

Initial Establishment of Riparian Vegetation after Disturbance by Debris Flows in Oregon

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ABSTRACT.—Three debris flows in the western Oregon Cascades were sampled near the end of the first growing season following disturbance. Vegetative regrowth accounted for 77% of the initial re-establishment of cover, but 67% of the individuals were seedlings. Surface deposit characteristics and intensity of scour were the most important influences on debris flow revegetation. Total cover (15%) and vegetative regrowth (14% cover, 28 shoots/m²) were highest on light intensity scour. Seedling establishment was highest on gravel and fine deposits (2–3% cover, 37–46 seedlings/m²). In contrast to previous studies which highlighted the role of seedlings, revegetation patterns in these debris flows were determined by the response of both vegetative sprouts and seedlings.

INTRODUCTION

Disturbance is a frequent event in most ecosystems (White, 1979; Sousa, 1984; Pickett and White, 1985), including riparian habitats. Initial revegetation patterns after disturbance are important because they determine how quickly soil and nutrient losses are reduced (Marks and Bormann, 1972) and because early revegetation patterns can have long-term effects on community dynamics (Glenn-Lewin, 1980; Franklin, 1981; Humphrey, 1984; McCune and Allen, 1985). Although patterns of early succession are well-documented, mechanisms—especially the role of propagule sources and means of establishment—are poorly understood. Plant successional theory in general concentrates on the importance of seed dispersal following disturbance (*see* Egler, 1954; Connell and Slatyer, 1977; Connell, 1978). Yet studies of early succession after fire show that vegetative regrowth and seedling establishment from onsite propagule sources often contribute more to initial revegetation than dispersal from external sources (Archibold, 1978; Hopkins and Graham, 1984; Stickney, 1986; Tsuyuzaki, 1987; Young *et al.*, 1987).

Debris flows are a major cause of disturbance to riparian vegetation in humid mountainous areas (Swanston, 1978; Veblen and Ashton, 1978). They can be very erosive and intense disturbances, exerting impact forces up to 4000 newtons/m² and scouring all soil to bedrock (Costa, 1984). Yet debris flows sometimes only shear off the aboveground vegetation without removing any substrate or propagules (Costa, 1984), and vegetative resprouting from transported fragments within deposits can dominate early succession on mass movement sites (Adams *et al.*, 1987). Debris flows can also 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 mass movement sites (Adams and Sidle, 1986; Miles and Swanson, 1986). This variation in scour and deposition produces variability in cover and species composition (Veblen and Ashton, 1978; Hull and Scott, 1982; Miles and Swanson, 1986; Smith *et al.*, 1986). The composition of the adjacent undisturbed vegetation can also influence revegetation patterns after debris flows (Hull and Scott, 1982; Hupp, 1983; Miles and Swanson, 1986; Smith *et al.*, 1986).

Some (Veblen and Ashton, 1978; Hull and Scott, 1982) hypothesize that differences in

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revegetation patterns after debris flows result from differences in the composition and density of seed dispersed from the adjacent vegetation and creation of different safe sites by scour and deposition for seedling establishment. However, these hypotheses have not been tested with studies of initial debris flow succession. Because riparian species distribution corresponds to topographic changes with distance from the stream (Campbell and Franklin, 1979), revegetation patterns after debris flows may also differ with topographic position.

In this study, we documented initial revegetation patterns after debris flows. Our specific objectives were to determine the relative contributions of seedlings and vegetative sprouts to initial revegetation, to examine differences in revegetation patterns on areas of scour and deposition and to examine the influence of the composition of the adjacent undisturbed vegetation and topographic position relative to the stream on revegetation following debris flows.

STUDY AREA

This study was conducted in the W-central Cascade Mountains near the town of Blue River, Oregon. 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 soil mass movements. These mass movements occur particularly in the lower elevation forests (below 850 m), which are underlain by hydrothermally altered volcanoclastic rocks (Swanson and James, 1975).

We selected as study sites three first-order streams experiencing debris flows in February 1986. 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.

WS10 faced SW and ranged in elevation from 463–610 m. Before it was clear-cut in 1975, a 450-yr-old stand of *Pseudotsuga menziesii* (nomenclature according to Hitchcock and Cronquist, 1973) dominated the site. The canopy of the riparian community also included individuals of *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 clear-cutting, *Acer circinatum* and *Epilobium angustifolium* dominated the site. The debris flow affected 220 m of stream length and averaged 8 m in width.

