0.0
Hypericum perforatum	147.3	0.0	13.7	0.0
Juncus balticus	0.0	0.0	1.7	0.0
Juncus effusus	374.3	6.6	66.0	0.0
Juncus ensifolius	437.2	7.0	19.2	0.0
Lactuca murialis	10.7	0.0	9.2	0.0
Linnaea borealis	26.8	0.0	1.5	0.0
Lotus purshiana	42.2	0.0	18.8	0.0
Luzula parviflora	23.7	0.0	25.1	0.0

Table 3-7. (Continued).

SPECIES	RESIDUAL PROPAGULE BANK		TRANSPORTED PROPAGULE BANK	
	# seeds/m^2	# buds/m^2	# seeds/m^2	# buds/m^2
Madia gracilis	0.0	0.0	4.2	0.0
Mimulus dentatus	2.3	16.7	2.5	0.0
Mitella ovalis	94.3	7.4	8.4	0.7
Montia sibirica	2.3	0.0	0.0	0.0
Oxalis oregana	5.6	40.3	2.1	11.2
Oxalis trillifolia	9.0	59.0	0.0	0.0
Petasites frigidus	0.0	68.1	0.0	7.3
Poa palustris	48.3	0.0	35.9	7.6
Polystichum munitum	0.0	5.2	0.0	0.0
Ribes bracteosum	53.7	0.0	0.0	0.0
Rubus leucodermis	46.8	0.0	13.0	0.0
Rubus parviflorus	24.5	0.0	2.9	0.9
Rubus ursinus	28.4	59.3	12.1	51.8
Senecio sylvaticus	46.8	0.0	81.9	0.0
Sonchus asper	0.0	0.0	9.2	0.0
Stachys cooleyae	23.0	102.9	0.0	11.2
Stellaria crispa	0.0	0.0	31.8	0.0
Tellima grandiflora	0.0	0.0	3.3	0.0
Typha latifolia	10.7	0.0	0.0	0.0
Tiarella unifoliata	0.0	0.0	0.0	0.5
Tolmiea menziesii	116.6	8.1	21.8	21.4
Trientalis latifolia	0.0	8.5	0.0	0.0
Veronica americana	10.7	0.0	3.3	0.0
Viola sempervirens	0.0	34.6	0.0	0.0
Whipplea modesta	0.0	0.0	2.5	0.0
unknown monocot	1142.1	0.0	50.6	0.0
unknown dead	361.3	28.9	306.6	23.2
Totals	7792.6	544.8	4484.4	247.3

Table 3-8. Composition and average numbers of seeds dispersed into the experimental site between March 25, 1987 and August 25, 1987.

SPECIES	TOTAL # SEEDS	SEEDS/M^2
Boykinia elata	8	5.2
Carex deweyana	2	1.3
Epilobium watsonii	4	2.6
Hypericum perforatum	1	0.6
Prunus emarginata	27	17.5
Vicia sp.	1	0.6
Unknown	4	2.6
Total	47	30.7

DISCUSSION

Disturbance intensity: predictions vs. results

We hypothesized that community revegetation patterns after debris flows result from differences in how scour and deposition affect propagule availability. Based on this hypothesis, we predicted that increased disturbance intensity of both scour and deposition would decrease total cover and vegetative regrowth, but that the effects of intensity on seedling establishment and the relative contribution of seedlings to revegetation would differ with disturbance type (Table 3-1). Our experimental results are consistent with these predictions for total cover and vegetative regrowth. This agreement supports our hypothesis that the effects of scour and deposition on propagule availability is a crucial mechanism in the development of early successional patterns after debris flows.

But these results are only partially consistent with our predictions for seedling establishment and the relative contribution of seedlings to revegetation. There was no significant difference in seedling establishment with increasing intensity of either deposition (matching the prediction) or scour (not matching the prediction). Seedling contributions to revegetation increased with increasing intensity of both deposition (matching the prediction) and scour (not matching the prediction).

We feel that the inability to predict seedling response to scour based on differences in propagule availability can be explained in two ways. Either the predictions were based on insufficient information or our hypothesis is incomplete. We based our predicted responses to deposition on empirical evidence from studies in a variety of communities and following several types of disturbance. The predicted responses to scour were based on assumed propagule banks characteristics and revegetation evidence following a single disturbance type (fire). That is, information on deposition effects was much more extensive than information on scouring effects. Based on our observations and results from this study, we suggest several refinements concerning the effects of scouring on propagule availability.

