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ABSTRACT

Sixteen understory plant communities in the riparian zones of small streams are identified and described. They range from pioneer communities on gravel and rock to well-developed shrub communities on flood plains and terraces. Several other vegetation types are discussed.

Distribution of communities within the riparian zone is also discussed. A survey of nine small streams shows the Acer circinatum community to have the widest distribution and highest cover, but the Rubus spectabilis/Ribes bracteosum community is somewhat more common in the active zone.

Biomass estimates are made for riparian vegetation along three stream segments. Total foliar production for 1976 is calculated for all vegetation, for communities, and for individual species. The percentage of each type of foliage which may reach the stream directly, indirectly, or not at all is estimated.

Abscission and fall senescence for thirteen species was monitored. Leafy and herbaceous detrital input is timed. Rates of leaf fall and decadence are related to environmental factors.

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RIPARIAN VEGETATION IN OREGON'S WESTERN CASCADE MOUNTAINS: COMPOSITION, BIOMASS, AND AUTUMN PHENOLOGY

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INTRODUCTION

In recent years, the Coniferous Forest Biome has sponsored efforts to quantify biological activity in streams. Vegetation along small streams is an important component of the riparian ecosystem. It produces the detrital substrate on which much of the instream system is based; it cycles nutrients; and it modifies the aquatic environment. This study of riparian vegetation in the central western Cascade Range of Oregon includes community descriptions, distribution surveys, biomass estimates, and observation of detritus production.

In 1976, riparian communities on Mack Creek and Watershed 2 (WS 2) in the H. J. Andrews Experimental Ecological Reserve (EER) were described and their distribution in relation to the stream was recorded and mapped (see Appendix). The next year, eight additional stream segments in three other watersheds were surveyed for the quantity and distribution of these riparian communities. Detritus contributions of riparian vegetation to the aquatic system was estimated by calculating 1976 production of leaves and herbage and average production per square meter and running meter of communities and individual species.

Leafy material is in readily digestible form when it enters a stream, and it produces a surge of nutrient material, much of which breaks down on the spot. To determine the timing of this nutrient input, woody and herbaceous species were monitored through late summer and fall. Rate of decadence and rate of leaf fall were related to weather and temperature.

This paper defines some riparian plant communities common to small streams in western Oregon and describes their habitats and distribution. It gives estimates of yearly foliage production of herbs and shrubs along three stream segments and discusses the timing and rate of leaf fall and decadence of herbs.

STUDY AREAS

Location

All streams studied are located in the Tsuga heterophylla transition zone of the western Cascade Range of Oregon. The rugged mountain topography has a mature ridge and valley conformation. Ridgetops reach 1,000 to 1,400 m elevation. Slopes are steep and deeply incised by streams. Gradients generally range between 10° and 35°, although backslopes and rocky outcrops range from 45° through 90°. Intermittent first-order streams are common.

Primary center for this work is the H. J. Andrews EER located 75 km east of Eugene. WS2, Mack Creek, and Lookout Creek are second-, third-, and fifth-order streams in the reserve (Figure 1). Five other streams of comparable size in the area were also sampled. Carpenter 75B and Clover are just north of the reserve on the northwest side of Carpenter

Mountain. Hagan Creek and Tiny Trout Creek are in the proposed Hagan Block Research Natural Area 13 km west of the reserve. All are part of the McKenzie River drainage. The Black Hole is located in the proposed Middle Santiam Research Natural Area 34 km to the north of the reserve in the Middle Santiam River watershed. Table 1 lists physical features.

Streams were selected in collaboration with the stream research group of the Coniferous Forest Biome and the Pacific Northwest Natural Area Committee. All streams are located in mature to overmature stands of Douglas-fir (Pseudotsuga menziesii) and other conifers, with the exception of a segment on Mack Creek in a clearcut.

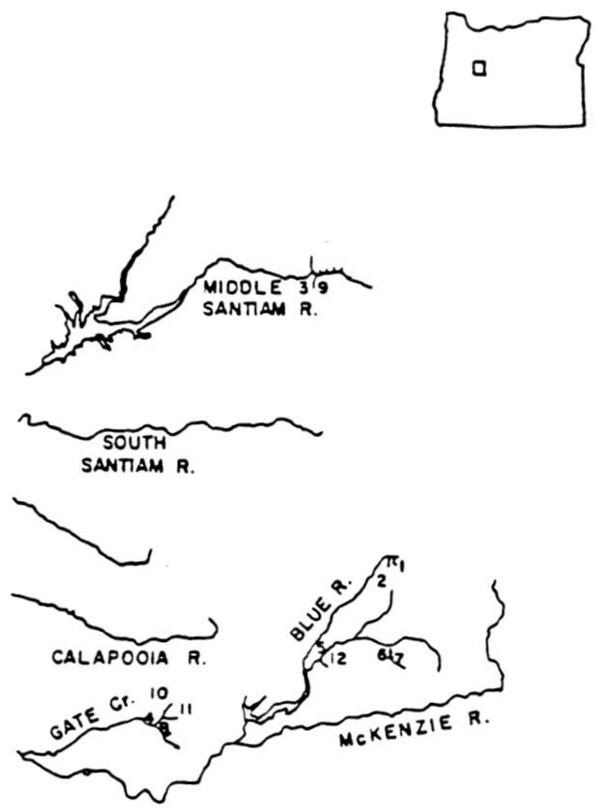


Figure 1. Map of Oregon showing the study area. Stream segments are indicated by numbers: (1) Carpenter 75B, (2) Clover, (3) Black Hole, (4) Hagan, (5) Lookout, (6) Mack Creek clearcut, (7) Mack Creek old-growth, (8) Tiny Trout, (9) Upper Black Hole, (11) Upper Tiny Trout, (12) WS 2.

Weather

Climate is typical for Western Oregon---mild wet winters and mild dry summers. At the weather station on WS 2 at about 500 m, the January mean is 2.3°C and the July mean 20.6°C (Rothacher et al. 1967). On Mack Creek at about 800 m, the January mean was 1.6°C and the July mean was 12.9°C in 1977. The 25-year average annual precipitation at the WS 2 weather station is 2,290 mm. Precipitation is strongly seasonal; 72% occurs from November through March. A considerable portion of this falls as snow at the higher elevations. Evapotranspiration is not a problem except upon rock surfaces which dry rapidly.

Soils

Soils in stream bottoms are chiefly colluvial or alluvial and are not developed or are poorly developed. At upper elevations, particularly along small streams, soil creep and minor slides combined with channel erosion create a sharp V-shaped channel with steep gradients and no terrace formation. Soils are those of the surrounding forest. At

Table 1. Location and physical description of sampled streams.

Stream	Order	Approximate elev. (m)	Aspect	Approximate gradient (deg)	Location	Average bank slope (deg)	Stream width (m)	Average transect length (m)	Stand age (years)
Carpenter 75B	1	800	NW	10	T15S R5E Sec 1	33	3.0	21	75
Clover	1	750	NW	10	T15S R5E Sec 10	45	2.8	19	135
Upper Tiny Trout	1	680	W	25	T16S R3E Sec 13-14	33	1.9	17	90
Upper Black Hole	1	700	N	20	T12S R5E Sec 19	38	2.5	25	Old-growth
Tiny Trout	2	560	W	9	T16S R3E Sec 14	36	2.5	22	90
Upper Hagan	2	530	SSW	8	T16S R3E Sec 14	32	4.5	29	90
Black Hole	2	610	N	20	T12S R5E Sec 19	37	5.9	27	Old-growth
Hagan	3	475	SW	1	T16S R3E Sec 14-15	36	6.4	43	90
WS 2	2	530	NW	14	T15S R5E Sec 31	46	1.5	11	Old-growth
Mack Creek	3	800	N	7	T15S R5E Sec 35	--	3.0	36	Old-growth and clearcut
Lookout Creek	5	460	SW	1	T15S R5E Sec 31	--	12.0	--	Old-growth

lower elevations the gradients decrease abruptly into flood plain, alluvial fan deposits, and some terrace formation (Swanson and James 1975).

Streams

Stream order

The studies center on first- through third-order streams (Table 1). Typically, first-order streams are small, rich in debris, and very steep. Gradients of upper ends and headwalls range up to 40°. Streambed morphology is commonly a stairstep series of small pools separated by freefall zones. Accumulations of organic debris dam the flow, thus reducing the effective gradient. The substrate is usually loose rocks and gravel of weathered tuff and breccia. Bedrock is exposed along several of the study reaches. Water flow varies from summer dry to as much as 1,000 liters/sec at the peak of winter flow.

Second-order streams are somewhat larger, and they vary considerably in gradient. Slopes of those we studied ranged from approximately 8° to 20°. Less debris allows a somewhat freer water flow.

Third-order streams are large enough to influence the surrounding forest and to produce canopy openings. Gradients are less than smaller streams; some occupy valley bottoms with slopes of about 1°. Organic debris must be very large to remain in place through heavy winter flows, and less of the stream area is occupied by logs. Weathered rock is the common substrate. Surface water flows all year. Winter high-water periods are brief, and water height is extremely variable.

Bedrock may be present regardless of order. Bedrock controls the gradient, forming a series of high falls and deep pools or, in some cases, a chute of uniform slope several meters long. Little organic debris accumulates in the channel in areas of exposed bédrock.

Streamside morphology

Historically, riparian vegetation is defined as vegetation rooted at water's edge. Plants rooted well back from the stream, however, also influence stream structure and chemistry, and the stream influences vegetation well beyond its water line. We have defined the border of the riparian zone (the break) as the point beyond which shrubby vegetation no longer interacts with the stream.

The break is frequently marked by a change in slope or in vegetation, commonly the top of a cliff, a pile of debris, or an abruptly more xeric community. The zone varies greatly in width.

Topography of a stream bottom controls both the distribution and the effect of communities on the stream. The area covered by moving water at least part of the year supports a specially adapted flora that has an immediate effect upon stream processes. Farther from the water, vegetation has a delayed or indirect influence. We have identified zones parallel to the stream in which we could classify communities by both habitat and function. We divided the area of riparian influence into three zones: active zone, border zone, and outer zone (Figure 2).

The active zone is subject to annual streamflow. Plants are rather permanently placed, but the water-covered area expands and contracts, so a portion of the streambed is sometimes active and sometimes not. For this study, the active zone was broadly drawn and includes any area from which vegetation could fall directly into water at high water. Organic contributions to the stream from these areas are defined by Boling et al. (1975) as "aggregated whole organic matter greater than 1 mm."

The border zone is any area from which leaves and debris can reach the stream after some delay. Slopes greater than 50° are a good example, as are cut banks with herbs growing at the top, and areas where litter may be entrailed by flood-level backwater. Dissolved and suspended materials wash into the stream from these points and surface-creep carries in larger particles.

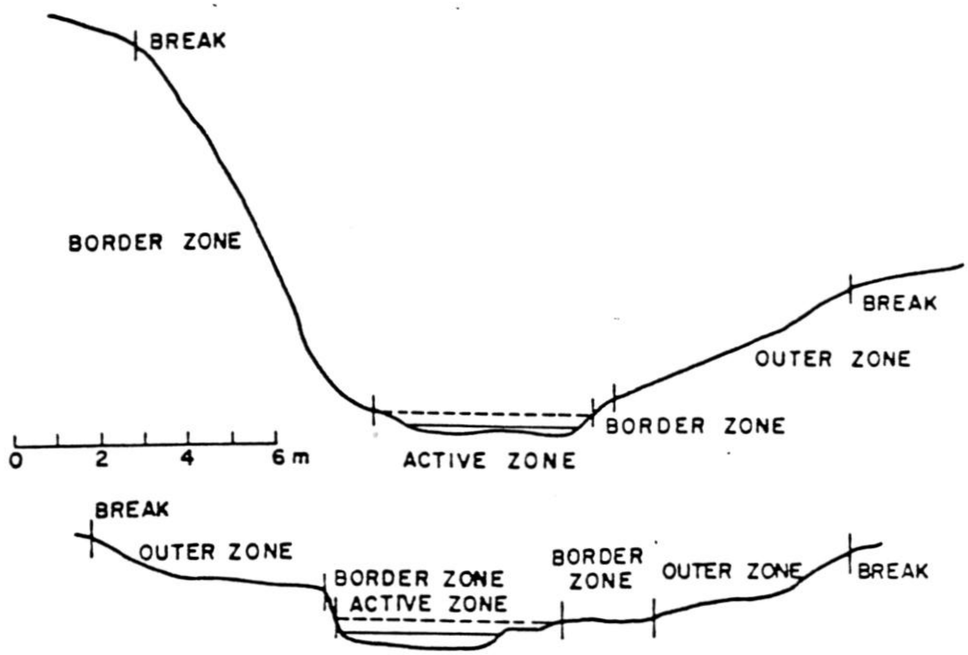


Figure 2. Position of the break and areas which can be designated active, border, and outer zones. The riparian zone as defined in this study extends from break to break.

The outer zone is the area within riparian influence, by topography or vegetation or both, from which leaves cannot reach the stream.

Unfortunately, a single plant may occupy two zones. An example is Acer circinatum, a sprawling shrub that roots well up on a slope but reaches over the stream (Figure 3). Roots may be at the outer edge of the riparian area, but leaves may be over the stream. Generally, the larger the plant, the more diffuse its influence, as we discuss in the biomass section.

Most of the work, including community descriptions, biomass estimates, and part of the phenology was done along two segments of Mack Creek, one in old-growth and one in a clearcut, and along a segment of WS 2 in old-growth where the stream had rock substrate. The three segments are diverse physically and vegetationally.

Mack Creek is a third-order stream at about 800 m elevation. The old-growth section has a gradient of about 7° and falls in a series of riffles and pools with a substrate of boulders to fine gravel and silt, and well-developed gravel armor on the bottom (Sedell et al. 1974). Waterflow is estimated at 100 to 140 liters/sec in late summer and 5,000 liters/sec during winter freshets (Art McKee, personal communication 1978). The riparian zone averaged 36 m wide, 24 m of bank and 12 m of stream channel. Several old channels and berms are included in the widest portions.

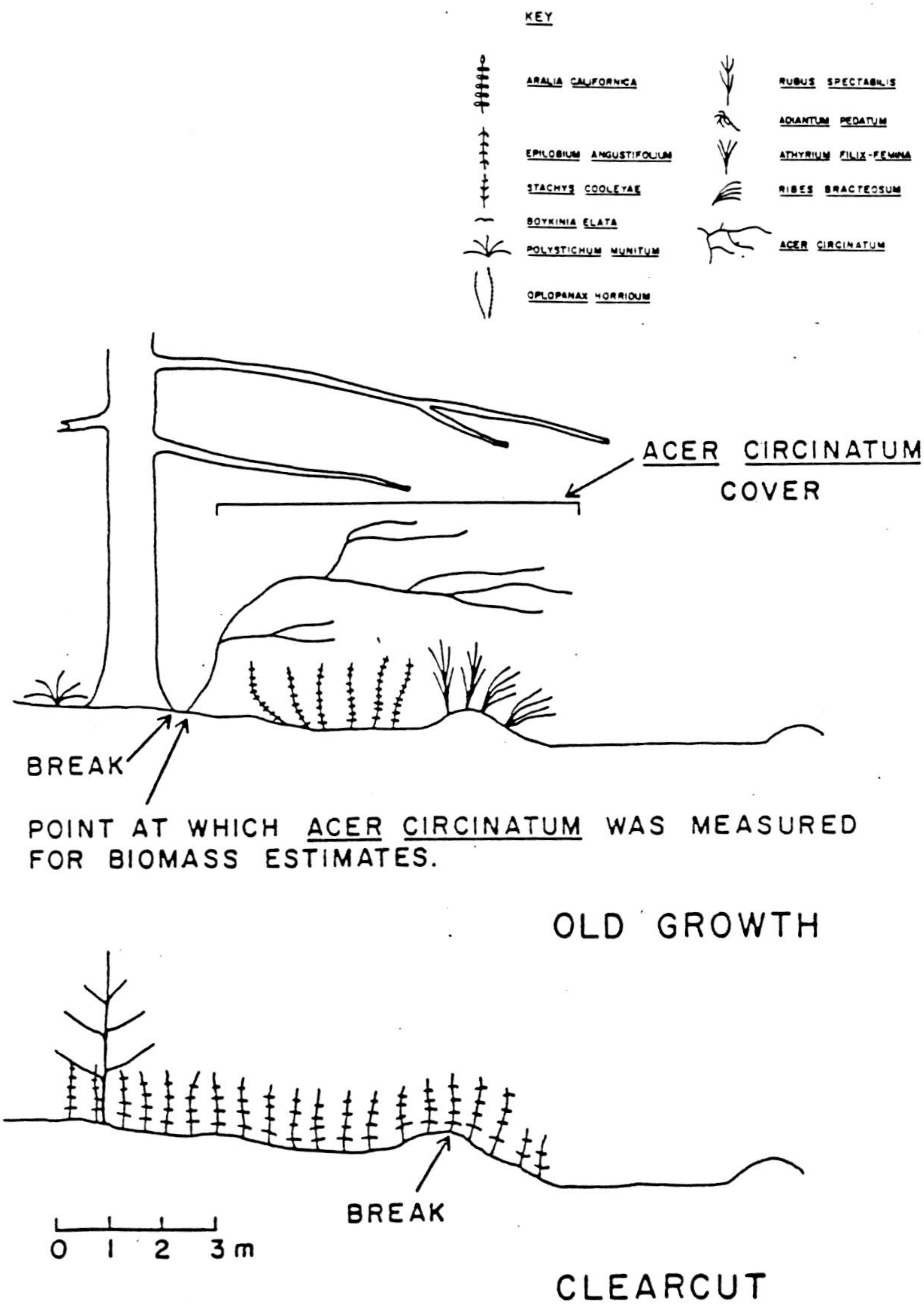


Figure 3. Cross sections of a stream in old-growth and a stream in a clearcut. Note the much wider zone of vegetation-stream interaction in old-growth. (See key.)