The Mack Creek Road site had a NW exposure and ranged in elevation from 561–732 m. The length of the flow was 480 m, and its average width was 15 m. We identified three distinct reaches on the site, each with different land-use histories. The upper reach where the debris flow originated was clear-cut in 1982 (V. Puleo, pers. comm.). Because the stream was close to the boundary of the harvest unit, an *Acer circinatum*-dominated clear-cut bordered this reach on only the western side. A *Tsuga heterophylla*-*Thuja plicata*/*Acer circinatum* forest bordered the eastern 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 yr ago (F. J. Swanson, pers. comm.) and had a mixed hardwood stand of *Alnus rubra*, *Populus trichocarpa*, *P. tremuloides*, *Pseudotsuga menziesii* and *Acer macrophyllum*.

Zeolite Creek had a NW exposure for the majority of the length sampled, but two of the upper sampling transects were on a SW-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. Debris flow width averaged 10 m. 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, pers. comm.). The upper 130 m of the debris flow path was clear-cut in 1976. An *Acer circinatum*-dominated community bordered this reach.

METHODS

Sampling.—On each site, we placed 20–25 transects perpendicular to the stream. We sampled the portion of the debris flow in which the disturbance removed most of the aboveground 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 20 by 50 cm plots at 2-m intervals along each transect and recorded total cover, species cover and the cover and number of seedlings and vegetative sprouts. Cover was estimated to the nearest percent. We defined total cover as the percentage of ground obscured by vegetation. We summed the cover of all individuals establishing by seed or by vegetative means in order 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: (a) it was an annual species; (b) cotyledons were present, or (c) 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. The remaining few unidentifiable seedlings were tallied as unknowns.

Each plot was classified into one of eight disturbance surface types: (1) light scour: all aboveground vegetation and litter removed with the residual mineral soil left intact; (2) moderate scour: all aboveground vegetation and at least some of the residual mineral soil removed; (3) intense scour: all above- and belowground vegetation and substrate removed to the underlying bedrock; (4) fine deposits: all material less than or equal to 4 mm in diam; (5) gravel deposits: inorganic material between 4 and 64 mm in diam; (6) cobble deposits: inorganic material with a diam larger than 64 mm; (7) debris deposits: deposits of bark, branches, stumps, logs and downed trees or shrubs; and (8) unstable: regardless of scour or deposition, the remaining or newly deposited soil unstable due to secondary effects of slumping, surface erosion or redeposition of substrate.

To describe the topographic position of each plot 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 included 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

TABLE 1.—Percentages of scour and depositional surfaces on each of the three study sites. n = number of plots on each site

Surface	WS10 n = 99 (%)	MACK CR RD n = 197 (%)	ZEOLITE CR n = 102 (%)
Light scour	33	4	13
Moderate scour	24	2	9
Intense scour	6	1	18
Total scour	63	7	40
Fine deposits	8	60	15
Gravel deposits	0	23	23
Rock deposits	0	2	8
Debris deposits	20	8	13
Total deposition	28	93	59
Unstable surfaces	9	0	1

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 the type of disturbance surface, the predisturbance vegetation and the topographic position relative to the stream. We also used analysis of variance to examine differences in revegetation patterns among the three study sites. Further exploration of significant relationships was through Fisher's Protected Least Significant Difference (FPLSD) analysis of means (Steel and Torrie, 1980). We used the two-tailed t-test to examine differences between seedling and vegetative sprout establishment. Regression models identified factors which significantly reduced variation in revegetation patterns of total cover, seedling establishment and vegetative regrowth. Regression models were developed for each site and for all sites combined. The data were first log-transformed, as this particular transformation was best at stabilizing variances and obtaining normal distributions of errors.

RESULTS

Differences among study sites.—Large differences occurred among the sites in the frequency of the three scour surfaces and in the deposits of both fine material and gravel (Table 1).

Although total cover did not differ significantly among the three sites (ANOVA, $P > 0.05$), the cover and density of vegetative sprouts and seedlings differed significantly (ANOVA, $P < 0.0005$ for vegetative sprout and seedling cover and $P < 0.0001$ for numbers of vegetative sprouts and seedlings, Table 2). Vegetative regrowth was greatest in the scour-dominated WS10 (10% cover, 28 sprouts/m²). Seedling density was greatest (FPLSD analysis of means, $P < 0.05$) on the deposition-dominated Mack Creek Road (44 seedlings/m²) but the seedling cover was higher on Mack Creek Road (2%) and Zeolite Creek (3%).