Two possible explanations for the lack of change in seedling establishment with increased soil removal are that (1) the vertical distribution of seeds in this community differs from most forest and lakeshore communities and (2) germination was stimulated more on scoured plots than on the controls. Seed banks in many forest and lakeshore communities do not extend below 5 cm, with most of the seed concentrated in the upper few cm of soil (Harper 1977, Moore and Wein 1977, Nicholson and Keddy 1983, Pratt et al. 1982, Strickler and Edgertown 1976). Seed banks in other wetland communities, however, extend to depths of 10-20 cm (Leck and Graveline 1979, Leck and Simpson 1987, Kellman 1978, McGraw 1980, Young et al. 1987). Seed bank densities in these communities either gradually decline with depth (Leck and Simpson 1982, Leck and Graveline 1979, van der Walk and Davis 1979) or a concentration of seed occurs between two to four cm (Kellman 1974, Young et al. 1987).

Since very high numbers of seedlings established on the 2.5 and 5 cm scour treatments (304-313 seeds/m^2), we suggest that the seed bank of our study site extended below a depth of 5 cm, with high numbers of seeds to this depth. We interpret this vertical profile as a result of the deep burial (> 2.5 cm) of the seed of several dominant species. The high cover of *Boykinia elata* on both scour treatments (2.8-3.1%) suggests a uniform distribution of seed between 2.5 and 5 cm. The high cover of *Epilobium watsonii*, *Senecio sylvaticus* and *Cirsium vulgare* on 2.5 cm scour (3.6-9.0%) and of *Carex deweyana* on 5 cm (3.1%) suggests that the seed of these species was concentrated just below these depths.

The vertical distributions of bud banks within a community are unstudied. Most studies of the depth distributions of individual species have shown that their vegetative perennating structures extend over a greater range of depths than seed banks. For example, Antos and Zobel (1984) found rhizomes of *Achlys triphylla* between depths of 1.4-20.0 cm and the rhizomes of Tiarella unifoliata between 3.4-8 cm. (These species, although present in the predisturbance community were not abundant.) Because the number of vegetative sprouts decreased from 141.0/m^2 on the controls and 128.8m^2 on 2.5 cm scour to only 46.5/m^2 on 5 cm scour, we suggest that the decrease in vegetative perennating structures with depth was sharp below 2.5 cm in this community. This sharp decrease would explain the unexpected increase with scour of the relative contribution of seedlings to revegetation.

Factors other than differences in propagule availability could also explain the inconsistencies between our predicted responses and the experimental results. Since there were no significant differences in mortality on any of the experimental treatments, these explanations center on factors affecting the emergence and initial establishment of individuals.

We suggest that germination was stimulated more on scour than on the controls. The less rapid reestablishment of a vegetative cover on scoured plots exposed seeds to the high light intensities and increased temperature fluctuations necessary for germination (Bazzaz 1983, Thompson et al. 1977). The scouring action itself may have stimulated germination through scarification (Mayer and Poljakoff-Mayber 1982). In addition, there was less competition from vegetative sprouts during the establishment phase as scour drastically reduced vegetative regrowth.

The density of buried seed on our site was high (7793 seeds/m^2). Although scour undoubtedly removed some seed, there were abundant seed reserves left at depths of 2.5 and 5 cm. This seed was able to germinate and establish because of favorable conditions on the scour treatments.

Several (Bazzaz 1983, Grime 1977, Runkle 1985, Sousa 1984) suggest that seedling establishment on disturbed sites increases in importance with disturbance intensity, because of the increased success of seedling establishment from dispersed seed. In our study, the contribution of dispersed seed to site revegetation was very low. Since dispersal contributed only 31 seeds/m^2 to revegetation and the two propagule banks contributed between 4484-7793 seeds/m^2, most seedlings probably originated from one of the two propagule banks and not from dispersed seed. Seedlings increased in importance relative to vegetative sprouts with scour because of increased importance of establishment from the on-site and disturbance-transported seed sources. The increased importance of these two seed sources to revegetation resulted from the lack of change in seedling establishment combined with the dramatic decrease in vegetative regrowth.