The width of the riparian zone in the clear-cut section of Mack Creek averages 11 m. Berms closely border the stream for most of its length. Because there is no overstory, the riparian zone is narrowly confined (Figure 3). Other physical characteristics of the clear-cut segment of Mack Creek are similar to those of the old-growth section.

Watershed 2 is drained by a second-order stream with an average gradient of 14° (Swanson, pesonal communication 1977). Streamflow ranges from 0.1 liter/sec in late summer to 990 liter/sec at peak flow (Harr 1976). Watershed 2 in the sampled area runs over bedrock scoured by a debris torrent in the late 1940's. There is little gravel, and accumulations of fine particles are severely disturbed by each high flow. The riparian zone, including 1.5 m of stream, averaged 11 m wide. Steep and often rocky side walls characterize the sampled section.

METHODS

Community Description

Stand tables were developed for 16 communities found along Mack Creek, WS 2, and Lookout Creek. Because the communities differ physiognomically, they could be stratified by preliminary visual reconnaisance. For estimating cover in shrub communities, 10-m transects were located in six or more stands where the vegetation was homogeneous in the lower strata. Each stand was well within a community type. Shrub cover was estimated in ten adjacent 1-m^2 quadrats along each transect--at least 60 samples from six stands. Herb cover was estimated in a 50- x 20-cm plot nested within each of the larger quadrats. Extreme variability in slope made it necessary to place all quadrats parallel to the ground surface.

Small herbaceous communities in the riparian zone are typically fragmented. When possible, transects were composed of ten adjacent 20- x 50-cm plots. More frequently the vegetation was isolated on rocks in the active streambed, in cracks on a cliff face, or on small gravel bars. In these cases, quadrats were laid through the available vegetation. Because stands were sampled with unequal numbers of quadrats, constancy was used in place of frequency. Cover estimates were made for each quadrat. Cover classes were estimated at 1% intervals up to 5%, and at 5% intervals thereafter. Substrate type, water and rock cover, slope, and relation to the stream were noted for all plots. Slopes over 60° in some communities required the use of climbing aids.

Conspicuous differences between communities made it possible to dispense with computer-assisted sorting. A simple application of Sorenson's modified Bray-Curtis (1957) ordination technique provided visual dimension to intercommunity relations.

Community Distribution

Community distribution was surveyed on eight segments of representative first- through third-order streams. They are 75B, Clover, Upper Tiny Trout, Tiny Trout, Upper Hagan, Hagan, the Black Hole and Upper Black Hole. Ten transects were established at 31.6-m intervals on each segment. Each transect, 3.16 m wide, was composed of adjacent 10-m^2 plots (3.16 x 3.16 m). Transects ran from break to break and were therefore different lengths. Cover, by community type, was estimated within each plot to the nearest 5%. Where there was no recognizable (described) community, dominant vegetation was recorded.

Each plot was assigned a zone designation. Frequently the zone was prorated because of abrupt changes in terrain. Slope, aspect, debris cover and class, major stem size, overstory cover, and substrate were recorded. Data were then summarized for total and proportional cover by stream, stream order, and zone.

Biomass Estimates

A 290-m stretch of Mack Creek in old-growth, a 220-m stretch of Mack Creek in a clearcut, and a 115-m stretch of WS 2 were systematically sampled in late July and early August of 1976 for standing foliar biomass of understory riparian species. We later stratified the samples into appropriate groups to estimate the average for individual understory communities and vegetation types. Systematic sampling assured that each community was sampled in proportion to its occurrence in the stream sections. Depauperate stands are therefore included in the average biomass estimates for communities in the correct proportion.

Transects were laid perpendicular from stream center to the break. On Mack Creek, transect lengths varied from 8 m to 39 m, plus about 12 m of stream. On WS 2, transects varied from 4 m to 18 m. Herbaceous communities in the active zone and on cliff faces were sampled with a 0.5-m wide transect in each 5 m of stream. Quadrats were adjacent 20- x 50-cm plots. Shrub communities from water to the break were sampled with a 1-m wide transect in each 10-m interval. Quadrats were adjacent 1-m^2 plots. All were a 10% sample (Figure 4). Each quadrat was coded active, border, or outer riparian zone and assigned to a community. Quadrats were not included in communities if they were bare, sterile, debris covered, or such, but were included in overall averages. In addition, slope was estimated with a clinometer, and aspect and surface cover were recorded.

All vegetation rooted within a quadrat was measured by species-specific units suitable for conversion to biomass; for example, Rubus spectabilis was measured for basal diameter, Epilobium angustifolium for height, and Adiantum pedatum for total length. We developed biomass estimation formulas for species limited to the riparian zone (Gholz et al. in press). Equations for other species are those of Gholz, Russell (1973), Grier (1974), and Kessel (personal communication 1977). If we had no equation for species of minor importance, we harvested the

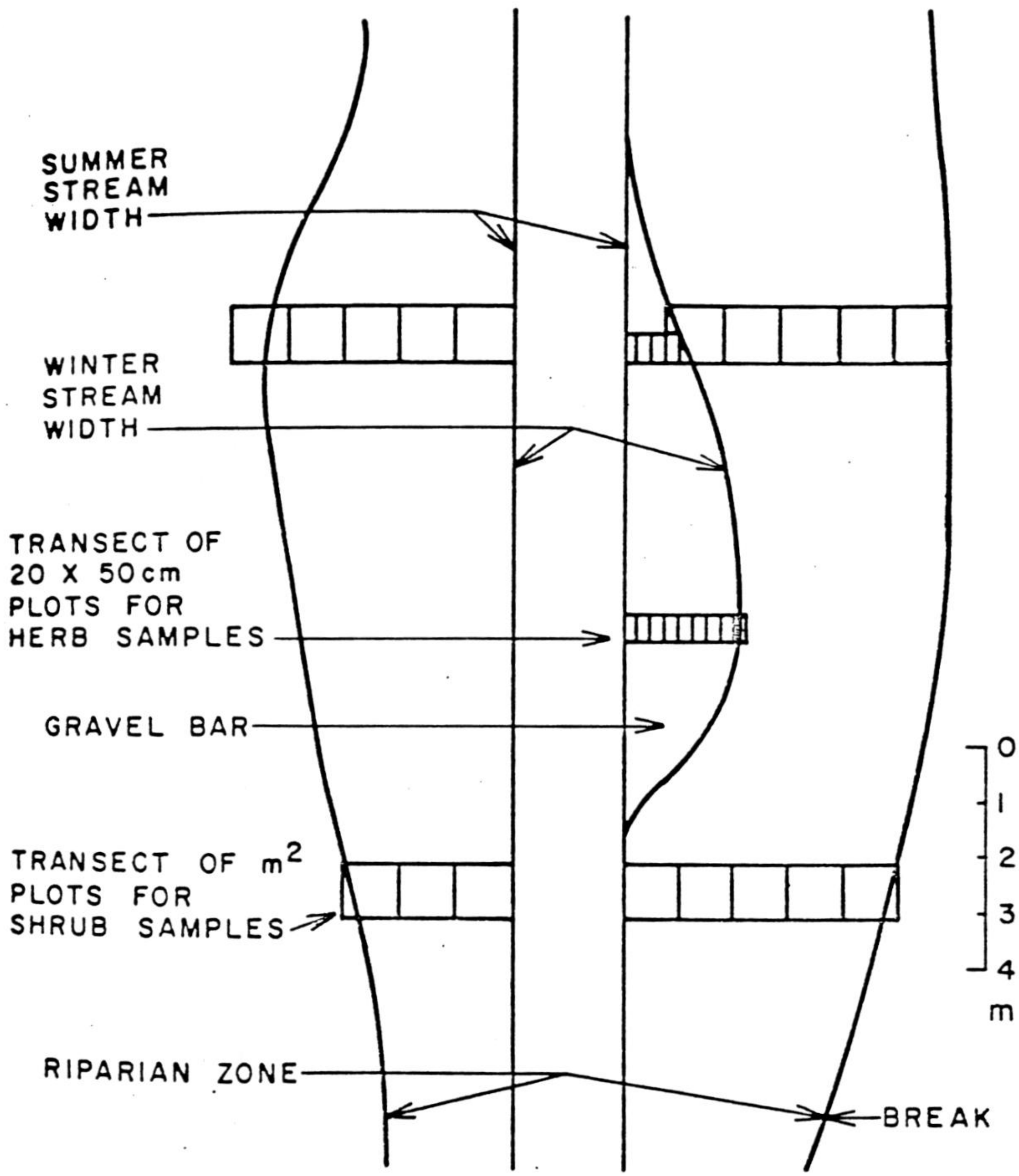


Figure 4. Diagram of the riparian zone with appropriate biomass sampling transects superimposed.

year's production. This was especially necessary in the clearcut, where over 100 species were found, and among small herbs in the active zone in old-growth.

Biomass was calculated and summarized on the Oregon State University computer with the help of Alfred T. Brown.

Rating and Timing Leaf Fall and Senescence

Weekly surveys of Mack Creek, Lookout Creek, and WS 2 were made from July 7 to November 21, 1977 to determine when foliage or entire herb plants entered the stream system. Weekly leaf counts were made on a minimum of 20 marked branches of seven species of deciduous trees and shrubs at each site (Table 2). The number of leaves per branch varied because of structure of the species; Acer circinatum averaged 100 but Oplopanax horridum only 13. The eight herbaceous species were rated on a scale of 0 (no visible deterioration) to 5 (down and dead in the water). Twenty to sixty quadrats were observed at each site for each species. Temperature records came from Mack Creek and the climatic station at WS 2. Stream flow records came from the WS 2 gauging station.

Table 2. Location and elevation of species observed weekly for leaf fall and senescence.

Species	Mack Creek (800 m) Old-growth	Mack Creek (800 m) Clearcut	Lookout Creek (470 m) River bar	WS 2 (530 m) Old-growth
Leaf fall				
Acer circinatum	X		X	
Acer macrophyllum	X			
Alnus rubra	X		X	
Oplopanax horridum	X			
Ribes bracteosum	X			
Rubus spectabilis	X			
Salix sitchensis		X	X	
Senescence				
Adiantum pedatum	X			X
Aralia californica				X
Athyrium filix-femina	X			X
Boykinia elata		X		X
Epilobium angustifolium	X	X		
Mimulus guttatus	X	X	X	
Petasites frigidus	X	X	X	
Stachys cooleyae	X	X	X	

If abscission is considered a threshold event, the number of leaves falling each day should follow a normal curve. When numbers are plotted against time, the percent of leaf fall may be plotted against days on probit paper, and the resulting straight line (Sarvas 1972) represents the rate of abscission.

COMMUNITIES AND THEIR DISTRIBUTION

Riparian understory communities, like bog, salt marsh, and beach strand vegetation, aggregate spatially rather than floristically. Within the riparian habitat are numerous microhabitats connected in space by the waterway but sufficiently different to support sharply disparate vegetation.

Streamside vegetation patterns depend upon many factors: general topography, stream gradient, and substrate type are important. Forest fires, recent floods, and debris torrents leave clear evidence in present communities.

In spite of diverse elements, we find several general riparian vegetation patterns, an obvious one connected with stream size. First-order streams in mature stands tend to be totally dominated by the surrounding forest. The first-order stream is squeezed into a narrow strip, and riparian vegetation is distributed sparsely along the stream, like a string of beads. Forest understory intrudes upon the riparian zone and evergreen trees overtop all. Second- and third-order streams are large enough to exert more influence on the forest, creating and maintaining open space.

Small herb communities are adapted to several temporary habitats found most often at the stream edge (Table 3). Their total quantity,

Table 3. Percent of vegetation cover of understory communities on nine small streams. Starred communities are described in this paper. Vegetation not clearly included in described communities is given under the dominant species.

Vegetation Type	Carpenter 75B	Clover	Upper Black Hole	Upper Tiny Trout	Black Hole	Tiny Trout	Upper Hagan	Hagan	WS 2
Active zone									
* Small pioneer herbs	2								
* *Boykinia elata*		19		9	4		4	1	28
Mitella ovalis					2			2	11
* *Tolmiea menziesii*					9				9
* *Athyrium filix-femina*	1	2		6	5	11	13	2	4
* *Adiantum pedatum*	3	2		6	1		1	1	2
* *Petasites frigidus*		11		1					7
Mixed fern									
Aralia californica		14		5		9	1		34
* *Oplopanax horridum*						15			
* *Rubus spectabilis/*									
Ribes bracteosum	6			19	48	28	25	36	
Large shrubs				3			6	9	
Corylus cornuta									
Osmaronia cerasiformis									
Rhamnus purshiana									
* *Acer circinatum*	2	40	29	5	23	27	31	40	
Forest shrub invasives	2	1		11	1	6		3	
Polystichum munitum		5	1	5	5	4	3	1	7
Oxalis oregana			29	14	11	9	10	6	
Forest herbs				2					
Outer zone									
* Small pioneer herbs									
* *Boykinia elata*									
Mitella ovalis						1			
* *Tolmiea menziesii*					2				
* *Athyrium filix-femina*			4	1	15	7	15	8	
* *Adiantum pedatum*					1				
* *Petasites frigidus*						2	1		
Mixed fern									
Aralia californica									
* *Oplopanax horridum*						9			
* *Rubus spectabilis/*									
Ribes bracteosum					10	10	7	23	
Large shrubs				1		2	9	16	
Corylus cornuta									
Osmaronia cerasiformis									
Rhamnus purshiana									
* *Acer circinatum*		36	55	25	22	30	37	34	
Forest shrub invasives	9	21		24	4	5	7	6	
Polystichum munitum	7	22	46	42	24	39	33	42	
Oxalis oregana			21	24	12	33	31	16	
Forest herbs		1	1	2				1	

Table 3 (cont.)

Vegetation Type	Carpenter 75B	Clover	Upper Black Hole	Upper Tiny Trout	Black Hole	Tiny Trout	Upper Hagan	Hagan	WS 2
Border zone									
* Small pioneer herbs	8								
* *Boykinia elata*								2	6
Mitella ovalis									2
* *Tolmiea menziesii*					4	7			3
* *Athyrium filix-femina*		2	100	14	17	16	19	27	3
* *Adiantum pedatum*		2	50			3		4	4
* *Petasites frigidus*		2							3
Mixed fern									18
Aralia californica	1	19		41		4	3		10
* *Oplopanax horridum*						15			
* *Rubus spectabilis/*									
Ribes bracteosum				40	11	8	47	26	
Large shrubs				38			1	3	
Corylus cornuta									
Osmaronia cerasiformis									
Rhamnus purshiana									
* *Acer circinatum*	5	18			28	73	40	63	7
Forest shrub invasives	12	8		4	3	6		2	5
Polystichum munitum	4	39		2	16		7	45	30
Oxalis oregana					43	20	45	2	
Forest herbs	1			14					3
Entire riparian zone									
* Small pioneer herbs	2								
* *Boykinia elata*		3		2			1		13
Mitella ovalis					1	1			5
* *Tolmiea menziesii*					4	1		1	5
* *Athyrium filix-femina*		1	5	3	13	8	15	8	5
* *Adiantum pedatum*		1	1	2	1			1	3
* *Petasites frigidus*	1	2				2	1		4
Mixed fern									12
Aralia californica		4		3		2	1		17
* *Oplopanax horridum*						11			
* *Rubus spectabilis/*									
Ribes bracteosum	2			6	21	13	13	25	
Large shrubs				2		1	8	13	
Corylus cornuta									
Osmaronia cerasiformis									
Rhamnus purshiana									
* *Acer circinatum*	2	35	45	19	23	34	36	37	9
Forest shrub invasives	5	17		20	2	5	5	5	4
Polystichum munitum	4	21	31	31	18	28	26	35	13
Oxalis oregana			21	21	15	27	28	14	
Forest herbs				2				1	2

measured as a percent of the total riparian area, remains fairly constant on first- and second-order streams (except on bedrock, where it is much higher). We believe two factors contribute to the general constancy. First, the understory cover on first-order streams is generally low; second, a first-order stream may consist of stream edges only--the water course is essentially absent. Sites suitable for small herbs are, therefore, a high percent of the total riparian area, but vegetation in general is sparse under old-growth canopies, and the two factors tend to cancel each other. Small herb cover tends to drop on larger streams because suitable sites compose a very low percent of the riparian area.

Similar patterns are shown by large herbs. First-order streams generally do not support a high cover because of drought and competition. The second-order stream has a constant water supply and a somewhat larger suitable area. On third-order streams, the area covered by large herbs may increase, but the riparian zone increases more; therefore the proportion of cover decreases.