Overall, vegetative sprout cover was greater than seedling cover (two-tailed t-test, $P < 0.05$) and accounted for 77% of the initial re-establishment of cover. Seedling density was greater than vegetative sprout density and 67% of the individuals establishing at the end of the 1st year were seedlings.

TABLE 2.—Percent cover (C) and density (D) of seedlings (S) and vegetative sprouts (SPR) within each site and for all sites combined (mean \pm standard error). Means with different letters within a column are significantly different at $P < 0.05$ (FPLSD analysis of means). TC = total cover, n = number of plots on each site

	TC (%)	SPR C (%)	S C (%)	SPR D (no./m ²)	S D (no./m ²)
WS10 (n = 99)	11 \pm 1.7 ^a	10 \pm 2.0 ^a	1 \pm 0.3 ^b	28 \pm 4.2 ^a	11 \pm 2.3 ^c
MACK CR RD (n = 197)	7 \pm 0.9 ^a	5 \pm 0.9 ^b	2 \pm 0.2 ^a	9 \pm 1.1 ^b	44 \pm 4.4 ^a
ZEOLITE CR (n = 102)	8 \pm 1.3 ^a	5 \pm 1.3 ^b	3 \pm 0.7 ^a	9 \pm 1.4 ^b	15 \pm 2.0 ^b
All sites (n = 398)	8 \pm 0.7	6 \pm 0.7	2 \pm 0.2	14 \pm 1.2	28 \pm 2.2
ANOVA (2 df)	P > 0.05	P < 0.0005	P < 0.0005	P < 0.0001	P < 0.0001

Species composition.—Thirty species established primarily as vegetative sprouts, including the dominants, *Petasites frigidus*, *Aralia californica* and *Epilobium angustifolium*. Seventeen species, such as *Epilobium watsonii*, *Cirsium vulgare* and *Alnus rubra*, established predominantly as seedlings, and 10 species, including *Agrostis alba* and *Boykinia elata*, were equally abundant as seedlings and vegetative sprouts (see Gecy, 1988, for further details).

Herbaceous species dominated initial revegetation, in terms of number of species, cover and density (Gecy, 1988). 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. Herbaceous species accounted for 93% of the seedlings and 98% of the vegetative sprouts on WS10 and 84% of the seedlings and 94% of the vegetative sprouts on Zeolite Creek.

Effects of scour and deposition.—Significant relationships existed between the types of disturbance surfaces and total cover, vegetative regrowth and seedling establishment (ANOVA, $P < 0.0001$, Table 3). Total cover was highest (FPLSD analysis of means, $P < 0.05$) on light intensity scour (15%). Vegetative sprout cover was also high (14%) on light scour. It was not significantly higher, however, than the vegetative cover on debris deposits or moderate scour, the next largest categories. The cover of seedlings was highest on three surfaces, light scour (2%) and fine (3%) and gravel deposits (2%). Vegetative sprout density

TABLE 3.—Percent cover (C) and density (D) of seedlings (S) and vegetative sprouts (SPR) on each of the disturbance surfaces (mean \pm standard error). Means with different letters within a column are significantly different at $P < 0.05$ (FPLSD analysis of means). TC = total cover, n = number of plots on each surface