Disturbance can produce both favorable and unfavorable conditions for the germination of seeds and buds (Bazzaz

1983, Canhan and Marks 1985, Leakey et al. 1977a and b, Mayer and Poljakoff-Mayber 1982, Sousa 1984). Both seedlings and vegetative sprouts respond favorably to the temporary release from competition and the increased resource availability (Bazzaz 1983). Disturbance can also cause physical damage to the preexisting vegetation, thereby decreasing the growth and survival of individuals. Since vegetative cover was 50% lower on 2.5 cm scour where large numbers of vegetative buds remained, we suggest that not all species present on the site were able to produce high cover after the severing, fragmentation or other damage to their vegetative perennating structures. Such individualistic responses to rhizome damage have been experimentally demonstrated (Hakansson and Wallgren 1972, Mann and Cavers 1979, Schmid and Bazzaz 1987, Sobey and Barkhouse 1977). Some species respond poorly if their rhizomes are severed in the early spring (Hakansson and Wallgren 1972, Mann and Cavers 1979), while the response of other species to rhizome damage may depend on the degree of clonal integration (Schmid and Bazzaz 1987) or rhizome growth rate (Sobey and Barkhouse 1977).

Two important points emerge from these alternative explanations: (1) the vertical distribution of propagules is not constant among species or communities and (2) an understanding of how species respond to disturbance may be crucial to understanding revegetation mechanisms. Since other studies also suggest that vertical distributions of propagules can differ within a single community (Archibold 1981, Thompson 1986), between similar communities (Rowe 1983, van der Walk and Davis 1979, Watt 1944) and through time (Granstrom 1982, Harper 1977, Young et al. 1987), we feel that further research on the factors contributing to differences in propagule availability among communities is necessary to understand the mechanisms of revegetation following disturbance.

Species responses

Although only 38% of the species responded to the experimental treatments, these species contributed 59% of the cover and the responses of these species varied considerably. Three explanations for the differences in species responses to the experimental treatments are: (1) differences in propagule availability between the two propagule banks, (2) propagule removal by scour and (3) species-specific responses to disturbance as a result of differences in physiological tolerances or morphological characteristics.

Differences in the establishment of six species correspond to differences in propagule availability between the residual and disturbance-transported propagule banks. _Epilobium paniculatum_, _Gnaphalium microcephalum_, _Madia gracilis_ and _Stellaria crispa_ occurred only in the transported propagule bank, and *Collomia heterophylla* and *Conyza canadensis* were more abundant in the transported propagule bank than in the residual propagule bank. All six of these species established almost exclusively on deposits, with significantly higher cover on these treatments. Since most of these species, except for *Stellaria crispa*, are important early successional species after clearcut and burns (Halpern 1987), we feel the seed for these species probably came from the upland clear cut soil added to the depositional mixture.

Oxalis trilliifolia, *Oxalis oregana*, and *Galium triflorum* propagules were more abundant in the residual soil than in the transported soil. These species established mostly on the control and 2.5 cm scour treatments. Their low establishment on the deposits probably resulted from a lack of propagules in the transported propagule bank and an inability of the somewhat succulent vegetative shoots establishing from propagules in the residual soil to penetrate even shallow deposits.

The restriction of *Galium triflorum* to the controls and the low cover of the two species of *Oxalis* on deep scour can best be explained by the removal of propagules by scour. *Galium triflorum*, which established both by seed and vegetative means, had high cover only on the controls. We observed its rhizomes running along the soil surface and suggest that its seed may also be buried at shallow depths.

Scour probably removed both Galium triflorum seed and rhizomes. We also observed exposed Oxalis rhizomes on 2.5 cm scour, but since the cover of these two species did not decrease much on this treatment, we suggest the two Oxalis species are tolerant of some rhizome exposure or damage. We interpret the strong decrease in Oxalis cover with further scour as a result of rhizome removal.

The high cover of Alnus rubra on 2.5 cm scour is somewhat difficult to interpret. The seed was available in the residual soil and both the control and scour treatments provided the necessary requirements for alder germination--high light, exposed mineral soil and adequate moisture--(U.S. Forest Service 1948, D. Hibbs, personal communication)--but alder established predominantly on the 2.5 cm scour. This is surprising as these results suggest a concentration of Alnus rubra seed just below 2.5 cm. Yet, the short-lived alder seed is dispersed in late November and December (U.S. Forest Service 1948) and does not usually become incorporated into a persistent seed bank, particularly to a depth of 2.5 cm (D. Hibbs, personal communication). It is possible that some of the recently-dispersed seed was buried by fluvial deposition during a winter storm and that very shallowly buried seed was removed by the raking of the litter during the experimental set-up. The low cover of Alnus rubra on the depositional treatments probably resulted because there were few propagules in the transported soil and the timing of treatment application occurred after most of the previous year's production of seed was dispersed from the adjacent canopy.