Shrubs show a different pattern. First-order streams where the forest overshadows and suppresses vegetation and where gradients are high have few shrubs. Along these streams, cover for the Rubus spectabilis/ Ribes bracteosum community (see Descriptions of Communities) averages 2%. As the stream gradient lessens and the stream broadens enough to allow light penetration, cover climbs to 25% or more. The large shrubs Osmaronia cerasiformis and Rhamnus purshiana showed similar patterns (Table 4).

The pattern of vegetation in response to stream size is modified by the character of the stream itself. The precise proportion of each community type depends upon elevation, light availability, sediment movement, and such. No one stream segment has all communities; no community was found on all streams. For example, small pioneer herbs (2% cover) are found on Carpenter 75B (Table 3, Entire Riparian Zone), which has sections of low gradient and high sediment deposit, but the Tolmiea menziesii community is missing. Tolmiea menziesii community is particularly strong (4% cover) along the Black Hole, which has dense shade and northerly aspect, but the Boykinia elata community is

Table 4. Percent of cover for vegetation types in the riparian zone of three stream orders. Starred communities are described in this paper. Vegetation not clearly included in described communities is given under the dominant species.

Vegetation grouped by physiognomic class of dominant species	1st-order streams	2nd-order streams	3rd-order streams	WS 2, 2nd-order rock substrate
Small herb				
* Small pioneer herbs	< 1	-	-	-
* *Boykinia elata*	1	1	< 1	13
Mitella ovalis	-	1	-	5
* *Tolmiea menziesii*	-	2	1	5
Oxalis oregana	5	2	1	-
Total	6	6	2	23
Large herb				
* *Athyrium filix-femina*	2	12	8	3
Aralia californica	1	1		17
* *Adiantum pedatum*	1	< 1	1	3
* *Petasites frigidus*	1	1	-	4
Mixed fern	-	-	-	12
Total	5	14	9	39
Shrub				
* *Oplopanax horridum*	< 1	3	-	-
* *Rubus spectabilis/ Ribes bracteosum*	2	16	25	-
Total	2	19	25	
Large shrubs				
Corylus cornuta var. californica	< 1	1	< 1	-
Osmaronia cerasiformis				
Rhamnus purshiana	< 1	2	13	-
Total	< 1	3	13	
* *Acer circinatum*	26	31	37	9
Polystichum munitum	21	24	35	19
Forest shrub intrusives				
Berberis nervosa	3	< 1	< 1	-
Rhododendron macrophyllum	< 1	-	-	-
Gaultheria shallon	2	< 1	1	-
Vaccinium parvifolium	3	4	4	-
Linnaea borealis	1	-	-	1
Total	9	4	5	1
Forest herb				
Oxalis oregana	6	18	13	-
Vancouveria hexandra	1	3	1	2
Total	7	21	14	2
Pteridium aquilinum	-	2	3	-

missing. The Boykinia elata community has greatest cover (3%) on Clover Creek under a relatively open canopy.

The average total cover for all communities dominated by small herbs in nonbedrock segments (including Mack Creek), is just under 6%. The total cover on WS 2, a bedrock-based stream scoured by a debris torrent in the late 1940's, increases dramatically to 23% (Table 4). The large herb-dominated vegetation increases to 39%. Visual survey of some segments of other streams not rigorously sampled suggests that these estimates are reasonable for other rock substrate streams.

Habitat type clearly is intrinsic to many of the following community descriptions. Habitat and distribution across the stream, therefore, will be covered under the community headings.

Descriptions of Communities

Sixteen potential communities have been identified, and stand tables prepared. Several clans and other vegetation types are discussed. All of the communities described are seral, part of the permanently immature vegetation of unstable habitats, and are composed of herbs or shrubs. The overstory is treated as a constant factor and is not included in descriptions. Broadleaf riparian forests dominated by alder (Alnus rubra) and cottonwood (Populus trichocarpa), found on terraces of larger streams, are also not included in this study.

"Community" is used here to mean a repeating assemblage of plants. A more precise terminology would require selection from the terms of several theorists and might imply hierarchy where there is none. Clans are not necessarily part of synusiae, nor do synusiae, particularly on smaller streams, always belong to the surrounding forest association. When descriptions have been assembled from a wider area it will be possible to rank and classify them.

Because the moss flora of waterways is a broad subject, and because this study deals with vascular communities, only mosses with major cover values are recorded. Two communities are more properly Bryophyte communities and should be redefined on that basis later: Bryophyte/Montia parvifolia, found on summer dry rocks, and Petasites frigidus/Brachythecium frigidum, found in seeps. Detailed analysis of moss species is needed for Bryophyte communities, where there are probably several associations, and vasculars are unimportant. Only mosses grow in numerous places on streams, particularly in old-growth stands on rock faces and seepage areas.

These riparian communities are described and discussed in approximate order of maturity:

- Pioneer communities
  - Small-herb community
  - Pioneer Boykinia elata community
  - Pioneer Tolmia menziesii community

Rhyzomatous clans and communities
- Petasites frigidus clan
- Stachys cooleyae clan
- Mimulus guttatus clan
- Petasites frigidus community
- Stachys cooleyae community
- Hydrophyllum tenuipes community

Well-developed herbaceous communities
- Boykinia elata community
- Tolmiea menziesii community
- Mitella ovalis/Marchantia community
- Athyrium filix-femina community
- Mixed fern-large herb vegetation

Shrub communities
- Rubus spectabilis/Ribes bracteosum community
- Oplopanax horridum community
- Acer circinatum community

Topographic climax communities
- Bryophyte/Montia parvifolia community
- Adiantum pedatum/precipice community
- Petasites frigidus/Brachythecium frigidum community

Small-herb pioneer communities

The small-herb community is seral to the Tolmiea menziesii community and is poorly defined floristically. The community develops rapidly on newly deposited sand and gravel less than about 3 cm diameter and persists where streamflow batters the surface but does not dislodge the substrate. Usually the habitat is below mean high water.

Total cover of vascular plants is 31% (Table 5). Montia sibirica and Galium triflorum, ubiquitous wet area species, are most frequent, and the common wet-forest indicator Oxalis oregana is third in frequency. No species occurs in more than 70% of all quadrats.

Species richness is moderate (21 species recorded from the measured plots). Only four species; Montia sibirica, Galium triflorum, Circaea alpina, and Oxalis oregana, have greater than 1% cover.

The moss layer is less developed than in more mature herb communities or on solid rock surfaces. Total moss cover averages 32%; exposed rock, gravel, or sand averages 54%.

The community is at best poorly defined and variable. It is composed of hydrophytic plants which establish readily in fairly fine material, generally by seed, and survive winter abrasion unless the roots are dislodged. These species are not adapted to survive heavy deposition of gravel or sand. Community composition is essentially accidental and depends upon seed sources and particle size in the seed bed.

Table 5. Stand tables for pioneer riparian communities. Cover and constancy are in percent. N = number of plots.

	Small herb community											
	In-stream gravel substrate								Gravel and soil substrate			
	N = 10		N = 10		N = 10		N = 10		N = 10		All plots	
Species	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	Ave. cover	Con-stancy
Vascular												
Montia parvifolia							0.4	10	0.1	10	+	4
Montia sibirica	5.6	70	8.5	100	5.2	60	3.4	90	0.4	10	4.6	66
Galium triflorum	4.8	70	2.0	30	5.3	60	19.1	90	9.0	60	8.0	62
Circaea alpina	0.6	20	0.5	30	0.6	10	3.0	30	1.2	50	1.2	28
Oxalis oregana	0.2	20	0.4	30	15.8	80	5.6	70	22.5	70	8.9	54
Trisetum canescens	0.9	40	0.1	10	1.0	30	0.5	10	1.5	30	0.8	24
Festuca subulata	0.4	10					1.5	30	1.2	30	0.6	14
Stellaria crispa	+	10					0.3	20	0.1	20	+	10
Boykinia elata	0.1	20	0.1	20							+	8
Tolmiea menziesii	+	10			0.1	10	1.0	20	0.6	20	0.3	12
Mitella ovalis	0.5	10	0.2	10	0.2	10	0.4	20	+	10	0.3	12
Tiarella unifoliata	1.0	10							1.5	10	0.5	4
Petasites frigidus												
Adiantum pedatum												
Aruncus sylvester	+	10									+	2
Hydrophyllum tenuipes	0.1	10			0.5	20					0.1	6
Stachys cooleyae												
Epilobium angustifolium												
Athyrium filix-femina							0.2	10			+	2
Rubus parviflorus									6.5	20	1.3	2
Hieracium albiflorum	0.2	10									+	2
Vancouveria hexandra	0.3	10									+	2
Smilacina stellata												
Trientalis latifolia												
Luzula parviflora	0.4	10									+	2
Linnaea borealis												
Listera caurina												
Agrostis exarata	+	10							5.0	20	1.0	6
Rubus spectabilis									1.5	20	0.3	4
Polystichum munitum												
Sambucus racemosa												
Acer circinatum									10.0	10	2.0	2
Tsuga heterophylla												
Acer macrophyllum							0.5	10			0.1	2
Total Vascular	14.7		11.8		28.8		35.9		61.1		30.5	
Bryophyte												
Leucolepis menziesii			0.8	10	10.3	60			15.0	80	5.2	30
Stokesiella praelongum			3.1	80	5.2	80	33.6	10	16.9	10	11.8	36
Brachythecium frigidum					15.2	40			1.9	30	3.5	14
Rhacomitrium aciculare	6.5	50									1.3	10
Stokesiella oreganum							6.5	30			1.3	6
Scleropodium obtusifolium	16.4	50									3.3	10
Marchantia												
Plagiomnium insigne			17.1	100			6.8	80	5.6	60	5.9	48
Total Bryophyte	22.9		21.0		31.0		46.9		39.5		32.3	

The pioneer small-herb community made up 9% of all riparian vegetation cover in the active zone on Mack Creek. It was found on only one of nine other stream segments surveyed, a low gradient first-order stream with considerable siltation and low shrub cover. It covered less than 2% in the active zone but 8% on minislides in the border zone.

	Pioneer *Boykinia elata* community						Pioneer *Tolmiea menziesii* community							
	Bedrock substrate						Bedrock; large-boulders							
	N = 10		N = 10		All plots		N = 10		N = 10		N = 10		All plots	
Species	cov.	con.	cov.	con.	Ave. cover	Con-stancy	cov.	con.	cov.	con.	cov.	con.	Ave. Cover	Con-stancy
Vascular														
Montia parvifolia			0.1	10	+	5	0.3	20	18.0	80	2.0	40	6.8	47
Montia sibirica							1.4	40	0.1	10	1.1	20	0.9	23
Galium triflorum	+	10	1.5	70	0.8	40	0.9	20	1.6	30	2.0	40	1.5	30
Circaea alpina			0.6	20	0.3	10	1.0	20	0.3	10	0.4	20	0.6	17
Oxalis oregana							0.8	40	0.8	20	0.1	20	0.6	27
Trisetum canescens	0.3	50	1.3	80	0.8	65	0.3	10	1.9	50	2.3	50	1.5	37
Festuca subulata	0.2	20	1.2	60	0.7	40			2.9	40	3.7	40	2.2	27
Stellaria crispa									0.5	10	0.1	20	0.2	10
Boykinia elata	39.0	100	70.5	100	54.8	100	0.1	20			0.9	40	0.3	20
Tolmiea menziesii			0.5	10	0.3	5	14.8	100	8.9	100	10.1	100	11.3	100
Mitella ovalis	6.9	80	3.3	50	5.1	65	0.1	10			0.4	30	0.2	13
Tiarella unifoliata														
Petasites frigidus			1.5	20	0.8	10								
Adiantum pedatum														
Aruncus sylvester														
Hydrophyllum tenuipes														
Stachys cooleyae														
Epilobium angustifolium														
Athyrium filix-femina														
Rubus parviflorus														
Hieracium albiflorum									0.2	10			+	3
Vancouveria hexandra														
Smilacina stellata	0.1	10			+	5								
Trientalis latifolia	+	10			+	5								
Luzula parviflora														
Linnaea borealis	2.7	30	2.5	10	2.6	20								
Listera caurina			0.2	30	0.1	15								
Agrostis exarata														
Rubus spectabilis														
Polystichum munitum	1.2	20			0.6	10								
Sambucus racemosa											3.0	10	1.0	3
Acer circinatum														
Tsuga heterophylla											1.0	10	0.3	3
Acer macrophyllum														
Total Vascular	50.4		83.2		66.8		19.7		35.2		27.1		27.3	
Bryophyte														
Leucolepis menziesii	0.2	20	0.2	10	0.2	15								
Stokesiella praelongum	41.2	100	77.0	100	59.1	100	9.0	90	1.0	10	2.0	20	4.0	40
Brachythecium frigidum	27.7	100	4.5	70	16.1	85	41.5	100	57.5	100	63.0	100	54.0	100
Rhacomitrium aciculare	10.0	70	0.5	10	5.3	40	22.5	80	10.5	100	18.0	100	17.0	93
Stokesiella oreganum														
Scleropodium obtusifolium			10.7	70	5.4	35	5.0	70	6.5	90	4.0	40	5.1	67
Marchantia	1.0	10			0.5	5								
Plagiomnium insigne														
Total Bryophyte	80.1		92.9		86.5		78.0		75.5		87.0		80.1	

Wet-rock pioneer communities

Wet-rock pioneers Boykinia elata and Tolmiea menziesii are capable of colonizing moss-covered rock faces or large boulders that remain wet all year. These locations are frequently badly battered by high winter streamflow.

Some sediment may be deposited during the spring and summer months. The moss layer may be washed clean during the winter but also reaches the depth of substrate found in the Bryophyte/Montia parvifolia stands (Figure 5).

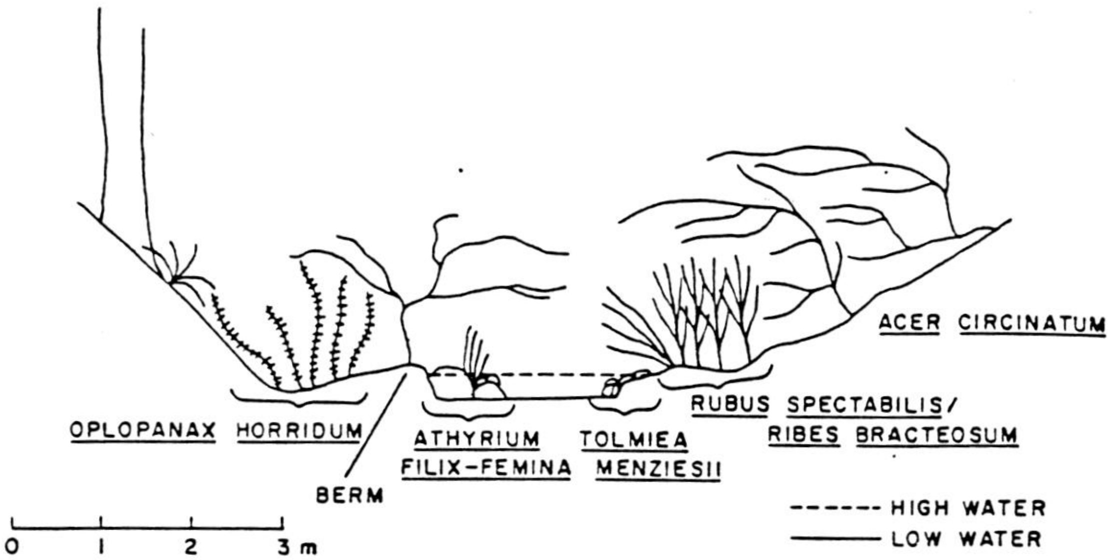


Figure 5. Cross section of a small moderate-gradient stream with some common vegetation patterns. Winter water table shown as a broken line.

Pioneer Boykinia elata *community*.--Boykinia elata stands occur in warm, sunny locations, which suggests sensitivity to cold and shade. Total vascular cover averages 67%. Only three vascular species exceed 1% cover, Boykinia elata 55%, Mitella ovalis 5%, and Linnea borealis, a forest intrusive (Table 5). Trisetum canescens and Festuca subulata have 65% and 40% constancy, respectively, but less than 1% cover.

The moss layer, typically well developed, averages 87% cover. Brachythecium and Stokesiella praelongum, common mosses of wet places, have highest cover. Scleropodium obtusifolium, a moss found beside fast moving water, is found in 7 of 20 plots, Rhacomitrium aciculare is found in 8.

Pioneer Tolmiea menziesii *community*.--Tolmiea menziesii occupies sites analogous to Boykinia in cooler, darker locations. Average cover for Tolmiea in sampled stands is 11% (Table 5). Total vascular cover is 27%. Several species, including Galium triflorum and the grasses Trisetum canescens and Festuca subulata, are found with constancy between 23% and 36% and cover values of 1% or 2%. Montia parvifolia occurs in 47% of sampled stands and has an average cover of 6.8%.

In the moss layer, Brachythecium frigidum replaces Stokesiella praelongum as dominant (100% frequency and 54% cover). Rhacomitrium aciculare, a species of splash zones, has 96% constancy and 17% cover. Total moss cover is 80%; the remainder is bare rock.

Rhyzomatous clans and communities

Petasites frigidus, Hydrophyllum tenuipes, Stachys cooleyae, Mimulus guttatus, and, to a certain extent, Epilobium angustifolium survive streamflow with a dense, matted root system. They may reestablish themselves from rootstocks, even after major disturbances such as debris torrents. Because they reproduce clonally, they tend to form clans rather than communities.