	TC (%)	SPR C (%)	S C (%)	SPR D (no./m ²)	S D (no./m ²)
Light scour (n = 32)	15 \pm 3.4 ^a	14 \pm 4.2 ^a	2 \pm 0.7 ^{ab}	28 \pm 5.5 ^a	22 \pm 5.6 ^b
Moderate scour (n = 49)	8 \pm 1.4 ^b	7 \pm 1.4 ^{ab}	1 \pm 0.3 ^{bc}	26 \pm 5.6 ^a	13 \pm 3.1 ^{bc}
Intense scour (n = 33)	0.1 \pm 0.1 ^c	0.1 \pm 0.1 ^c	0 ^d	3 \pm 0.3 ^d	0 ^d
Fine deposits (n = 142)	10 \pm 1.5 ^b	7 \pm 1.5 ^{bc}	3 \pm 0.6 ^a	12 \pm 1.8 ^{bc}	46 \pm 5.2 ^a
Gravel deposits (n = 69)	6 \pm 1.0 ^b	4 \pm 1.0 ^{cd}	2 \pm 0.3 ^a	7 \pm 1.6 ^c	37 \pm 4.6 ^a
Cobble deposits (n = 13)	2 \pm 1.5 ^c	0.5 \pm 0.4 ^{de}	0.4 \pm 0.3 ^{cd}	2 \pm 1.0 ^d	14 \pm 6.5 ^{bc}
Debris deposits (n = 51)	10 \pm 2.0 ^b	9 \pm 1.9 ^{ab}	1 \pm 0.3 ^{cd}	19 \pm 4.8 ^{ab}	11 \pm 3.0 ^c
Unstable (n = 9)	0.4 \pm 0.2 ^c	0.2 \pm 0.2 ^c	0.2 \pm 0.1 ^c	2 \pm 1.5 ^{cd}	3 \pm 1.7 ^{cd}
ANOVA (7 df)	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001

TABLE 4.—Percent cover (C) and density (D) of seedlings (S) and vegetative sprouts (SPR) for each of the vegetation types (mean \pm standard error). Means with different letters within a column are significantly different at $P < 0.05$ (FPLSD analysis of means). TC = total cover, n = number of plots within each vegetation type

	TC (%)	SPR C (%)	S C (%)	SPR D (no./m ²)	S D (no./m ²)
Clear-cut (n = 181)	11 \pm 1.3 ^a	10 \pm 1.4 ^a	2 \pm 0.5 ^c	21 \pm 2.6 ^a	16 \pm 1.9 ^b
Hardwood (n = 61)	9 \pm 2.1 ^a	5 \pm 1.9 ^b	3 \pm 0.6 ^a	9 \pm 2.3 ^b	49 \pm 8.6 ^a
Conifer (n = 156)	5 \pm 0.6 ^b	3 \pm 0.5 ^b	2 \pm 0.2 ^b	7 \pm 0.9 ^b	34 \pm 3.9 ^a
ANOVA (2 df)	$P < 0.03$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$

was highest on light and moderate scour (26–28 sprouts/m²). Seedling density was highest on fine and gravel deposits (37–46 seedlings/m²). Few individuals established on intense scour or unstable surfaces and cover was correspondingly low on these surfaces.

Effects of vegetation type and topographic position.—Significant statistical relationships also existed between the predisturbance vegetation type and revegetation patterns (ANOVA, $P < 0.03$ for total cover, $P < 0.0001$ for cover and density of vegetative sprouts and seedlings, Table 4). Cover was higher (FPLSD analysis of means, $P < 0.05$) on the clear-cut (11%) and hardwood-influenced reaches (9%) than on the reaches where the adjacent vegetation was dominated by conifers (5%). Vegetative sprouts were most dominant in clear-cut reaches (85% of the total cover). Both cover (10%) and density (21 sprouts/m²) were higher (FPLSD analysis of means, $P < 0.05$) on clear-cut reaches than on the conifer or hardwood reaches. Seedling cover was highest on the hardwood-dominated reaches, averaging 3% and contributing to 39% of the total cover. Seedlings were more dense on both the hardwood and conifer-dominated reaches than on the clear-cut reaches (Table 4). More than 84% of individuals within these two vegetation types were seedlings.

The species of trees establishing within the hardwood and conifer-dominated reaches were often those present in the adjacent undisturbed vegetation. *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, $P < 0.04$). Seedling cover was lowest (FPLSD analysis of means, $P < 0.05$) where zones were undistinguishable (2%). Seedling cover was highest in the active zone (3%) where moisture was available throughout the growing season.

Regression models.—The overall regression models for both total and seedling cover included as significant terms surface type, predisturbance vegetation type, site and topographic position relative to the stream ($P < 0.05$, Table 5). All 16 significant models included surface type as an important characteristic affecting revegetation and in nine it was the only characteristic that explained any of the variability. None of the models explained more than 39% of the variation in either total cover or the means of establishment.