Recent fluvial deposition could also explain the establishment of Cirsium vulgare on 2.5 cm scour, as others (Pratt et al 1982, Strickler and Edgerton 1976) report the seed of this species only at very shallow depths.

Petasites frigidus and Polystichum munitum were more abundant in the residual soil than in the transported soil. Since they established more readily on deposits than on scour, their differential establishment was not a result of differential propagule availability, but can be better explained as a result of physiological intolerances to scour and morphological adaptations for penetrating deposits.

Three observations of Petasites frigidus can explain its response to these experimental treatments: (1) since Petasites rhizomes were visible on scour, propagules were available for regrowth on these treatments; (2) there were dramatic differences in vigor between individuals establishing from visible fragments (small, distorted, anthocyanic leaves) and individuals known to originate from the residual propagule bank (large, symmetric, green leaves); and (3) Petasites' early spring growth form was compact. We suggest that Petasites was not able to produce high cover on scour because it was intolerant of rhizome exposure and damage. We also suggest that the most vigorous sprouts on the depositional treatments originated from the residual propagule bank. Petasites frigidus commonly forms large monotypic stands after clear cutting of riparian communities as it can easily outcompete other species for light (Campbell and Franklin 1979). The high cover of Petasites on the deposits probably resulted because its compact early spring growth form allowed easy penetration of deposits and the increased light stimulated vigorous growth.

Zobel and Antos (1987) noted that while normal aerial shoots of many herbaceous species are tall enough to reach the surface of deposits, many fail to grow through deposits. They suggest that most aerial shoots are poorly adapted to grow through soil. Polystichum munitum leaves are commonly longer than 20 cm (Hitchcock et al. 1964), but this species was unable to penetrate 10 cm deposits. Perhaps its slow growth subjected leaves to the deleterious effects of reduced gas exchange (Zobel and Antos 1987) longer than on the 5 cm deposits which it could penetrate. Elongation of shoots through the additional 5 cm of deposits could have also caused excessive tearing and abrasion of the leaf surface preventing emergence with increased burial depth.

Propagule availability, physiological tolerances to disturbance and germination requirements can also explain the lack of significant responses of many species to the treatments. The composition and abundance of seeds was very similar between the two propagule banks. Three of the most important seedling species establishing on our site, *Epilobium watsonii*, *Carex dewyana* and *Boykinia elata* dominated both propagule banks. In addition, the abundance of *Senecio sylvaticus* was similar between the two propagule banks. The seed of all four species appeared to be deeply buried in the soil. These four species probably also have similar germination requirements, as the germination of both early successional species (*Epilobium watsonii* and *Senecio sylvaticus*) and late seral streamside species (*Carex dewyana* and *Boykinia elata*) is stimulated by fluctuating temperatures in a high light environment accompanied by increased soil aeration (Bazzaz 1983, Thompson et al. 1977). We interpret the lack of treatment response of these important seedling species as a result of uniform propagule availability between scour and depositional treatments, deeply buried seed that was not removed by scour and similarity in germination requirements.

Stachys cooleyae established equally well on scour and deposition, but it was more abundant in the residual soil. Therefore, its lack of treatment response cannot be explained by uniform propagule availability. *Stachys* cooleyae, like Petasites frigidus, is a vigorous perennial able to successfully outcompete even Petasites for light (Campbell and Franklin 1979). Although we observed Stachys regenerating from vegetative fragments, we feel that much of its vigorous growth originated from vegetative buds in the residual soil. This robust perennial was able to penetrate even the deepest deposits and also readily established on scour. Since its rhizomes were visible on the scour treatments, its fairly high cover on scour shows a tolerance of this species to rhizome exposure or damage. We suggest that Stachys cooleyae's lack of response to the experimental treatments resulted from morphological adaptations allowing deposit penetration, physiological tolerance to the potentially detrimental effects of scour and deposition an ability to increase cover with the increased light environment associated with the creation of a gap.