The pattern of clan distribution is interesting. In clearcuts, Petasites frigidus, Mimulus guttatus, Stachys cooleyae, and Epilobium angustifolium crowd out other species by developing vigorously and are typically separated along temporal and spatial gradients. The spatial arrangement is Mimulus guttatus nearest the center of the active channel, Petasites frigidus next, Stachys cooleyae at the edge of the active zone, and Epilobium angustifolium on the bank. Light availability seems to be a factor in the close competition. The short Mimulus guttatus creeps furthest into full sunlight.

Mimulus guttatus develops under water in the early summer and pushes farthest into the active channel. It emerges at about the time that Petasites frigidus is flowering at the channel edge. Mimulus guttatus develops fully, reaches 100% cover by midsummer, and declines. By this time, Petasites frigidus flowers have died, and the strong growing leaves begin to eclipse Mimulus guttatus.

Stachys cooleyae can overtop Petasites frigidus and so hold its own along the bank, although Petasites frigidus is a species which can colonize even dry berm tops if the soil is coarse enough to permit free rhizome penetration. Epilobium angustifolium, commonly found in clearcuts, becomes exceedingly vigorous beside the stream. Stachys and Epilobium reach maturity in late summer and early fall.

Although the above clans are true of the clearcut, under old-growth canopy, three rhyzomatous herbs appear in riparian stands with numerous other species. Although their extent was limited, these stands were sampled for community stand table descriptions. Petasites frigidus and Stachys cooleyae were sampled in 10 quadrats and Hydrophyllum tenuipes in 20.

Petasites frigidus *community*.--Petasites frigidus is found in open places in running water where it may form large monotypic stands. Under old-growth canopy other species compete successfully, and a seral community dominated by Petasites frigidus results. In these stands Petasites frigidus has 36% of a total vascular cover of 77% (Table 6). Only 14 species were found in the measured stands. Tolmiea menziesii (17% cover), found in the shade, Epilobium

Table 6. Stand tables for *Rhyzomatous* communities and the *Athyrium filix-femina* community. Cover and constancy are in percent. N = number of plots.

	Rhyzomatous communities									
	Petasites fridigus		*Hydrophyllum tenuipes*						*Stachys cooleyae*	
	N = 10		N = 10		N = 10		All plots		N = 10	
Species	cov.	con.	cov.	con.	cov.	con.	Ave. cover	Constancy	cov.	con.
Vascular										
Montia parvifolia			0.3	20			0.2	10		
Montia sibirica	0.3	30	0.5	40	1.1	20	0.8	30	4.3	50
Galium triflorum	3.8	60	4.3	60	5.8	20	5.1	40	11.2	90
Circaea alpina	0.1	10	1.1	30	0.4	20	0.8	25	0.3	10
Oxalis oregana	0.8	40	1.1	20	14.4	100	7.8	60	7.6	80
Trisetum canescens	1.3	40	1.5	30	0.1	10	0.8	20		
Festuca subulata	1.5	10			0.1	10	+	5	5.3	70
Boykinia elata	0.1	10	3.5	10	+	10	1.8	10	12.5	50
Tolmiea menziesii	17.0	90	4.2	20	2.2	20	3.2	20	0.6	20
Mitella ovalis	0.2	10			0.3	10	0.2	5	0.5	10
Tiarella unifoliata			0.1	10			+	5		
Petasites frigidus	36.3	70								
Adiantum pedatum										
Aruncus sylvester	3.5	10								
Hydrophyllum tenuipes			36.9	100	56.5	100	46.7	100	11.1	60
Stachys cooleyae									25.5	30
Epilobium angustifolium	6.5	20							2.5	10
Athyrium filix-femina									8.6	40
Rubus parviflorus										
Streptopus amplexifolius			0.3	10			0.2	5		
Vancouveria hexandra			0.1	10			+	5		
Epilobium watsonii									2.2	30
Trientalis latifolia									8.2	50
Luzula parviflora										
Linnaea borealis									1.0	10
Gymnocarpium dryopteris	5.0	10								
Anemone lyallii	1.0	10	+	10			+	5		
Agrostis exarata										
Viola sp.										
Osmorhiza chilensis									0.3	20
Anemone deltoidea										
Rubus spectabilis										
Acer circinatum										
Total Vascular	77.4		53.9		80.9		67.4		101.7	
Bryophyte										
Rhizomnium glabescens					0.5	10	0.3	5		
Leucolepis menziesii			1.5	10	0.5	20	1.0	15	7.5	30
Stokesiella praelongum	1.5	30	1.0	20	2.5	10	1.8	15	18.5	50
Brachythecium frigidum	18.0	60	17.0	60	22.2	90	19.6	75	12.0	40
Rhacomitrium aciculare			1.0	20	1.5	30	1.3	25		
Scleropodium obtusifolium					0.3	10	0.2	5	8.5	50
Plagiomnium insigne									11.5	60
Rhytidiadelphus triquetrus	1.5	30					24.0			
Total Bryophyte	21.0		20.5		27.5				58.0	

angustifolium (7% cover), found in disturbed clearings, and Galium triflorum (4% cover), are the most common associates, which shows the adaptability of Petasites frigidus.

Moss cover is only 21%; Brachythecium frigidum averages 18%. Moss cover is not consistant; total frequency is only 60%.

	Athyrium filix-femina community									
	N = 10		N = 10		N = 10		N = 10		All plots	
Species	cov.	con.	cov.	con.	cov.	con.	cov.	con.	Ave. cover	Constancy
Vascular										
Montia parvifolia					0.1	10			+	3
Montia sibirica	0.4	20	2.0	60	1.9	50	0.1	10	1.1	35
Galium triflorum	1.5	30	0.6	20	0.2	20	1.5	30	1.0	25
Circaea alpina			+	10	1.1	20	3.1	70	1.1	25
Oxalis oregana	3.3	30			1.6	60	15.8	100	5.2	48
Trisetum canescens			0.1	10	1.0	10			0.3	5
Festuca subulata	0.6	20							0.2	5
Boykinia elata	0.1	10			+	10	8.5	50	2.2	18
Tolmiea menziesii	2.5	10	1.4	30	3.8	40	7.9	80	3.9	40
Mitella ovalis			0.2	10			0.2	10	0.1	5
Tiarella unifoliata										
Petasites frigidus										
Adiantum pedatum	11.0	30					2.0	10	3.3	10
Aruncus sylvester										
Hydrophyllum tenuipes			0.3	10	1.5	10			0.5	5
Stachys cooleyae							6.5	30	1.6	8
Epilobium angustifolium	8.0	10							2.0	3
Athyrium filix-femina	76.0	100	28.0	100	77.0	100	5.5	40	46.6	85
Rubus parviflorus							40.0	100	10.0	
Streptopus amplexifolius										
Vancouveria hexandra			5.0	10					1.3	3
Epilobium watsonii										
Trientalis latifolia										
Luzula parviflora	5.0	20							1.3	5
Linnaea borealis										
Gymnocarpium dryopteris	7.5	10							1.9	3
Anemone lyallii										
Agrostis exarata			2.3	30	+	10			0.6	10
Viola sp.			1.6	20					0.4	5
Osmorhiza chilensis					0.2	10			+	3
Anemone deltoidea										
Rubus spectabilis					10.0	20			2.5	5
Acer circinatum	10.0	100							2.5	3
Total Vascular	125.9		41.5		98.4		91.1		89.2	
Bryophyte										
Rhizomnium glabescens			9.0	30			0.5	10	2.4	10
Leucolepis menziesii	0.5	10	0.9	20	0.2	10	1.0	20	0.7	15
Stokesiella praelongum	0.5	10	4.0	20	15.0	50	20.5	50	10.0	33
Brachythecium frigidum	20.0	40	17.0	70	19.0	60	20.0	60	19.0	58
Rhacomitrium aciculare										
Scleropodium obtusifolium	6.0	20			5.0	20			2.8	10
Plagiomnium insigne							2.0	30	0.5	8
Rhytidiadelphus triquetrus										
Total Bryophyte	27.0		30.9		39.2		44.0		35.3	

Stachys cooleyae *community*.--Stachys cooleyae is found most often in open, sunny situations, including the edges of third-order and larger streams, clearcuts, and gravel bars. It may develop fully in areas that are never free of running water.

In the seral stands sampled under old-growth, Stachys averages 26% (Table 6). Sixteen species were represented, 12 with more than 1% cover. Total cover of 102% reflects the mature community but also the sunny habitat. Boykinia (13%) and Epilobium angustifolium (3%) also indicate relatively open situations.

Moss cover is 58%. Brachythecium frigidum, Stokesiella praelongum and Plagiomnium insigne, wet land species, each cover more than 10%. Frequency is low; Stokesiella occurs in only 50% of the sampled quadrats.

Hydrophyllum tenuipes *community*.--Hydrophyllum tenuipes dominates in the shade along stream banks, generally where there is some soil, water speed is moderate at high flow, and where the water-free season is relatively long.

Hydrophyllum tenuipes contributes 47% cover out of a total of 67% (Table 6). Measured plots had 15 species, five with more than 1% cover. Moss cover averages 24% with Brachythecium frigidum contributing 20%.

Hydrophyllum tenuipes and its close relative Hydrophyllum fendleri are also found as common understory herbs in very wet forests. Low incidence of Epilobium angustifolium and Boykinia elata indicate cool shaded conditions.

The community is closely related to the Athyrium filix-femina community described later and may belong to a complex of communities in which Athyrium is the key species.

Well-developed herbaceous communities

Boykinia elata *community*.--The Boykinia elata community represents a mid-seral successional stage on soil but is climax on wet logs in the stream. Boykinia elata is sensitive to cold and shade and is confined to elevations below 800 m. Stands are usually found on fine soil or organic matter that is permanently wet. The substrate appears to have little resistance to water action. The best examples of Boykinia elata types are in scoured areas that have then remained undisturbed for 10 years. Periodic flooding with no battering is common.

Total vascular cover in the herbaceous layer averages 110% (Table 7). In addition, a high overstory of shrubs (or Aralia californica) is not uncommon. Average shrub overstory is 33%. As might be expected, the total of vascular species increases to 29; however, four are overstory and one, Rubus ursinus, intrudes from adjacent habitats.

Boykinia elata has 62% cover. Mitella ovalis, the most frequent associate, has 13% cover. The aggressive and ubiquitous Petasites frigidus constitutes 11% cover.

The moss layer is 50%; low cover is caused by the basal diameters of the vasculars. Important components almost exactly parallel the Tolmiea menziesii community, but Leucolepis menziesii is more common.

Table 7. Stand tables for the *Boykinia elata*, *Tolmiea menziesii* and *Mitella ovalis*/*Marchantia* communities. Cover and constancy are in percent. N = number of plots.

	Boykinia elata community									
	N = 10		N = 10		N = 10		N = 10		All plots	
Species	cov.	con.	cov.	con.	cov.	con.	cov.	con.	Ave. cover	Constancy
Vascular										
Montia parvifolia	0.1	20							+	5
Montia sibirica			+	10					+	3
Galium triflorum	2.4	50	1.2	70	0.6	30	4.1	30	2.1	45
Circaea alpina										
Oxalis oregana	4.0	40	3.1	30					1.8	18
Trisetum canescens			0.1	10	0.1	40	2.8	50	0.8	25
Festuca subulata	2.4	70	2.0	60	0.1	10	2.1	30	1.7	43
Stellaria crispa	0.2	20	+	20					+	10
Boykinia elata	68.5	100	60.0	100	64.5	100	53.5	100	61.6	100
Tolmiea menziesii	8.5	20	0.1	10	0.7	20	6.0	30	3.8	20
Mitella ovalis	20.4	100	16.8	100	4.2	60	9.9	80	12.8	85
Tiarella unifoliata	1.1	40	2.4	30	1.8	30	0.2	10	1.4	28
Petasites frigidus	13.5	30	27.5	30	2.7	20	1.0	10	11.2	23
Adiantum pedatum					9.5	20	22.5	30	8.0	13
Aruncus sylvester							2.4	30	0.6	8
Hydrophyllum tenuipes										
Stachys cooleyae										
Athyrium filix-femina			+	10					+	3
Ranunculus uncinatus			0.1	10					+	3
Galium oreganum			+	10					+	3
Blechnum spicant			1.5	10					0.4	3
Carex sp.					5.3	50	0.2	20	1.4	18
Rubus ursinus					0.3	20			+	5
Adenocaulon bicolor					2.1	30			0.5	8
Streptopus amplexifolius					1.0	10	5.7	40	1.7	13
Hieracium albiflorum					0.2	10			+	3
Vancouveria hexandra					0.1	10			+	3
Trientalis latifolia							0.1	10	+	3
Linnaea borealis										
Listera caurina	0.5	20							0.1	5
Achlys triphylla										
Aralia californica	30.0	30					70.0	70	25.0	25
Vaccinium parvifolium	15.1	50	15.0	20					7.5	18
Tsuga heterophylla	2.8	20			+	10			0.7	8
Acer macrophyllum	0.5	10	1.0	10					0.4	5
Total Vascular	170.1		130.8		93.3		180.4		143.6	
Bryophyte										
Hylocomium splendens	1.0	10							0.3	3
Dicranum fuscescens	1.2	30							0.3	8
Rhizomnium glabrescens	6.7	70	2.0	40			2.7	40	2.9	38
Leucolepis menziesii	35.0	100	25.2	90	5.0	20	3.0	40	17.1	63
Stokesiella praelongum					5.0	30	1.5	20	1.6	13
Brachythecium frigidum	12.6	80	17.1	60	25.5	70	47.5	100	25.6	78
Stokesiella oreganum			0.5	10	1.5	20			0.5	8
Hypnum circinale			0.1	10					+	3
Marchantia	+	10							+	3
Plagiomnium insigne	0.7	80	0.2	20	+	10	3.2	40	1.0	38
Rhytidiadelphus triquetrus	1.1	30			1.5	20			0.9	13
Total Bryophyte	58.3		43.3		38.5		58.9		49.8	

The Boykinia elata community is found in the wettest sites. On WS 2 where it is well established, it is four times more common in the active zone than in the border zone. On other surveyed streams it is found only in the active zone (Table 3, Figure 6).

Table 7 (cont.)

Species	*Tolmiea menziesii* community						*Mitella ovalis/Marchantia* community					
	N = 10		N = 10		All plots		N = 10		N = 10		All plots	
	cov.	con.	cov.	con.	Ave. cover	Con-stancy	cov.	con.	cov.	con.	Ave. cover	Con-stancy
Vascular												
Montia parvifolia	1.0	20	0.3	10	0.7	15						
Montia sibirica	0.5	10	2.9	40	1.7	25	0.1	10			+	5
Galium triflorum	8.7	70	8.1	70	8.4	70	1.2	60	1.7	40	1.5	50
Circaea alpina	7.3	50	7.7	90	7.5	70	0.6	20	1.3	50	1.0	35
Oxalis oregana	7.7	60	5.6	60	6.7	60						
Trisetum canescens	2.6	50	0.4	10	1.5	30	0.1	10			+	5
Festuca subulata	1.1	40			0.6	20						
Stellaria crispa	0.1	10	+	10	+	10						
Boykinia elata	6.1	50			3.1	25	27.4	100	45.9	100	36.6	100
Tolmiea menziesii	17.2	100	22.7	100	20.0	100	0.2	10			0.1	5
Mitella ovalis	2.8	50	0.6	20	1.7	35	31.1	100	30.5	100	30.8	100
Tiarella unifoliata			0.5	10	0.3	5	10.2	90	5.4	50	7.8	70
Petasites frigidus			1.0	10	0.5	5			14.5	30	7.3	15
Adiantum pedatum									2.5	10	1.3	5
Aruncus sylvester												
Hydrophyllum tenuipes	0.1	10			+	5						
Stachys cooleyae			1.5	20	0.8	10						
Athyrium filix-femina												
Ranunculus uncinatus							0.3	10			0.2	5
Galium oreganum												
Blechnum spicant							7.5	30			3.8	15
Carex sp.									2.1	50	1.1	25
Rubus ursinus							0.8	10	4.4	50	2.6	30
Adenocaulon bicolor							2.4	20	1.6	20	2.0	20
Streptopus amplexifolius												
Hieracium albiflorum												
Vancouveria hexandra												
Trientalis latifolia												
Linnaea borealis									1.0	10	0.5	5
Listera caurina												
Achlys triphylla							2.0	10			1.0	5
Aralia californica							100.0	100	100.0	100	100.0	100
Vaccinium parvifolium												
Tsuga heterophylla												
Acer macrophyllum												
Total Vascular	55.2		51.3		53.3		183.9		210.9		197.4	
Bryophyte												
Hylocomium splendens												
Dicranum fuscescens												
Rhizomnium glabrescens	1.0	20	1.0	10	1.0	15	6.0	80	5.5	80	5.8	80
Leucolepis menziesii	10.5	50	1.0	10	5.8	30						
Stokesiella praelongum	3.5	20	15.0	30	9.3	25	11.5	50	3.5	50	7.5	50
Brachythecium frigidum	54.0	80	22.5	70	38.3	75	28.5	80	1.0	10	14.8	45
Stokesiella oreganum												
Hypnum circinale												
Marchantia							50.5	100	89.0	100	69.8	100
Plagiomnium insigne	4.0	20	3.5	30	3.8	25	3.0	40	1.0	20	2.0	30
Rhytidiadelphus triquetrus	5.0	10			2.5	5						
Total Bryophyte	78.0		43.0		60.5		99.5		100.0		99.8	

Tolmiea menziesii *community*.--The Tolmiea menziesii community is well developed for a community in an active channel. Stands are found on stabilized sand and gravel deposits and occasionally on boulders and logs (Figure 5).