DISCUSSION

Scour and deposition.—These results agree with the results of previous studies (Veblen and Ashton, 1978; Hull and Scott, 1982; Miles and Swanson, 1986; Smith *et al.*, 1986) that variation in scour and deposition is the most important factor affecting the development of successional patterns after shallow mass movements. Hull and Scott (1982) and Veblen and Ashton (1978) suggest that this results from differential creation of microsites for seedling

TABLE 5.—Disturbance characteristics (DIST CHAR) included in the regression models for each of the vegetation attributes (VEG ATTRIB), and the percentage variation (% VAR) accounted for by the models, as determined by R^2 , the regression coefficient of determination. Only sites in which regression models were significant are included. S = surface, VT = vegetation type, Z = riparian subzone, WS10 = Watershed 10, MCR = Mack Creek Road

VEG ATTRIB	Site	DIST CHAR	% VAR (R^2)
Total cover	All	S, VT; Z or Site	24
	WS10	S	38
	Zeolite	S	39
Sprout cover	All	S	16
	WS10	S	28
	Zeolite	S	32
Sprout density	All	S	18
	WS10	S	17
	Zeolite	S, VT, Z	34
Seedling cover	All	S, VT, Z, Site	26
	WS10	S	17
	Zeolite	S, Z	32
	MCR	S, VT, Z	39
Seedling density	All	S, VT, Z, Site	36
	Zeolite	S	33
	MCR	S, Z	33

establishment by scour and deposition. Some investigators (Flaccus, 1959; Hupp, 1983; Sousa, 1984) hypothesize that microsite availability for seedling establishment is crucial following rapid mass movement events. These intense disturbances are assumed (Flaccus, 1959; Hupp, 1983; Sousa, 1984) to remove all pre-existing vegetation, including the stored propagules, making dispersal the only source of revegetation.

Both seedlings and vegetative sprouts, however, contributed to the revegetation of our study sites. More importantly, the surfaces on which seedlings and vegetative sprouts had their greatest cover and density differed. Because the majority of species regenerated from a single source, differences in seedling and vegetative sprout establishment could produce differences in species composition on scour and deposition. Thus, differential establishment of seedlings alone cannot explain the initial revegetation patterns we observed. We propose that scour and deposition affect species composition, density and cover mainly by altering the relative contributions of seedlings and vegetative sprouts to revegetation.

Initial revegetation patterns can be important determinants of later successional patterns (Egler, 1954). Because our data are from the first growing season after disturbance, caution must be used in extrapolating the results to subsequent years. Seedling establishment patterns, in particular, may change considerably. We did not assess seedling establishment from either autumn-dispersing species or those species requiring stratification, and abundant bare ground was available for their colonization. In addition, several fast-growing species established primarily as seedlings (*e.g.*, *Alnus rubra*) so that seedling cover may dramatically increase in the next few years. Long-term studies are necessary to determine the significance of the initial revegetation patterns to succession.

Effects of vegetation type and topographic position.—The effect of the vegetation type in initial debris flow revegetation was complex on the three debris flows 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 source of seed dispersed into a disturbed area and can influence the light regime of a disturbed site. (Kellman, 1974; Hull and Scott, 1982; Swanson *et al.*, 1982; Hupp, 1983). Some seed undoubtedly dispersed from the adjacent vegetation onto these narrow (6 to 28-m wide) debris flow sites, since we observed some compositional similarity between the tree seedlings establishing on the debris flows and the dominant tree species in the adjacent canopy and the seed of most tree species is conspicuously absent from seed banks (Thompson, 1978; Pratt *et al.*, 1982; Silvertown, 1982).

The cover and density of vegetative sprouts also changed dramatically with vegetation type. Vegetative regrowth was much higher on clear-cut reaches than on conifer or hardwood reaches. Relatively abundant vegetative regrowth has occurred in other clear-cut communities following volcanic eruption, fire and mass movements (Stickney, 1986; Halpern, 1987; Smith *et al.*, 1986). These observations are consistent with the suggestions by Franklin *et al.* (1988) that rapid regrowth of previously clear-cut communities following a second disturbance occurs because the species present in early successional communities possess adaptations allowing vigorous resprouting, whereas the species present in late successional communities are less able to respond vegetatively to disturbance.

The topographic position of the disturbed surfaces relative to the stream by itself had no significant influence on total cover and vegetative regrowth. This was surprising as Campbell and Franklin (1979) identified strong relationships between riparian community structure and the riparian subzone. Although 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; Padgett, 1982; McBride and Strahan, 1984), these results support the conclusions of Wood and del Moral (1987) that community gradient patterns do not develop until later in succession.

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