Until July, the cover of Aruncus sylvester was very high only on the controls. Severe browsing damage by deer in July virtually eliminated this species from the control plots. The non-significant response of Aruncus sylvester to the experimental treatments probably resulted from differential herbivory of the robust individuals on the controls.

Species influences on community patterns

The overall lack of pattern to seedling establishment reflected the individual species responses to the experimental disturbances. Several dominant seedling species (Carex dewyana, Boykinia elata, Epilobium watsonii) were ubiquitous and showed no significant differences in cover among the treatments. Other seedling species responded to the treatments, but their cover often was low. For example, the cover of Stellaria crispa, Gnaphalium microcephalum and Epilobium paniculatum was significantly higher on one or more of the depositional treatments, but none of these species had more than 0.9% cover. Five seedling species providing higher cover did show strong responses to the treatments. The increased cover of Madia gracilis, Collomia heterophylla and Conyza canadensis on the depositional treatments was offset, however, by the increased cover of Alnus rubra and Cirsium vulgare on scour. This resulted in an overall lack of patterns to seedling establishment even though individual species showed strong treatment responses.

Whereas seedling establishment was variable and showed no overall treatment response, the decrease in total cover with increasing disturbance intensity paralleled the decrease in vegetative regrowth. Thus, the decrease in total cover can best be explained as a consequence of the effects of disturbance on vegetative regrowth. The decreased vegetative regrowth can in turn be explained by the effects of disturbance on a few species. The effects of intensity on these species changed according to disturbance type. The cover of the Oxalis species decreased much more rapidly with deposition than with scour. Conversely, the cover of Petasites frigidus and Polystichum munitum decreased rapidly with scour, but not with low depths of deposition. Galium triflorum decreased in response to any disturbance, while Stachys cooleyae and Rubus ursinus showed little difference in cover among the treatments. Thus, although these species responded differently to deposition and scour, decreased cover of a few resprouting species on deposition was offset by a decreased cover of other on scour. This resulted in similar decreases in both vegetative regrowth and total cover as the intensity of both disturbance types increased.

Conclusions

Disturbance intensity was very important in determining initial revegetation through effects on vegetative regrowth. Seedling establishment was more variable than vegetative regrowth and showed no significant response to the treatments. Seedling contributions to revegetation increased with increasing disturbance intensity mainly because of the dramatic decrease in vegetative regrowth.

The responses of a few species to disturbance type and intensity affected overall community patterns. Propagule availability, germination requirements and abilities to emerge through deposits or tolerate rhizome exposure affected the responses of these species.

Our hypothesis that early successional patterns result from differences in how scour and deposition affect propagule availability allowed us to make accurate predictions of some early successional patterns and enabled us to interpret the responses and lack of responses of some species. But our hypothesis did not allow us to make accurate predictions of seedling responses to scour and was insufficient to explain the observed patterns of many species. We suggest that because some predictions were not consistent with our results, further research is needed on the factors influencing propagule availability within a community. We also suggest that our hypothesis is incomplete without consideration of (1) the factors influencing species responses to disturbance and (2) how species-specific responses influence revegetation.

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Chapter 4

CONCLUSIONS

In this thesis I used an observational study to generate hypotheses of the mechanisms through which debris flows affected the revegetation of riparian communities. I followed this preliminary descriptive study with a field experiment in which I simulated the effects of a debris flow. In both studies, I examined the roles of seedlings and vegetative sprouts, propagule sources and disturbance characteristics in early riparian succession.

Direct comparisons of the experimental and observational results show that the cover values and densities were much higher on the simulated debris flow treatments than on the actual debris flows (Tables 2-5 and 3-2). For example, total cover on the debris flow low intensity scour surface was much less (14.8%) than the cover (58.9%) on the lowest intensity experimental scour treatment--2.5 cm scour. The highest densities of seedlings (46/m^2) and vegetative sprouts (28/m^2) on the three debris flows were also much less than the lowest densities of seedlings (168/m^2) and vegetative sprouts (42/m^2) on the simulated debris flow treatments. The differences in cover and densities of individuals between the two studies probably occurred because the range of depths used in the simulated debris flow treatments represented hypothesized thresholds of response to increasing intensity of scour and deposition, and not the full range of intensities actually occurring on debris flow sites. The range of scour and depositional depths on debris flows generally exceed the range of depths used in my experimental study (D. Harr, personal communication, F.J. Swanson, personal communication).