Total vascular cover averages 53% (Table 7); pioneer communities average 30% and 27%. Tolmiea menziesii is found in 100% of all quadrats. There are only 15 vascular associates compared with 21 in the small-herb community. The smaller number is due in part smaller sample size, but also to the exclusion of species such as Hieracium albiflorum which cannot compete in the dense vegetation found in the Tolmiea menziesii community.

Moss cover averages 50%, and 10% to 15% of the substrate, ordinarily rock, is exposed. The addition of Rhizomnium glabescens, Leucolepis menziesii, Plagiomnium insigne, and Rhytidiadelphus triquetrus common on undisturbed sites and on soil, and the loss of Rhacomitrium aciculare and Scleropodium obtusifolium characteristic of exposed rock, reflect the change in habitat from colonized rock to stabilized gravel and soil.

Tolmiea menziesii is a community of wet areas. On WS 2 it is 3 times more common in the active zone than in the border zone. It was found in the active zone at Mack Creek and The Black Hole, but in the border on Tiny Trout. The species Tolmiea menziesii is adaptable to the deep litter of streamside forests, particularly on low terraces, and may reach 100% cover. Because other characteristics of a Tolmiea community are missing, it is merely a characteristic species of the hardwood forest.

Mitella ovalis/Marchantia *community*.—Occasionally a semiporous barrier will be deposited upon a slightly sloping, nonporous surface across which water seeps all year, such as a small log impeding drainage from an almost flat rock. If there is no disturbance, organic matter and extremely fine inorganic particles build up and form an aqueous muck. Sampled depths varied from 1 to 6 cm.

The bryophyte layer nears 100% and Marchantia, the dominant species, averages 70% cover (Table 7). This is the only community where Marchantia is not rare. Brachythecium frigidum is the most common associate.

The vascular species closely approach those of the Boykinia elata community but lack some of the larger herbs and disturbed-earth invasives. Cover of Boykinia elata and Mitella ovalis averages 37% and 31%, respectively (62% and 13% in the Boykinia community). A 100% overstory of Aralia californica was present in all stands.

The Mitella ovalis/Marchantia community was found only on WS 2. It occupies less than 1% of the riparian area and is found only in the border zone. Nonetheless, it has practical importance as an indicator beyond its area or biomass. Marchantia and Mitella give the surface a flat firm appearance, but the smooth, almost slimy consistency of the muck and lack of surface irregularities in the bedrock substrate make the footing treacherously slick.

Arthyrium filix-femina *community*.--The largest and most well-developed herb communities are dominated by Athyrium filix-femina. Athyrium can colonize cracks in rocks and crevises between rocks and so can be a true pioneer species. More frequently it is found as a dominate on perennially wet soil with other herbs.

Athyrium can survive severe battering if the roots are protected and in constant contact with water. In the sampled stands, Athyrium averaged 47% cover, but 100% cover is not uncommon (Table 6). Total cover averages 89%. The most frequent associates are Tolmiea menziesii, Montia sibirica, and Oxalis oregana. The low herb associates are, in fact, much the same as the Tolmiea menziesii or Boykinia elata communities. Rubus parviflorus was found infrequently but with high cover (40%) in those quadrats where it occurred. Twenty-four vascular species were found in these stands; fifteen with cover values greater than 1%.

The moss layer averages only 35% total cover. Part of the remainder is plant bases. Brachythecium frigidum, found in permanently wet areas, covers 20%, and the wet soil species Stokesiella praelongum covers another 10%.

Only fragments of this community develop on very small streams, commonly in the border zone. On WS 2 it is distributed about equally between active and border zones. On larger streams it is usually found in the border zone (Figure 6).

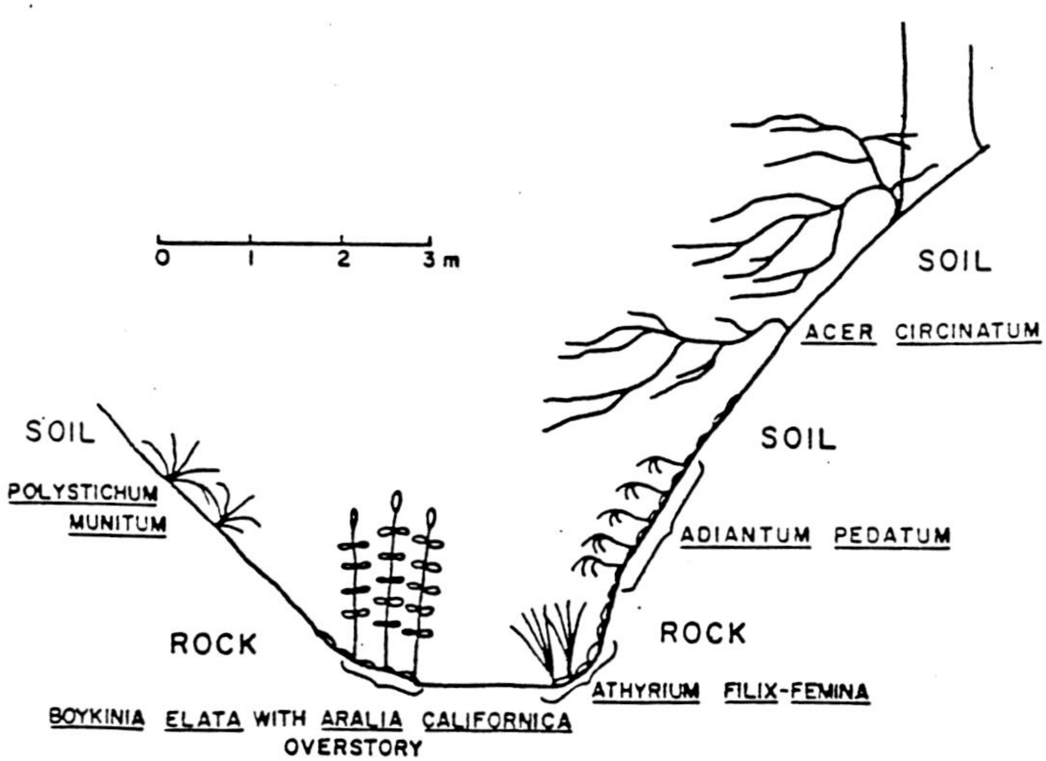


Figure 6. Cross section of a rock substrate stream with some common vegetation patterns.

The three communities dominated by the rhyzomatous herbs mentioned earlier (Petasites frigidus, Stachys cooleyae and Hydrophyllum tenuipes) may merely be phases of the Athyrium filix-femina community. They were not found on other stream segments sampled. The arrangement of streamside communities makes broken and isolated stands appear distinctive. A more extensive area might have a more homogeneous appearance. Observations on Mack Creek since sampling lead to the hypothesis that under an old-growth canopy all three phases would develop into some type of Athyrium filix-femina stand.

Mixed fern-mixed large herb vegetation.—One floristically rich herb community, probably a stage in succession, did not occur frequently enough to be sampled. It is dominated by a wide assortment of large perennial herbs such as Aruncus sylvester, Athyrium filix-femina, Aralia californica, and Heracleum lanatum. A single stand was found on WS 2 and another on Mack Creek. No other such stands were found on the stream segments surveyed. These stands occupy habitats scoured several decades previously (on WS 2 about 30 years before) in which shrub communities are slow to develop. In the WS 2 stand, the slope is 45° to 55°, soil thin and unstable and shade dense. On Mack Creek, the slope is 10°, winter overflow regular and probably not violent, but scientist impact had sheared the shrubby layer and allowed full development of herbs.

Shrub communities

Rubus spectabilis/Ribes bracteosum *community*.--The Rubus spectabilis/Ribes bracteosum community is the most common shrub complex rooted on the stream bottom alluvium in the western Cascade Range. Generally the overstory canopy is somewhat open, which is ideal for development of Rubus spectabilis. The soil is generally rocky alluvium but may contain a high percentage of fines and a humus layer. Leaf litter on some of the sampled stands was sufficiently thick to exclude mosses. In more typical open stands, moss flora similar to that of the Tolmiea menziesii community develops on the ground. The community as a whole cannot withstand significant water damage but is frequently found in the winter active channel of streams with low effective gradients. It appears intolerant of drought.

Rubus spectabilis cover varies from 0% to 96% in the sampled areas (Table 8). Rubus spectabilis is a shrub wide-spread in the Cascade and Coast Ranges on wet habitats, including wet hillsides, avalanche tracks, seeps, and stream bottoms. In the areas sampled, however, it was generally found in a mosaic with Ribes bracteosum, which averaged from 0% to 100% cover. Ribes bracteosum is almost always found near permanent water sources, such as stream edges, while Rubus spectabilis ranges from streamside to many meters from the stream. In the Oregon Cascade Range, summer drought appears to prevent hillside colonization and confines the community to bottoms.

Table 8. Stand table for the *Rubus spectabilis/Ribes bracteosum* community. Cover and constancy are in percent. N = the number of plots

	N = 6		N = 9		N = 13		N = 9		N = 7		N = 8		N = 8		All plots	
Species	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	Ave. cover	Con-stancy
Ribes bracteosum			77.8	100	67.3	100	100.0	100	100.0	100	41.9	100	43.8	75	64.3	90
Rubus spectabilis	95.8	100	64.0	100	52.6	100					81.3	100	66.3	100	50.3	73
Athyrium filix-femina					51.9	69	38.9	100			0.8	38	33.1	75	21.6	45
Polystichum munitum			3.3	11	7.1	15	2.2	22			14.0	50			4.2	15
Acer circinatum			5.0	22			8.9	22	2.1	29			13.7	38	4.1	15
Oplopanax horridum	16.8	33	13.9	22							1.3	13	0.6	13	4.0	10
Tolmiea menziesii	4.3	33	8.4	22			2.8	11	0.3	14	6.5	25			3.0	13
Dryopteris austriaca							4.4	11	5.7	29					1.3	5
Blechnum spicant							1.7	22	7.1	14					1.1	5
Gymnocarpium dryopteris							0.7	22	1.4	14					0.3	5
Hydrophyllum tenuipes	5.8	33	1.7	33	1.9	23	•		1.0	29					1.4	17
Galium triflorum	1.5	33	0.4	22			0.9	22	3.6	14	0.9	38	0.6	13	1.0	18
Circaea alpina	8.5	33	1.3	44			0.4	22	1.3	14	0.3	25			1.3	18
Oxalis oregana	3.8	50	0.4	22					0.4	29	0.3	13			0.5	13
Stachys cooleyae	10.0	33	2.0	22			0.2	11	+	14					1.3	10
Epilobium angustifolium	1.5	33	1.7	22			1.7	11	3.6	14					1.1	10
Mitella ovalis	0.5	17	1.0	22			1.1	11			4.1	25	2.4	50	1.2	17
Montia sibirica	+	17					+	11			0.1	13			+	5
Boykinia elata	+	17	0.2	11					0.3	14					+	5
Agrostis exarata	0.8	17													+	2
Aruncus sylvester	+	17	+	11	0.7	8									0.1	5
Luzula parviflora							+	11			4.4	13			0.6	3
Epilobium watsonii							0.2	11							+	2
Heracleum lanatum							1.1	11							0.2	2
Tiarella unifoliata	0.7	33	0.2	11	1.2	85	1.3	44					1.9	37	0.8	35
Smilacina stellata					9.1	54	2.1	22							2.3	15
Vancouveria hexandra					0.2	8	+	11							+	3
Trillium ovatum					0.4	8	+	11							+	3
Achlys triphylla			0.7	11			2.8	11							0.4	3
Anemone lyallii			+	11											+	2
Rubus ursinus									2.1	29					0.2	3
Asarum caudatum											4.4	13			0.6	2
Actaea rubra													12.5	13	1.7	2
Vaccinium alaskaense			1.0	11											0.2	2
Vaccinium parvifolium			+	11											+	2
Tsuga heterophylla									0.6	29					+	3
Thuja plicata													25.0	38	3.3	5
Acer macrophyllum							0.2	11	1.4	14					0.2	3
Total Cover	149.8		183.6		192.5		172.6		131.1		160.3		199.9		173.4	

Although the large fern Athyrium filix-femina has low constancy, it is third highest in cover. Oplopanax horridum occurs occasionally in this community.

The herb layer other than ferns averages only 18% in a total average vascular cover of 173%. The herb layer contains typical herbs from the Tolmiea menziesii community.

The Rubus spectabilis/Ribes bracteosum community is found in the active zone of very small streams, but not in the outer zone. Excepting WS 2, it is present and common in the active zone of all second- and third-order streams. On Mack Creek it has highest cover in the outer zone but is well represented in the active zone, especially by Ribes bracteosum leaning over the stream from the bank (Figures 5, 7).

Oplopanax horridum *community*.—The Oplopanax horridum community occupies much the same edaphic conditions as the Rubus spectabilis/ Ribes bracteosum community but prefers cooler, shadier conditions. The two communities occur together on sites at moderately high elevations with north exposures and a closed overstory. Although it is found as a forest understory in the Chamaecyparis nootkatensis/ Oplopanax horridum community, Oplopanax appears to have little drought tolerance. In a riparian setting it is found most often on wet, seepy hillsides with complete overstory. Oplopanax also occurs in overflow channels, particularly those fed by leakage through a berm, and on berms of coarse rock with an accessible water table.

Total vascular cover in the Oplopanax horridum community is 162%, of which O. horridum contributes 94% (Table 9). The herb layer is dominated by a variety of ferns having a total cover of 43%. Athyrium filix-femina is foremost (cover 16%), but Drypoteris austriaca averages 12% cover and in one stand under a broad-leaf canopy reaches 44%. Polystichum munitum averages 29% in one stand near the break and Gymnocarpium dryopteris reaches 16% cover on a berm top. Average total of other herbs is 7.5%, in contrast to 18% in the sunnier Rubus-Ribes plots. Total number of species is 26.

Table 9. Stand table for *Oplapanax horridum* community. Cover and constancy are in percent. N = number of plots.

	N = 10		N = 10		N = 10		N = 10		N = 10		N = 10		N = 10		All plots	
Species	cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	Ave. cover	Con-stancy
Oplopanax horridum	77.0	10	97.5	10	99.0	10	97.5	10	96.5	10	94.0	10	98.5	10	94.3	100
Athyrium filix-femina	50.5	9	25.5	4	31.0	5	6.5	4	0.4	1	0.5	1	0.5	1	16.4	36
Dryopteris austriaca	12.9	6	6.5	2	14.0	8	44.5	10	6.5	6					12.1	46
Ribes bracteosum	38.0	9					14.0	4			2.0	1			7.7	20
Polystichum munitum			3.0	2	29.0	8	0.5	1	1.8	3			1.5	2	5.1	23
Acer circinatum			7.5	2					10.5	5	0.5	1	17.0	4	5.1	17
Blechnum spicant	4.0	3			6.5	4	7.5	3	4.7	4			1.6	2	3.5	23
Adiantum pedatum			8.0	3			1.0	2	9.0	1			3.5	2	3.1	11
Gymnocarpium dryopteris	3.0	4			16.0	7	0.5	1	1.5	4					3.0	23
Hydrophyllum tenuipes	0.6	2	6.0	2									10.0	2	2.4	9
Tiarella unifoliata	0.4	4	1.8	3	5.9	6			2.2	5					1.5	26
Rubus spectabilis							5.0	2			3.5	2			1.2	6
Galium triflorum			+	1											+	1
Circaea alpina			+	1									1.0	1	+	3
Oxalis oregana	+	1	0.3	4											+	7
Mitella ovalis	4.1	4					1.0	2					+	1	0.1	10
Montia sibirica			5.3	2											0.1	3
Boykinia elata			0.5	1											+	1
Smilacina stellata					1.0	1			1.6	3					0.4	6
Vancouveria hexandra					+	1									+	1
Trillium ovatum					2.5	1									+	1
Clintonia uniflora					0.5	1			2.3	6					+	10
Achlys triphylla	1.0	1													+	1
Anemone lyallii					0.3	1			0.2	1	1.0	1			+	4
Rubus ursinus					0.3	1									+	1
Vaccinium parvifolium					+	1	2.5	1	1.3	3					0.1	7
Tsuga heterophylla							6.0	2					16.0	2	3.1	6
Log			1.0	1	7.5	2					16.0	3			3.5	-
Total Cover	191.6		161.9		206.1		186.5		138.5		101.5		149.6		162.6	

The Oplopanax horridum community is most frequent in the outer zone on Mack Creek (Figure 5) but also leans over the active channel from the bank. Its single other occurrence in the survey is also over the active channel and in the outer zone (Table 3).

Acer circinatum *community*.--Acer circinatum is widespread in both forests and clearcuts. In the open it grows as a dense shrub. In shade it elongates and sprawls, rooting wherever horizontal stems reach the ground. In riparian settings it forms a midlevel canopy which can be rooted at or above the break and yet can reach well over the stream in response to light in the opening. Acer circinatum is important in nutrient cycling and in physical structure of the zone. Therefore, although the Acer canopy spreads far beyond the area of rooting and overlaps other communities, we describe areas of fairly uniform Acer circinatum dominance as a community type.

Total vascular plant cover in the Acer circinatum community is 179% (Table 10), including a sparse Ribes/Rubus community which it frequently overtops. Acer circinatum averages 97%. Ferns are again the chief herbs with 44% cover. Polystichum munitum covers the greatest area (15%) and is much more constant (45%) than Athyrium filix-femina

Table 10. Stand table for *Acer circinatum* community. Cover and constancy are in percent. N = number of plots.

	N = 10		N = 10		N = 10		N = 10		N = 10		N = 10		All plots	
Species	cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	Ave. cover	Constancy
Acer circinatum	100.0	10	99.5	10	98.0	10	93.0	10	97.5	10	95.0	10	97.2	100
Polystichum munitum	25.5	7	14.3	7	34.5	5	1.8	2	9.0	4	6.0	2	15.2	45
Athyrium filix-femina	1.1	2	9.0	2	16.5	3			18.5	5	29.0	5	12.4	28
Rubus spectabilis	6.1	1			8.0	3	18.5	3	15.5	6	22.5	8	11.8	35
Vaccinium alaskaense	8.5	3			22.0	3	22.6	10	1.5	1			9.1	28
Gymnocarpium dryopteris	20.2	9	11.0	3			10.2	3	11.0	3			8.7	30
Ribes bracteosum			0.1	1					5.5	1	24.0	5	4.9	12
Hydrophyllum tenuipes									6.0	2	12.2	5	3.0	12
Blechnum spicant	10.0	1	5.0	1			1.0	1	0.6	2			2.8	8
Dryopteris austriaca			7.5	5	1.6	3	6.0	4					2.5	29
Adiantum pedatum			5.5	3	5.0	1			1.0	1	2.0	1	2.3	18
Oplopanax horridum									5.5	1	2.0	2	1.3	5
Tiarella unifoliata	1.1	5	3.3	5	3.6	3	0.7	3	0.4	2	4.0	2	2.2	33
Galium triflorum					0.1	2							+	3
Circaea alpina			+	1					0.2	2	0.3	1	+	7
Tolmiea menziesii											5.0	1	0.8	2
Mitella ovalis			+	1					+	1	0.3	1	+	5
Boykinia elata			+	1					+	1	+	1	+	5
Streptopus amplexifolius											1.0	1	+	2
Smilacina stellata							+	1					+	2
Trillium ovatum			1.0	1					+	1			+	3
Clintonia uniflora					1.6	1							+	2
Rubus ursinus											0.5	1	+	2
Goodyera oblongifolia	+	1											+	7
Cornus canadensis			+	1	0.7	1	0.3	2					+	2
Linnaea borealis			0.2	2									+	3
Asarum caudatum			0.4	1					+	1			+	3
Actaea rubra									1.0	1			+	2
Vaccinium parvifolium			2.7	4	1.0	2	1.6	2					0.8	13
Vaccinium membranaceum							2.5	1					+	2
Thuja plicata			20.0	3									3.3	5
Log			6.0	1			21.0	6	7.5	2	8.0	2	7.1	
Total Cover	172.7		179.9		192.6		158.3		168.1		203.9		179.3	

(12% cover, 28% constancy). Gymnocarpium dryopteris is third in cover (9%) but is found as frequently as Athyrium filix-femina. Cover of shrubs other than Acer circinatum is 28%. Rubus spectabilis is most important (12% cover, 35% constancy). Vaccinium spp. covers 10% (constancy 43%).

Acer circinatum is generally rooted in the outer zone (about 80% on Mack Creek) and only rarely in the active zone (3% on Mack Creek). The distribution of cover (over all surveyed segments) is different, however; Acer circinatum covers 23% of the active zone and 32% of the outer zone. The outer zone, generally larger than the active zone, had about 72% of total Acer circinatum cover and the active zone had 20% (Figures 3, 7).

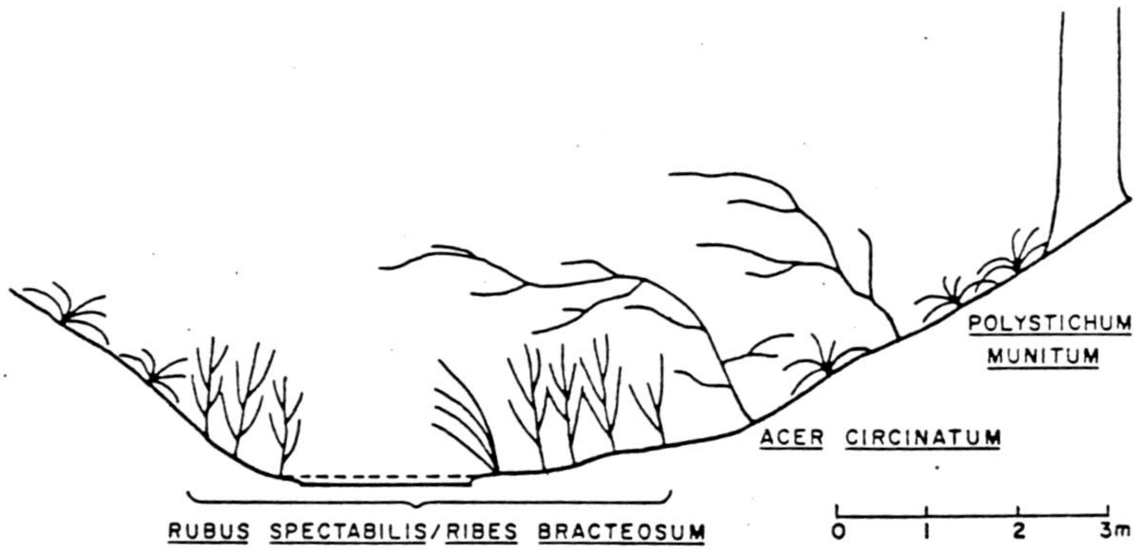


Figure 7. Cross section of a small low-gradient stream with some common vegetation patterns.

Topographic climax communities

Bryophyte/Montia parvifolia *community*.--Of little importance (except that it provides relatively firm footing) the Bryophyte/Montia parvifolia community is typically found on large boulders that are dry in the summer. Stands are above all but the high water flows. They occur in sunny and well shaded locations. Soil formation is 1 cm or less and is composed of accumulated litter and moss pollsters. Slopes are 0° to 90°, but rarely overhanging.

Total vascular cover averages 29% (Table 11). Montia parvifolia, the dominant herb, and Montia sibirica, also a frequent component, seed readily in moss. Cover of Montia parvifolia is 17%, a high value because of its runner-like growth pattern.

Table 11. Stand table for Bryophyte/*Montia parvifolia* and *Petasites frigidus*/*Brachythecium-frigidum* communities. Cover and constancy are in percent. N = number of plots. Degree of slope is shown where pertinent.

	Bryophyte/*Montia parvifolia* community							
	N = 10		N = 10		N = 10		All plots	
Species	cov.	con.	cov.	con.	cov.	con.	Ave. cover	Con-stancy
Vascular								
Montia parvifolia	3.7	90	13.5	100	32.6	100	16.6	97
Montia sibirica	2.5	50	12.1	40	0.8	40	5.1	43
Galium triflorum								
Circaea alpina	0.1	10			0.6	20	0.2	10
Oxalis oregana	0.1	10					+	+
Trisetum canescens	0.2	10	1.5	30	2.2	30	1.3	23
Festuca subulata	0.1	10			3.3	30	1.1	13
Boykinia elata								
Tolmiea menziesii	+	10	0.3	30	0.5	10	0.2	16
Mitella ovalis								
Tiarella unifoliata					0.3	10	0.1	3
Petasites frigidus					1.5	10	0.5	3
Aruncus sylvester								
Epilobium angustifolium			2.5	20			0.8	10
Athyrium filix-femina								
Epilobium watsonii			1.0	10			0.3	3
Mimulus guttatus			0.1	10	1.5	10	0.5	7
Rubus ursinus								
Streptopus amplexifolius								
Hieracium albiflorum								
Anaphalis margaritacea								
Equesetum telmatia								
Luzula parviflora								
Listera caurina								
Carex deweyana								
Viola sp.								
Aralia californica								
Sambucus racemosa			6.0	20			2.0	7
Acer circinatum					1.5	20	0.5	7
Salix sp.								
Alnus sinuata								
Total Vascular	6.7		37.0		44.8		29.2	
Bryophyte								
Brachythecium frigidum	1.3	40	1.3	10			0.9	17
Stokesiella praelongum	6.2	40	28.8	80	23.7	80	19.6	67
Philonotis fontana								
Leucolepis menziesii					1.5	10	0.5	3
Marchantia								
Scleropodium obtusifolium	48.0	80	55.5	80	35.0	60	46.2	73
Rhacomitrium aciculare	12.5	60	8.3	50	15.8	70	12.2	60
Plagiomnium insigne					2.0	10	0.7	3
Ceratodon purpureus	1.4	20	1.5	10	0.8	10	1.2	13
Rhacomitrium heterostichum			1.0	10			0.3	3
Unidentified	2.5	50	1.3	40	1.2	50	2.1	47
Total Bryophyte	71.9		97.7		80.0		83.2	

Moss cover averages 84% and bare rock 6%. Rhacomitrium acciculare, Stokesiella praelongum, and Scleropodium obtusifolium dominate.

This community is subject to extreme summer drought because the habitat lacks water storage capacity. Montia parvifolia is a perennial capable of developing to maturity by mid-June and remaining dormant through the summer.

Petasites frigidus/Brachythecium frigidum community													
N = 10		N = 10		N = 10		N = 10		N = 10		N = 10			
70°		42°		15°		15°		5°		5°		All plots	
cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	Ave. cover	Con-stancy
0.9	3							+	4	2.5	5	0.6	20
25.3	7	0.2	1	0.8	1	0.5	1	0.1	1			4.5	18
								+	2	+	1	+	5
3.1	2							2.1	5	13.2	9	3.1	30
		0.2	1									+	2
								0.2	3			+	5
3.7	7			1.6	3	12.4	5			0.3	2	3.0	28
		2.5	3									0.5	5
										0.1	1	+	2
26.0	6	56.5	10	27.0	10	36.5	10	34.5	10	35.5	10	36.0	93
4.0	1			0.5	1	0.2	1					0.8	5
						3.8	3					0.6	5
								0.4	4	0.6	6	0.2	17
								0.8	7	0.1	1	0.2	13
				0.1	1							+	2
3.3	2											0.6	3
						0.3	1					+	2
								0.2	1	0.2	1	+	3
				21.0	5	19.5	4	1.0	1			6.9	17
								0.1	1			+	2
		1.4	5									0.2	8
				2.6	4	0.3	2					0.5	12
										0.3	2	+	3
		100.0	10			11.0	2					18.5	20
						+	1					+	2
						0.2	1					+	2
66.3		160.8		53.6		84.7		39.4		52.7		76.2	
100.0	10	96.5	10	41.5	10	40.0	9	95.0	10	83.0	9	76.0	98
		2.5	1	55.5	10	59.5	10					19.6	35
				3.0	2			3.1	4	10.0	1	2.7	12
						0.5	1					+	2
		1.0	2									+	3
100.0		100.0		100.0		100.0		98.1		93.0		98.3	

The community is almost absent from the small first- and second-order streams surveyed, but is more common in third- to fifth-order streams with protruding rocks and some canopy openings.

Adiantum pedatum/precipice *community*.—Adiantum pedatum grows luxuriantly in wet cracks in rocks, especially on slopes too steep for Athyrium filix-femina. It prefers shaded north-facing slopes with a permanent water supply, but does not necessarily require seeps (Figure 6).

Slopes on sample sites average 83° and range from 50° to 110°. Substrates range from an overhanging dry rock face with little moss cover to a somewhat broken and decayed rock slope with slight soil formation and 100% moss cover. Typically, the bottom of the slope is slightly steeper than the top. Upper edges have more species, including some from the forest floor, than lower slopes. Old fern fronds still basally attached are the source of most of the accumulated litter.

Moss cover averages 58% but ranges from 5 to 100%. Wet, north-exposed faces have highest concentrations. Bryophytes found in the quadrats indicate the wide variation in surface condition; Ceratodon purpurens, typical of sterile rock cliffs, Hylocomium splendens, typical of forest floors, and Rhacomitrium aciculare indicating well-aerated water, are parts of the bryophytic flora at different locations (Table 12).

Vascular cover averages 78% but ranges from 21% to 125%. Adiantum pedatum averages 53% cover. Aruncus sylvester is fairly common on steep slopes and, being large, is second in vascular coverage (6%). Streptopus amplexifolius commonly eaten by deer, reaches large dimensions and full fruit in these inaccessible locations, but its cover is low. A total of 23 vascular species were recorded in the plots.

The Adiantum pedatum community covers approximately 2% of the riparian area on Mack Creek and is found only in the border zone. On WS 2 it covers about 3% of the riparian area, again in the border zone.

Petasites frigidus/Brachythecium frigidum *community*.—The well-defined Petasites frigidus/Brachythecium frigidum community occupies seepage areas, usually on rock surfaces, in the border zone. It was found in small quantities on Mack Creek, WS 2, and several other streams in the Andrews Reserve, but not on other streams sampled for community cover. Brachythecium frigidum forms thick 3- to 5-cm mats of moss in which Petasites frigidus, an adaptable species, can grow. The stands are found on seepage areas, with firm soil to solid rock, and on boggy muck. Gradients range from 5° to perpendicular and are not subject to scour. Most stands are in sunny locales. There is usually little soil formation, and the moss layer is the rooting medium for vascular plants. The locations are not subject to summer drought; at least a minimal amount of moisture was available all year in the dry summer of 1977.

Total cover of vascular plants is 76.2% for all stands (Table 11). One stand had 100% Aralia californica overstory cover. If this is removed, vascular cover averages 58%: 36% Petasites frigidus, 7% Equisetum telmatia, 5% Galium triflorum, and 3% Oxalis oregana. Twenty-six species were recorded.

Table 12. Stand table for *Adiantum pedatum* community. Cover and constancy are in percent. N = number of plots. Degree of slope given.

	Adiantum pedatum community													
	N = 10		N = 10		N = 10		N = 10		N = 10		N = 10			
	99°		98°		84°		78°		68°		72°		All plots	
Species	cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	cov.	freq.	Ave. cover	Constancy
Vascular														
Adiantum pedatum	21.0	10	45.0	10	55.0	10	48.0	10	79.0	10	67.0	10	52.6	100
Aruncus sylvester			5.0	3			1.2	3	17.0	6	10.0	6	5.5	30
Boykinia elata					1.0	3			0.2	2	19.0	10	3.4	25
Vancouveria hexandra					4.0	4			12.0	8	2.0	2	3.0	23
Oxalis oregana					10.2	6					5.2	5	2.6	18
Polystichum munitum					8.0	6	6.0	2					2.3	13
Achlys triphylla									11.0	10	2.0	2	2.1	20
Streptopus amplexifolius			1.0	1	0.4	2			0.2	1	9.0	3	1.8	12
Petasites frigidus									3.0	4	8.0	5	1.8	15
Montia parvifolia	+	1											+	2
Montia sibirica					0.2	2	0.2	1					+	5
Galium triflorum			+	1	+	6	0.4	5	0.2	2	1.8	7	0.4	35
Festuca subulata			+	1	0.2	1	5.0	3			0.2	1	0.8	10
Tolmiea menziesii			+	1			2.0	4					0.3	8
Epilobium watsonii							0.2	1					+	2
Polypodium glycyrrhiza			2.0	2	0.6	4	0.2	1					0.5	12
Hieracium albiflorum							0.2	1					+	2
Anaphalis margaritacea					0.2	1							+	2
Linnaea borealis			+	1	+	1							+	3
Heuchera micrantha							1.0	2					0.2	7
Stipa sp.							5.0	2			0.3	1	0.9	5
Bromus vulgaris					0.5	1							+	2
Total Vascular	21.0		53.0		80.3		69.4		122.6		124.5		78.3	
Bryophyte														
Stokesiella praelongum			3.0	6	36.0	10	30.0	10	13.0	8	30.2	8	18.7	70
Brachythecium frigidum			3.0	6	14.0	10	4.0	4	11.0	6	25.1	8	9.5	57
Hylocomium splendens					27.0	10	10.0	2					6.2	20
Ceratodon purpureus	4.2	7	6.0	6			1.0	3	14.0	5	10.0	6	5.9	45
Scleropodium obtusifolium	21.0										5.4	3	4.4	5
Leucolepis menziesii					+	1	+	1	13.0	6	5.2	2	3.0	15
Stokesiella oreganum					3.0	4	12.0	4					2.5	3
Porothamnion bigelovii			12.0	5									2.0	8
Rhacomitrium acciculare			6.0	6							5.0	4	1.8	15
Philonotus fontana									3.0	2	5.0	7	1.3	15
Rhyzomnium glabrescens							1.0	2			5.0	4	1.0	10
Marchantia											5.0	1	0.8	2
Neckera menziesii					5.0	4	+	1					0.8	8
Encalyptra sp.	2.8	2											+	3
Total Bryophyte	28.0		30.0		85.0		58.0		54.0		95.9		57.9	

The moss mat is complete except for water, surface debris, and projecting rocks, all of which account for 1.4% cover. Brachythecium frigidum covers 76% of all plots. On steeper slopes of 45° to 90°, Brachythecium frigidum may approach 100%. Stokesiella praelongum, the common associate, reaches 60% in a protected stand with low slope.