Even though the magnitude of the revegetation response differed between my observational and experimental studies, there were many similarities in early successional patterns between the two studies. Both seedlings and vegetative sprouts contributed to the revegetation of the debris flows and the simulated debris flow treatments. Vegetative regrowth dominated cover, but seedlings were more abundant than vegetative sprouts. Observations on the debris flows suggested that the establishment of individuals occurred from three sources: dispersed seed, the disturbance-transported propagule bank and the residual propagule bank. The experimental results confirmed that all three propagule sources could contribute to debris flow revegetation.

Variation in the intensity of scour and deposition on the three debris flow sites produced variation in early successional patterns. I hypothesized that differences in these patterns resulted from differences in how scour and deposition affected propagule availability. I used this hypothesis to develop predictions of effects of increasing intensity of scour and deposition on total cover, seedling establishment and vegetative regrowth. Most predictions were consistent with the experimental results. Thus, the results of both the observational and experimental studies suggest similar mechanisms of revegetation. However, some of the experimental results could not be explained solely on the basis of propagule availability as they also reflected individualistic species responses to disturbance.

I conclude from this research that: (1) models of early riparian succession after debris flows need to consider variation in disturbance characteristics, propagule availability and individualistic species responses to disturbance and (2) further research on the mechanisms of revegetation is necessary.

I propose several questions for further research. Does the exposure of riparian species to low intensity, recurrent flood disturbance lead to an ability to reestablish after catastrophic disturbance as many (for example Hupp 1983b, Hupp and Osterkamp 1985) suggest? The life history strategies that allow species to reestablish following recurrent disturbance in other communities (resprouting from below-ground perennating structures, incorporation into a large persistent seed bank) can also allow reestablishment following catastrophic disturbance (Fox and Fox 1986, Grime 1977, Young et al. 1987). The vigorous resprouting of a few species and a large persistent seed bank allowed the rapid reestablishment of cover on my experimental debris flow. Are these two adaptations common to riparian communities following different types and intensities of disturbances?

What determines the physiological tolerances of the riparian species dominating early succession? For example, why can Stachys cooleyae tolerate scour, but Petasites frigidus can not? How well do the dominant species respond to rhizome severing or fragmentation? What factors contribute to species' abilities to penetrate deposits? Little is known about how individual riparian species respond to disturbance, yet these responses may determine how a community recovers from disturbance.

How well do my experimental results generalize to other riparian communities and other disturbances? This question is particularly important in light of the strong influence of vegetation type on the revegetation of my observational sites. Would another experimental debris flow produce the same patterns if it were done on a clear-cut or old-growth stream?

Finally, how does the initial composition of a site determine future successional change? Roberts (1987) suggests that succession is not an unvarying process developing towards a climax, but rather a change away from seral conditions, with the trajectory of this change originally controlled by the pioneer species. This suggestion is important since others (Keeley and Keely 1984, Kellman 1974, Young et al. 1987) note that the species colonizing a site in the first year after disturbance may control further recruitment of individuals. The main source of propagules for recruitment can change from either the on-site propagule bank (Keeley and Keeley 1984, Young et al. 1987) or off-site dispersal (Kellman 1974) to seed input from the original colonizers. Observations in the second year of my experiment also show a shift in the sources of establishment. The main sources of new individuals in the first year were the two propagule banks. In year 2, the main source appears to have shifted to seed produced on-site by individuals that established in the first year. This autochonous seed rain may allow two important colonizers, Petasites frigidus and Epilobium watsonii, to increase their dominance. The autochonous seed rain may also reduce differences in species establishment on the experimental treatments. For example, Madia gracilis established only on deposits in the first year following the simulated disturbance because most of its seed was in the transported propagule bank. It flowered profusely last August, producing abundant seed and Madia seedlings established on all treatments this spring.

Continued monitoring of my experimental debris flow treatments should provide some answers to the questions I have proposed, but further research is needed on the mechanisms contributing to revegetation of different communities and following different disturbances.

Chapter 5

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Chapter 6

APPENDIX

Table 6-1. Species present on the experimental site prior to manipulation based on relevés made in October, 1986 and March, 1987.