Riparian Forest Succession

Permanent immaturity may be a prime characteistic of an active riparian zone, but increasing maturity of the adjacent forest does affect streamside vegetation. The effect of shade and competition from mature forest stands on the understory has been discussed previously. Successional patterns in the overstory are briefly considered here.

Succession patterns of the overstory generally begin following a major disturbance such as fire, logging, or flood. Red alder is the first tree species to invade mineral soil bordering the stream, willow the first on islands and edges in the active zone. On larger rivers, cottonwood stands are established on alluvial deposits and mature further from the stream than the more frequently disturbed zone colonized by alder. Cottonwood above alder above willows above water is a common sight along larger streams. On smaller streams only willow or alder may be present, and on first-order streams they too may be absent.

All of these species have special requirements for establishment which are not met in the understory of a mature stand. After 100 years or so of undisturbed growth (less for willow), the pioneers begin to die out. Big leaf maple, which seeds in deep humus and can tolerate moderate shade, is the most common deciduous replacement. Acer circinatum sprawls horizontally and vertically and survives as the broad-leaf or evergreen forest ages. Succession in coniferous stands leads to an overstory of hemlock and small quantities of western redcedar, but the maples remain.

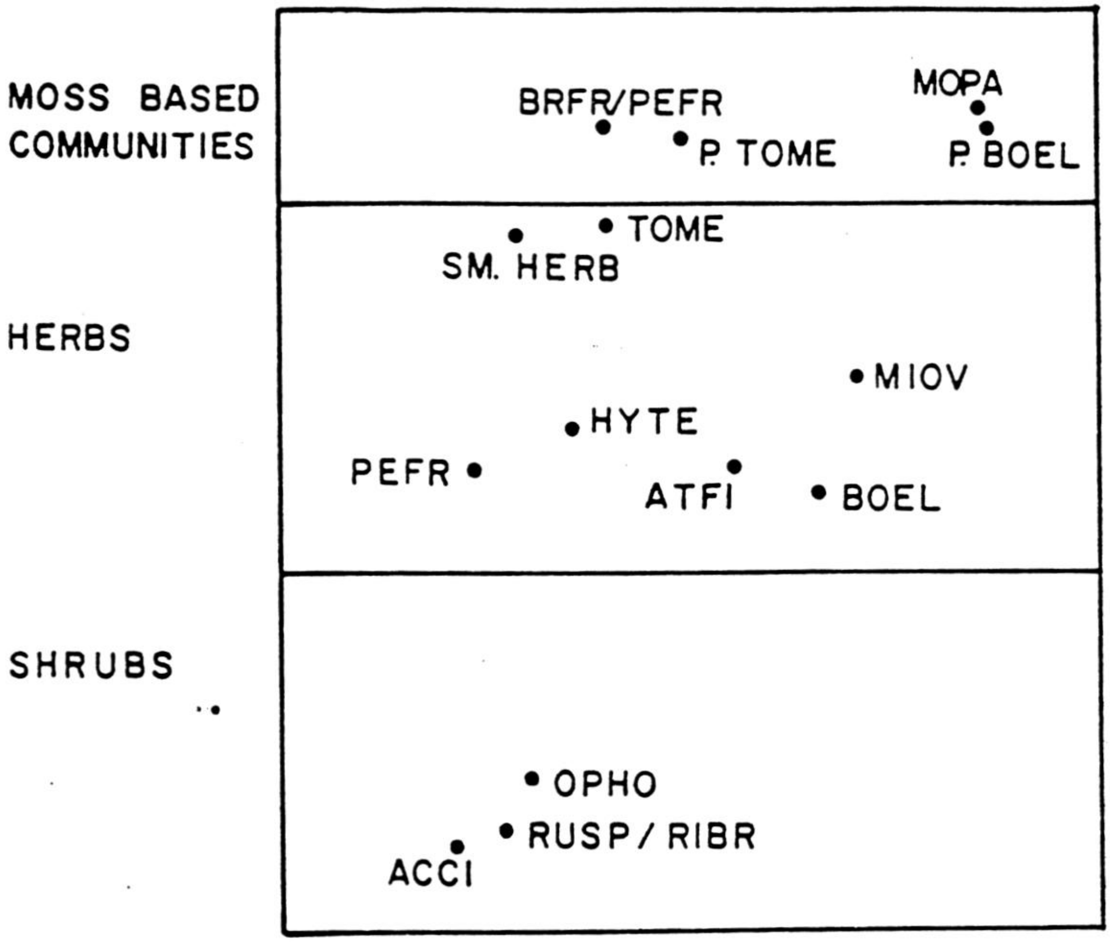
Establishment of riparian tree species may be precluded by shrub competition or small stream size. A very dense stand of Rubus spectabilis may delay or prevent establishment of tree species. A broadleaf riparian forest often does not form, especially on small streams, and only herbs, shrubs and evergreens are present.

Community Ordination

Communities were analyzed with Bray-Curtis ordination techniques (Bray and Curtis 1957) to display community relations visually. This analysis was not necessary to establish statistically that the moss-dominated Brachythecium frigidum/Petasites frigidus community was different from the Oplopanax horridum community (similarity index 0.005) or the invasive small-herb community (similarity index 0.162). The pattern of intercommunity relationship is interesting, however (Figure 8).

Overall similarities are low. Only 15% of all possible combinations showed similarities greater than 30%. In general, similarity was high among communities in the same successional groups. The closest relation was between the Pioneer Tolmiea menziesii and Tolmiea menziesii communities (58%). Similarities of less than 5% accounted for 38% of all combinations, which is to be expected when shrub-dominated hillsides are compared with wet, instream rocks covered by moss.

Broad arrays of this sort tend to produce lopsided displays on ordination planes. For instance, a reasonable axis might approximate successional state; end points could be Pioneer Tolmiea menziesii and Acer circinatum. But Acer circinatum is so dissimilar to the herb communities that they cluster at one end of the axis, even though Pioneer Tolmiea menziesii has similarities of over 40% with only two communities.



ACCI–ACER CIRCINATUM

ATFI–ATHYRIUM FILIX-FEMINA

BRFR/PEFR–BRACHYTHECIUM FRIGIDUM / PETASITES FRIGIDUS

BOEL–BOYKINIA ELATA

MIOV–MITELLA OVALIS

MOPA–MONTIA PARVIFOLIA

OPHO–OPLOPANAX HORRIDUM

P. BOEL–PIONEER BOYKINIA ELATA

PEFR–PETASITES FRIGIDUS

P. TOME–PIONEER TOLMIEA MENZIESII

RUSP/RIBR–RUBUS SPECTABILIS/ RIBES BRACTEOSUM

TOME–TOLMIEA MENZIESSI

SM. HERB–SMALL HERB

Figure 8. Ordination display of fourteen communities from old-growth riparian zones.

The best separation is achieved by using the two communities least related to all others for initial ordinates and two similar communities from two substrate types for second ordinates. The *Acer circinatum* and Bryophyte/ *Montia parvifolia* communities are end points for the first dimension, *Petasites frigidus* and Pioneer *Boykinia elata* end points for the second (Figure 8). This segregated the communities into moss, herb, and shrub dominated groups which roughly parallel successional stages. Herbs with affinity for a rootable substrate such as soil or sand segregate to the left, those oriented to rock substrates to the top and right.

BIOMASS ESTIMATES

Small stream ecosystems depend upon terrestrial vegetation as a source for most nutrient and energy sources (Cummins 1974, Sedell et al. 1975). In old-growth forests, a large share of this plant material enters streams as detritus from herbaceous or shrubby layers. In a clearcut, before young trees close in, the origin may be entirely herbaceous. To quantify detrital contributions to the aquatic system from the lower plant strata, biomass estimates were made on two segments of Mack Creek and one one of WS 2.

Distribution of biomass is uneven across the riparian zone. Some species are common, others sporadic, some are large and some small, and some are almost completely confined to a single zone. Vegetation growing well back from the stream, whatever its biomass, does not have the influence of that in the active zone. Therefore, to estimate proportional impact upon the stream, data are further classified under active zone, border zone, and outer zone.

Biomass and distribution data are presented here in three ways relating to detritus production: (1) as overall 1976 foliar biomass production for stream segments; (2) as average yearly production of different communities, including the many minor species; and (3) as weight and frequency of individual species that are a major source of detritus.

Overall biomass measurements for a stream segment are generally summarized per meter of stream length rather than by square meter of either land or water. Frequently vegetation overlaps the stream and the increased length of stream edge—by meander or island--will increase the material deposited in the stream. On the other hand, the stream can be 1 m or 10 m wide without necessarily changing the vegetation mass deposited along a given length. This is particularly true in the herb-dominated clearcut where no advantage is gained by additional light penetration. For this reason, summary by square meter of stream is unsatisfactory as a measure of detritus source. Data for a linear meter of stream may easily be translated to load per square meter of stream.

Aggregate Foliar Biomass

Total foliar biomass for understory species differs on each stream segment. The average per meter of stream increases from WS 2 to Mack Creek old-growth to the Mack Creek clearcut. Total foliar biomass on WS 2 averages 560 g/m of stream (Table 13). The relatively broad border zone accounts for two-thirds of the total and the active zone for about one-third. The outer zone is narrow to nonexistent on WS 2. Only about 6% of the total biomass originates there.

In the old-growth section of Mack Creek, the total production is estimated at 1,019 g per linear meter (Table 14). The active zone averages 133 g/m, about 13% of the total, and the border zone 296 g/m or 29% of the total. The outer zone averages 591 g/m--more than half of the riparian biomass in this stream segment.

Because two series of samples were taken in the active zone of Mack Creek old-growth, we can further divide the active zone into "instream" and "edge" segments. "Instream", which includes very low bars and islands, averages 40 g/m. The "edge", with its overhanging shrubs, contributes more than twice as much--92 g/m.

The clear-cut section of Mack Creek averages 2,022 grams biomass per meter of stream, the highest of any segment investigated (Table 15). More than half this total (1,090 g/m) was in the active zone. The border zone, narrow and spotty, averaged 330

Table 13. Estimated 1976 foliar production[a] of understory vegetation rooted in the riparian zone along 115 m of WS 2. Weight in grams.

	Active zone	Border zone	Outer zone	Total
Total	18,000	42,400	4,000	64,400
Average per running meter	157	368	35	560
SD (weights for 23 transects)	204	327		463
$S_{\bar{x}}$	43	68		48
Range	0–825	0–866		0–1,226
$S_{\bar{x}}$ as % of average	27%	18%		9%
Transects needed to estimate average ± 10%	416	312		273

[a]Foliage of deciduous plants, one year's evergreen production, entire herbaceous plant.

Table 14. Estimated 1976 production[a] of understory vegetation rooted in the riparian zone along 290 m of Mack Creek old-growth. Weight in grams.

	Active zone			Border zone	Outer zone	Total
	Instream	Edge	Total			
Total	11,700	26,700	38,500	85,900	171,300	295,600
Average per running meter	40	92	133	296	591	1,019
SD (weights for 29 transects)	49	124	135	311	457	623
$S_{\bar{x}}$	9	23	25	58	85	116
Range	0–155	0–421	0–467	0–1,659	0–1,638	176–3,064
$S_{\bar{x}}$ as % of average	22%	25%	19%	19%	14%	11%
Transects needed to estimate average ± 10%	593	763	432	431	239	149

[a]Foliage of deciduous plants, one year's evergreen production, entire herbaceous plant.

A comparison of production shows that in each stream segment different zones produce the highest percentage of the total biomass. On WS 2, the border zone produces two-thirds of the total; on the Mack Creek old-growth stand, the outer zone produces 58%; and on the Mack Creek clearcut, the active zone produces 54%.

Table 15. Estimated 1976 foliar production[a] of understory vegetation rooted in the riparian zone along 220 m of the Mack Creek clearcut. Weight in grams.

	Active zone	Border zone	Outer zone	Total
Total	239,800	72,600	132,400	444,800
Average per running meter	1,090	330	602	2,022
Transect halves in which each zone occurs	19	19	18	22
Average mass per transect half	631	191	368	1,011
SD_x transect halves	637	136	243	776
$S_{\bar{x}}$	146	31	57	165
Range (excepting zero)	<1-2,411	75-640	25-1,177	76-2,544
$S_{\bar{x}}$ as % of average	13%	16%	16%	16%

[a]Foliage of deciduous plants, one year's evergreen production, entire herbaceous plant.

Total foliar biomass production per meter is greatest in the clear-cut section of Mack Creek, almost twice the production per meter of the old-growth section and nearly 4 times the production of WS 2. Even more dramatic is the comparison between the active zones of the three segments, the areas where vegetation production most affects a stream. The active zone in the clearcut produces 7 times the mass of either old-growth section.

Biomass Production by Community

Average figures for community foliar biomass are summarized in Tables 16, 17, 18, and 19. The estimated weights range widely among the communities. Furthermore, a different set of communities is most important on each stream segment.

Table 16. Estimated 1976 foliar production[a] of some riparian vegetation types in the Mack Creek clearcut. Weight in grams.

	Petasites frigidus					
	Active zone	Border and outer zones	All zones	*Stachys cooleyae*	*Mimulus guttatus*	*Epilobium angustifolium*
Samples (m^2)	12	9	21	5	6	31
Average	397	115	277	189	64	195
SD_x	228	68	226	140	30	190
$S_{\bar{x}}$	65	23	49	62	12	34
$S_{\bar{x}}$ as % of average	17%	20%	18%	33%	19%	18%
95% confidence interval	±133	±47	±100	±122	±24	±69
Range	83-692	12-185	12-692	19-364	34-111	14-871
Quadrats needed to estimate average ± 10%			260	200	100	360

[a]Foliage of deciduous plants, one year's evergreen production, entire herbaceous plant.

Table 17. Estimated 1976 foliar production[a] of some communities rooted in the riparian zone in Mack Creek old-growth. Weight in grams.

	Oplopanax horridum	*Rubus spectabilis/Ribes bracteosum*: *Ribes bracteosum* dominant	*Rubus spectabilis/Ribes bracteosum*: *Rubus spectabilis* dominant	*Rubus spectabilis/Ribes bracteosum*: Combined community	*Acer circinatum*	*Athyrium filix-femina*	*Polystichum-Blechnum*: *Polystichum munitum* dominant	*Polystichum-Blechnum*: *Blechnum spicant* dominant	*Polystichum-Blechnum*: Combined community	*Vaccinium* ssp.
Samples (m^2)	79	38	36	74	98	9	51	22	73	65
Average	58	82	85	84	88	96	40	26	36	28
SD_x	54	74	91	82	94	59	33	22	31	29
$S_{\bar{x}}$	6	12	15	10	10	20	5	5	4	4
$S_{\bar{x}}$ as % of average	10%	15%	18%	11%	11%	21%	12%	18%	10%	13%
95% confidence interval	±12	±24	±31	±19	±19	±46	±9	±10	±7	±7
Range	4-299	<1-382	8-503	<1-503	2-472	6-228	<1-193	4-78	<1-193	<1-157
Quadrats needed to estimate average ± 10%	338	322	448	383	453	155	281	284	301	430

[a]Foliage of deciduous plants, one year's evergreen production, entire herbaceous plant.

Table 18. Estimated 1976 foliar production[a] of some communities in WS 2. Weight in grams.

	Aralia californica	Mixed Wet fern	*Polystichum munitum*	*Boykinia elata*	Pioneer *Boykinia*	*Mitella ovalis*	*Brachythecium frigidum/Petasites frigidus*
Samples (m^2)	21	16	33	19	12	3	8
Average	140	85	78	17	5	13	12
SD_x	64	46	65	8	3	10	5
$S_{\bar{x}}$	14	12	11	2	1	6	2
$S_{\bar{x}}$ as % of average	10	14	14	11	15	43	14
95% confidence interval	±30	±24	±22	±4	±2	±12	±4
Range	39-258	14-155	0-306	6-40	10-4	4-24	6-16
Quatrats needed to estimate average ±10%	83	117	276	85	108	218	61

[a]Foliage of deciduous plants, one year's evergreen production, entire herbaceous plant.

Although most vegetation fell into community types previously described, samples included some vegetation not described as communities but clearly dominated by a single species such as Polystichum munitum, Petasites frigidus, Stachys cooleyae, Mimulus guttatus, Epilobium angustifolium, and Aralia californica. The remaining vegetation type is mixed wet fern. Species in this group of quadrats fell somewhere

Table 19. Estimated 1976 foliar production[a] of some herbaceous communities in the active zone in Mack Creek old-growth. Weight in grams. Data are adjusted to equal 100% cover.