TREES

Acer macrophyllum
Alnus rubra
Pseudotsuga menziesii
Thuja plicata
Tsuga heterophylla

SHRUBS
Acer circinatum
Cornus nuttalii
Rhamnus purshiana
Rubus ursinus
Vaccinium parviflora

HERBS

Achlys triphylla
Adiantum pedatum
Anemone lyalli
Aralia californica
Aruncus sylvester
Asarum caudatum
Athyrium felix-femina
Blechnum spicant
Boykinia elata
Carex deweyana
Ciraea alpina
Disporum hookeri
Equisetum sp.
Festuca subulata
Galium triflorum
Gaultheria shallon
Lactuca murialis
Mitella ovalis
Montia sibirica
Osmorhiza purpureum
Oxalis oregana
Oxalis trilliifolia
Petasites frigidus
Polystichum munitum
Pteridium aquilifolium
Stachys cooleyae
Synthris reniformis
Tiarella unifoliata
Tolmiea menziesii
Trientalis latifolia
Trillium ovatum
Trisetum canescens
Vancouveria hexandra
Viola sempervirens

Table 6-2. Mean cover (%) of all vascular plant species that established on each of the experimental treatments after adjustment for the covariate of topographic position. A 0 cover value indicates the species did not occur on the treatment. The number of plots on which the species established (FREQ) is listed. The means through which each species was observed to establish are listed in parentheses after the species name (V=vegetative means, S=by seed or spore). S_D=average standard deviation of the differences between the adjusted means (Snedecor and Cochran 1967). *=P<.05, **=P<.01, ***=P<.001, NS=not significant.

SPECIES	CONTROL	SCOUR		DEPOSIT			FREQ
		2.5cm	5cm	5cm	10cm	19cm	
TREES AND TALL SHRUBS							
Acer circinatum (S)	0.0	0.5	0.0	0.0	0.0	0.0	1
Acer macrophyllum (V)	0.0	0.0	0.0	2.6	0.0	0.0	1
Alnus rubra (S)	0.4	1.2	0.3	0.1	0.1	0.1	22
Prunus emarginata (S)	0.2	0.3	0.4	0.4	0.4	0.3	37
Salix sitchensis (S)	0.0	0.5	0.6	0.0	<.1	<.1	4
Taxus brevifolia (S)	0.5	0.0	0.0	0.0	0.0	0.0	1
LOW SHRUBS AND HERBS							
Adiantum pedatum (S,V)	2.0	0.6	0.3	0.9	0.5	0.0	12
Agrostis exarata (S,V)	0.6	0.9	0.5	1.6	1.4	2.1	40
Anaphalis margaritacea (S)	0.5	0.6	0.2	0.3	0.8	0.8	17
Angelica arguta (S,V)	6.1	1.2	0.0	0.0	0.0	0.0	3
Aralia californica (S,V)	0.0	0.0	6.8	0.0	0.0	0.0	3
Aruncus sylvester (S,V)	4.8	2.8	1.9	2.1	<.1	0.6	24
Athyrium filix-femina (V)	<.1	1.5	<.1	0.3	0.1	0.0	4
Blechnum spicant (V)	1.0	0.0	0.1	0.5	0.0	0.0	3
Boykinia elata (S,V)	1.0	3.1	2.8	1.5	1.0	2.0	39
Bromus vulgaris (V)	0.1	0.0	0.0	0.0	0.0	0.0	2
Cardamine oligosperma (S)	0.0	0.0	0.0	0.0	0.1	0.2	5
Carex amplifolia (V)	0.0	0.0	0.0	0.0	0.3	1.0	3
Carex deweyana (S,V)	1.4	1.7	3.1	1.0	1.0	0.9	42
Chrysanthemem leucathum (S)	0.0	0.0	0.0	0.1	0.0	<.1	3
Circaea alpina (S,V)	0.0	0.0	0.0	1.0	0.0	0.3	3
Cirsium sp. (S)	0.0	<.1	0.1	1.0	0.0	0.3	5
Cirsium vulgare (S)	2.0	6.0	<.1	0.3	0.8	1.3	18
Collomia heterophylla (S)	<.1	0.0	1.7	1.8	2.7	1.7	28
Conyza canadensis (S)	0.0	<.1	0.2	0.7	1.0	3.1	22
Deschampsia elongata (S)	<.1	0.1	0.1	0.2	0.2	0.2	13
Disporum hookeri (V)	0.0	0.2	0.0	<.1	0.0	0.0	3
Epilobium angustifolium (V)	0.0	0.0	0.0	<.1	0.1	0.0	3

Table 6-2. (Continued).

SPECIES	CONTROL	SCOUR		DEPOSIT			
		2.5cm	5cm	5cm	10cm	19cm	FREQ
Epilobium minutum (S)	0.0	0.0	0.0	0.0	.1	0.0	1
Epilobium paniculatum (S)	0.0	0.0	0.0	<.1	0.2	0.9	10
Epilobium watsonii (S,V)	1.1	8.9	3.6	1.5	3.5	3.4	52
Equisetum sp. (S,V)	<.1	0.0	0.0	0.3	0.2	0.6	11
Festuca arundinoidea (S,V)	0.0	0.0	0.0	0.2	0.2	<.1	5
Festuca subulata (V)	0.6	0.0	0.0	0.0	0.0	0.0	2
Galium triflorum (S,V)	3.4	0.6	0.5	0.2	0.1	0.1	26
Gnaphalium microcephalum (S)	0.0	0.0	0.0	0.1	0.0	0.5	5
Hieracium albiflorum (S)	0.0	0.0	0.0	0.0	0.0	0.2	1
Holcus lanatus (S,V)	0.0	0.0	0.0	0.1	1.3	0.7	8
Hypericum perforatum (S)	1.1	0.7	0.8	0.1	0.1	0.1	23
Hypochaeris radicata (S)	0.0	0.0	0.0	0.6	0.5	0.0	4
Juncus effusus (S,V)	0.1	0.2	0.6	0.1	<.1	0.4	17
Juncus ensifolius (S,V)	<.1	0.3	0.4	<.1	0.1	0.1	15
Lactuca murialis (S)	0.7	0.2	0.0	0.0	0.4	0.1	10
Lotus purshiana (S)	0.2	0.6	0.0	1.3	0.3	1.5	23
Luzula parviflora (S,V)	0.7	0.7	0.9	0.3	<.1	0.1	21
Madia gracilis (S)	0.0	0.0	0.0	0.5	0.7	2.4	8
Mitella ovalis (S,V)	0.4	0.3	0.2	0.1	<.1	0.1	13
Montia sibirica (S,V)	0.9	0.0	0.0	0.2	0.1	<.1	8
Oxalis oregana and trillifolia (S,V)	18.2	12.1	1.9	6.0	0.5	<.1	21
Petasites frigidus (V)	31.3	12.6	5.9	28.2	26.4	18.8	46
Plantago lanceolata (S)	0.0	0.0	0.0	0.0	0.2	0.0	1
Poa palustris (S,V)	0.0	0.0	0.0	0.0	0.2	0.6	3
Polygonum minimum (S)	0.0	0.0	0.0	<.1	0.0	<.1	2
Polystichum munitum (V)	4.4	0.0	<.1	7.7	0.0	0.0	7
Ribes bracteosum (S)	0.0	0.0	0.0	0.0	<.1	0.0	1
Rubus leucodermis (S,V)	0.0	0.2	0.0	0.0	0.0	0.0	1
Rubus ursinus (S,V)	3.2	2.1	1.3	1.8	0.6	0.4	32
Senecio sylvaticus (S)	1.1	3.6	0.2	0.2	2.0	1.3	31
Sonchus asper (S)	0.0	0.5	0.0	0.0	0.0	<.1	2
Stachys cooleyae (S,V)	4.6	6.7	2.6	5.6	4.7	4.8	18
Stellaria crispa (S)	0.0	<.1	0.0	<.1	0.3	0.1	9
Tiarella unifoliata (S,V)	0.0	0.3	0.1	0.2	0.0	0.0	3
Tolmiea menziesii (S,V)	4.2	0.9	0.4	0.7	0.6	0.9	22
Trientalis latifolia (V)	1.2	0.0	0.0	<.1	0.1	0.2	7
Trifolium pratense (S)	0.0	0.0	0.0	0.0	0.0	0.5	1
Vancouveria hexandra (V)	0.0	0.2	0.0	0.0	0.0	0.0	1
Veronica americana (S)	0.0	0.1	0.0	<.1	0.0	0.0	3
Viola glabella (V)	<.1	0.3	3.2	<.1	0.0	0.0	4
Viola sempervirens (V)	0.1	0.0	0.0	0.0	0.0	0.0	1
unknown dicot	<.1	<.1	0.2	0.4	0.2	0.3	22
unknown monocot	0.1	0.2	0.0	<.1	0.1	<.1	7