	Small herb	Pioneer *Tolmiea menziesii*	Medium herb	*Athyrium filix-femina*
Samples (m^2)	61	76	30	16
Average	21	21	49	101
SD_x	10	9	21	61
$S_{\bar{x}}$	1	1	3	5
$S_{\bar{x}}$ as % average	6	5	6	5
95% confidence interval	±2	±2	±6	±11
Range	6-43	8-64	20-95	32-171
Quadrats needed to estimate average ± 10%	98	66	74	144
Average cover in the field	79%	43%	73%	76%

[a]Foliage of deciduous plants, one year's evergreen production, entire herbaceous plant.

between Adiantum pedatum and Athyrium filix-femina but contained generous if irregular amounts of Polystichum munitum and Aruncus sylvester, occasional Petasites frigidus, and some Rubus parviflorus. Weights are given as though these are described communities.

The single plots with the greatest biomass weights and the heaviest average community weights on the three stream segments contained tall vigorous herbaceous types. The average biomass of smaller herbs is low, but it is typically concentrated in the critical active zone. Shrubby communities have relatively consistent averages from community to community.

The heaviest rooted mass (692 g) measured from the Petasites frigidus clan growing in the active zone in the clearcut on Mack Creek (Table 16). The Rubus/Ribes community was next with 503 g (Table 17). Petasites frigidus stands also had the highest average weight per square meter, 277 g overall and 397 g in the active zone of the clear-cut.

Large-herb communities

The three vigorous large herbs from the clearcut have the highest average weights per unit area of all community groupings (Table 16) due to stand density and individual plant vigor. One quadrat contained 104 Petasites leaves, 19 Epilobium angustifolium plants more than 1 m tall, and a 15% cover of Mimulus guttatus. The sunlight in the clearcut clearly stimulates growth.

In the old-growth sections, the highest average is again produced by herbaceous species; Aralia californica in WS 2 averages 104 g/m^2 (Table 18). This large vigorous herb is not described here as a community type—it is associated with at least three small-herb communities—but where it overlaps Boykinia elata or Mitella ovalis communities its weight is so overwhelming that the small herbs can almost be ignored. Aralia has one of the least variable sample sets; its standard error of the mean is only 10% of the estimated average.

The Athyrium filix-femina community was sampled with both the instream 20- x 50-cm quadrats and the 1- x 1-m quadrats used for shrubs at the edge of the active zone. It is the only community sampled two ways (Tables 17 and 19). Average weights and variance for the two sample sets are from the same populations, as determined by t and F tests, respectively. Average mass for quadrats occupied by the Athyrium filix-femina community are 101 g/m^2 in the active zone and 96 g/m^2 on the edges. The heaviest quadrats are 171 g instream and 228 g at the edge. Because it is found chiefly in the active zone, this community is second only to Aralia in potential contribution of material directly to the water in old-growth areas.

Shrubby communities

Acer circinatum had the highest average weight of the shrubby communities, 88 g/m^2 (Table 17). Rubus/Ribes was close with 84 g/m^2 and had the heaviest single quadrat (503 g/m^2). Oplopanax horridum averages much less (58 g/m^2), but the range of values overlaps those of other shrubby communities.

Among the shrubs, individual quadrats with low biomass may be caused by less vigorous vegetation or by quadrats which have 100% cover produced by stems originating in Adjacent quadrats. (See Reliability of Biomass Estimates.)

Medium-size-herb communities

Communities composed only of medium-size herbs are found in the active zone. Under a forest canopy, the communities tend to be heterogeneous instead of forming clans as in clearcuts. Most of the species are soft and have many leaves. In addition, many stands are small and isolated by water or rock.

Three community types are represented in this group: Petasites frigidus, Hydrophyllum tenuipes, and Tolmiea menziesii. Because the average weights do not differ significantly, it seems practical to combine them (Table 19). Average biomass is 49 g/m^2. Interestingly, all the sampled square meters dominated by Petasites in the clear-cut active zone exceeded the average biomass of quadrats sampled for medium-size herbs, including Petasites, in the old-growth forest.

Small-herb communities

The small-herb community (including small amounts of Tolmiea menziesii), dominated by Montia sibirica, Galium triflorum, and Oxalis oregana, averages 21 g/m^2 of biomass, less than half the value for communities

The 17 g/m^2 of the Boykinia elata community is less than either the Tolmiea or small-herb communities, although superficially similar to them (Table 18). Boykinia elata tends to dominate an area (cover values to 100%), but it has little mass when compared with Tolmiea menziesii of equal size.

Two pioneer communities, Boykinia elata and Tolmiea menziesii, occupy similar situations (for example, isolated rocks). The Tolmiea averages 21 g/m^2, however, the same as small-herb communities, while the pioneer Boykinia averages only 5 g/m^2, the lowest value for any community (Table 18).

Biomass Production by Species

The herbaceous and leafy production of 16 riparian species is summarized in Tables 20, 21, and 22. A comparison of stream segments shows which species produce best in each location and which single species affects a zone most.

Table 20. Estimated 1976 foliar production[a] and frequency of major species along 115 m of WS 2. Weight in grams.

	Athyrium filix-femina	*Adiantum pedatum*	*Aralia californica*	*Petasites frigidus*	*Polystichum munitum*	*Blechnum spicant*	Small herbs
Active zone							
Total	1,700	218	10,600	1,050	370	123	3,290
Average (running meter)	15	2	92	9	3	1	29
Frequency in 23 transects	5	6	11	8	2	1	19
Border zone							
Total	3,200	4,530	11,500	—	17,300	1,690	
Average (running meter)	28	39	100	—	157	15	not separable
Frequency in 23 transects	10	17	12	—	14	9	
Total	4,900	4,700	22,100	1,050	17,700	1,810	
Average (running meter)	43	41	192	9	154	16	

[a]Foliage of deciduous plants, one year's evergreen production, entire herbaceous plant.

Different species are top producers on each stream segment. The scoured bedrock on WS 2 will not support shrubs. The largest production is from large herbs: Aralia californica, Athyrium filix-femina, and Adiantum pedatum. In old-growth forest along Mack Creek, Athyrium filix-femina and Adiantum pedatum are well represented, but the shrubs Ribes bracteosum, Rubus spectabilis and Oplopanax horridum are the heaviest producers. In the clearcut along Mack Creek, Mimulus guttatus, Stachys cooleyae, Epilobium angustifolium, and Salix sitchensis are the chief producers.

Table 21. Estimated 1976 foliar production[a] and frequency of major species along 290 m of Mack Creek old-growth. Weight in grams.

	Athyrium filix-femina	*Adiantum pedatum*	*Polystichum munitum*	*Blechnum spicant*	*Ribes bracteosum*	*Rubus spectabilis*	*Oplopanax horridum*	*Acer circinatum*	*Vaccinium* spp.
Active zone									
Instream subtotal	1,770	701	—	—	2,350	19	445	—	—
Average (running meter)	6	2	—	—	8	—	2	—	—
Frequency in 58 transects	8	2	—	—	6	1	1	—	—
Edge subtotal	4,900	28	1,000	153	11,300	3,190	3,800	1,630	45
Average (running meter)	17	—	4	<1	39	11	13	6	<1
Frequency in 29 transects	6	3	3	2	10	6	9	4	1
Total	6,680	728	1,000	153	13,620	3,210	4,240	1,630	45
Average (running meter)	23	3	4	<1	47	11	15	6	<1
Border zone									
Total	8,730	10,400	8,520	2,620	6,030	7,610	5,430	11,100	1,960
Average (running meter)	30	36	29	9	21	26	19	38	7
Frequency in 29 transects	11	9	17	13	5	12	7	11	7
Outer zone									
Total	9,080	261	28,600	11,200	4,840	16,600	16,500	47,800	12,600
Average (running meter)	31	1	99	39	17	57	57	165	43
Frequency in 29 transects	13	9	21	22	4	13	17	23	23
Total All Zones	24,500	11,300	38,100	14,000	24,500	27,400	26,200	60,600	14,600
Average (running meter)	84	39	131	48	84	95	90	209	50

[a]Foliage of deciduous plants, one year's evergreen production, entire herbaceous plant.

Because each of these species has a characteristic habitat, some species such as Vaccinium, which grow on relatively dry sites away from the stream, make little impact on the stream. Other species, particularly those growing in the active zone, contribute directly to the stream.

Species common to WS 2 and Mack Creek old-growth

The three most important species on WS 2 are limited to areas of abundant moisture (Table 23). Almost all of the riparian area in WS 2 is in active stream or on its border; consequently, all three species have direct impact on the stream. Aralia californica, a very large herb, averages 192 g/m of stream length. Athyrium filix-femina averages 43 g/m and Adiantum pedatum 41 g/m. Together they account for 49% of the riparian biomass on WS 2. Thirty-five percent of all Athyrium (Table 20) probably falls directly into the stream, as does 48% of the Aralia californica. Adiantum pedatum is generally found on ledges, however, and because its fronds are not deciduous, only 5% of its total production reaches the stream intact.

Athyrium filix-femina and Adiantum pedatum are also found in fairly large quantities on Mack Creek in the old-growth forest. Adiantum biomass per meter is almost the same same as on WS 2 (Table 24). This is probably due to Adiantum's affinity for the border zone; it prefers steep, continually moist slopes, cliff faces, and stable rock islands. Although Mack Creek and WS 2 are very different, the average width of their border zones is approximately 3 m.

Table 22. Estimated 1976 foliar production[a] and frequency of major species along 220 m of the Mack Creek clearcut. Weight in grams.

	Mimulus guttatus	*Petasites frigidus*	*Stachys cooleyeae*	*Epilobium angustifolium*	*Salix sitchensis*
Active zone					
Total	12,400	65,400	38,500	50,000	159,800
Average (running meter)	56	297	175	226	726
Frequency in 22 transects	9	13	5	15	14
Average (m^2)	14	76	45	58	186
Border zone					
Total	1,420	1,017	1,180	34,000	50,200
Average (running meter)	6	46	5	155	228
Frequency in 22 transects	2	13	3	16	7
Average (m^2)	2	14	2	47	69
Outer zone					
Total	—	31,800	176	53,000	18,300
Average (running meter)	—	144	1	241	83
Frequency in 22 transects	—	11	1	17	2
Average (m^2)	—	40	<1	68	24
Total All Zones	13,800	107,000	39,800	136,800	228,000
Average (running meter)	63	488	181	622	1,037

[a]Foliage of *Salix*, entire herbaceous plant.

Table 23. Estimated 1976 foliar production of major herb and shrub species of three stream segments. Weight in grams per running meter.

Species	WS 2	Mack Creek old-growth	Mack Creek clearcut
Aralia californica	192		
Athyrium filix-femina	43	84	
Adiantum pedatum	41	39	
Petasites frigidus	9	+	488
Ribes bracteosum		84	
Rubus spectabilis		94	
Oplopanax horridum		90	
Mimulus guttatus			63
Stachys cooleyae			181
Epilobium angustifolium			622
Salix sitchensis			1,037

Although the total contribution of Athyrium filix-femina in the old-growth segment on Mack Creek is larger than that of WS 2, biomass estimates from the active zone and the border zone are similar. The active zone on Mack Creek includes stable islands, a good habitat for Athyrium; but because this segment has a flood plain which remains damp, Athyrium; also grows well far beyond the immediate stream borders, and growth in the outer zone is 37% of total production.

Table 24. Estimated 1976 production of two ferns on two stream segments. Weight in grams per running meter.

Species		WS 2	Mack Creek old-growth
Adiantum pedatum	Active	2	3
	Border	39	36
	Outer	—	1
	Total	41	39
Athyrium filix-femina	Active	15	23
	Border	28	30
	Outer	—	31
	Total	43	84

Polystichum munitum and Blechnum spicant, species typical of much of the forest immediately surrounding a riparian zone, have patterns with some similarity on the two segments (Table 25). Only about 2% of these evergreen ferns overlap the streambed. Dead fronds remain attached to the main plant, even on steep slopes; hence, they are an unlikely major source of stream debris.

Table 25. Estimated 1976 production of evergreen ferns on two stream segments. Weight in grams per running meter.

Species		WS 2	Mack Creek old-growth
Blechnum spicant	Active	1	1
	Border	15	9
	Outer	—	39
	Total	16	48
Polystichum munitum	Active	3	4
	Border	151	29
	Outer	—	99
	Total	154	131
Combined	Active	4	4
	Border	165	38
	Outer	—	137
	Total	170	180

Species found chiefly in Mack Creek old-growth

Any similarities between Mack Creek old-growth and WS 2 end with the ferns. Aralia californica, which apparently requires a warmer, longer season, is absent from Mack Creek. Shrubs are almost absent from the sampled section of WS 2 but make heavy contributions on Mack Creek old-growth (Table 23).

The distribution of Ribes bracteosum and Rubus spectabilis, ordinarily found together along western Cascade Range streams, is shown in Table 26. Ribes is found on the margins of the stream, but Rubus competes well into the open wet forest. Oplopanax horridum is well developed on low berms and terraces with ready access to the water table. Figure 9 shows this relation graphically.

Table 26. Estimated 1976 foliar production of major shrubs in Mack Creek old-growth. Weight in grams per running meter. Distribution shown as percent of total production.

Zone	Species						Total major shrubs	
	Ribes bracteosum		*Rubus spectabilis*		*Oplopanax horridum*			
Active	47.0	56%	11.1	12%	14.6	16%	72.7	27%
Border	20.8	25%	26.2	28%	18.7	21%	65.7	24%
Outer	16.7	20%	57.2	61%	57.0	63%	130.0	49%
Total	84.4	100%	94.5	100%	90.3	100%	269.2	100%

All three shrubs have deciduous leaves which contribute readily utilizable materials to the stream. Approximately 27% of the foliar mass of the combined shrubs falls directly into the stream or onto margins which are covered at an average high water. Twenty-four percent probably falls in areas which delay entrance to the stream system so that some decomposition takes place; almost half of the total yearly foliar production in the riparian zone is believed to have decayed in place.

Acer circinatum was common on Mack Creek in the old-growth forest and estimates of foliar mass for the full riparian area are available (Table 21). It is important to note that biomass estimates are derived from basal measurements and any figures so derived apply to point or origin (Figure 3). Acer circinatum, especially in old-growth forest, may produce leaves meters away from its origin. Averaged cover distribution from eight streams sampled for community type indicates how much more of the litter directly affects the stream than is estimated from rooted biomass calculations (Table 27).

Table 27. Zone distribution of *Acer circinatum* foliage as percent of total *Acer circinatum* measured in the riparian zone.

Zone	Rooted biomass Mack Creek	Cover stream segments
Active	3	20
Border	18	8
Outer	79	72
Total	100	100

Species found chiefly in the Mack Creek clearcut

Species important on the clear-cut segment of Mack Creek are entirely different from those important in old-growth forest (Table 22), with the exception of Petasites frigidus, which can grow in wet gravel in either condition. Salix sitchensis is the only woody plant of importance on the stretch sampled. Additional herbaceous species are Mimulus guttatus, Stachys cooleyae, and Epilobium angustifolium.

The clearcut is still being invaded by Salix, and distribution is uneven. Cover over the segment averages 25%, ranging from 6% on the upper half to 35% on the lower half of the stream. Since the riparian zone of the lower half-segment is almost twice as wide as the upper half, it has greater weight in the calculated averages. The irregular distribution and size of Salix sitchensis required a separate biomass sample, a 250-m segment extending 15 m beyond each end of the rest of the sample. A transect 5 m wide was run in the center of each 25 m segment--a 20% sample.

Salix sitchensis averages 1,037 g foliage per meter of stream, the greatest production for any riparian species. Approximately 70% of all Salix foliage (726 g/m) falls in the active zone, and the percentage is that low only because many leaves fall on top of steep banks that tend to contain winter flow. Twenty-two percent of leaves fall in the border zone and only 8% in the outer zone (Table 22).

Mimulus guttatus grows almost exclusively in the active zone. It is probably more important for maturation and decay early in the season than for total biomass. Ninety percent of its yearly production is in the active zone (Table 22).

Stachys cooleyae is similarly restricted. Of an estimated average of 181 g of stream, 175 g (97%) was rooted in the active channel (Table 22).

Petasites frigidus is a vigorous, adaptable species. In the clearcut, large quantities are rooted in gravel deposits in the stream. It also grows on top of the rocky side banks lining the stream, although not as vigorously. The total weight distribution for this species is high in the active zone, drops markedly in the border zone, and rises in the outer zone (Figure 9), a pattern also apparent on a quadrat basis. Petasites frigidus produced approximately 297 g/m in the active zone (Table 22), second only to Salix.

Epilobium angustifolium must have reached its apogee in the riparian zone in the year of sampling. It was tall and vigorous. On 67% of transects it was found in the active zone on islands and bars. Detritus contribution to the active stream was 226 g/m, third after Salix and Petasites (Table 22). However, Epilobium overtops Petasites on the stream bank, particularly where water is near the surface. Epilobium is second (622 g/m) in total biomass estimates for the full width of the clear-cut riparian zone.

The distribution of biomass of these species as percent of total biomass is shown in Figure 9.

Reliability of Biomass Estimates

Biomass is irregularly distributed in the riparian zone and variation in total biomass from transect to transect is very high (Tables 13, 14, and 15). Standard deviations approach or surpass the average weights of the transects. Biomass prediction for the active zone is most important because this zone is most directly related to the stream. In the clearcut, the active zone is slightly less variable than in the other two zones. In the old-growth forest, the active zone is most variable. Figure 10 shows the distribution of sample weights from active-zone transects on Mack Creek. Along this segment,

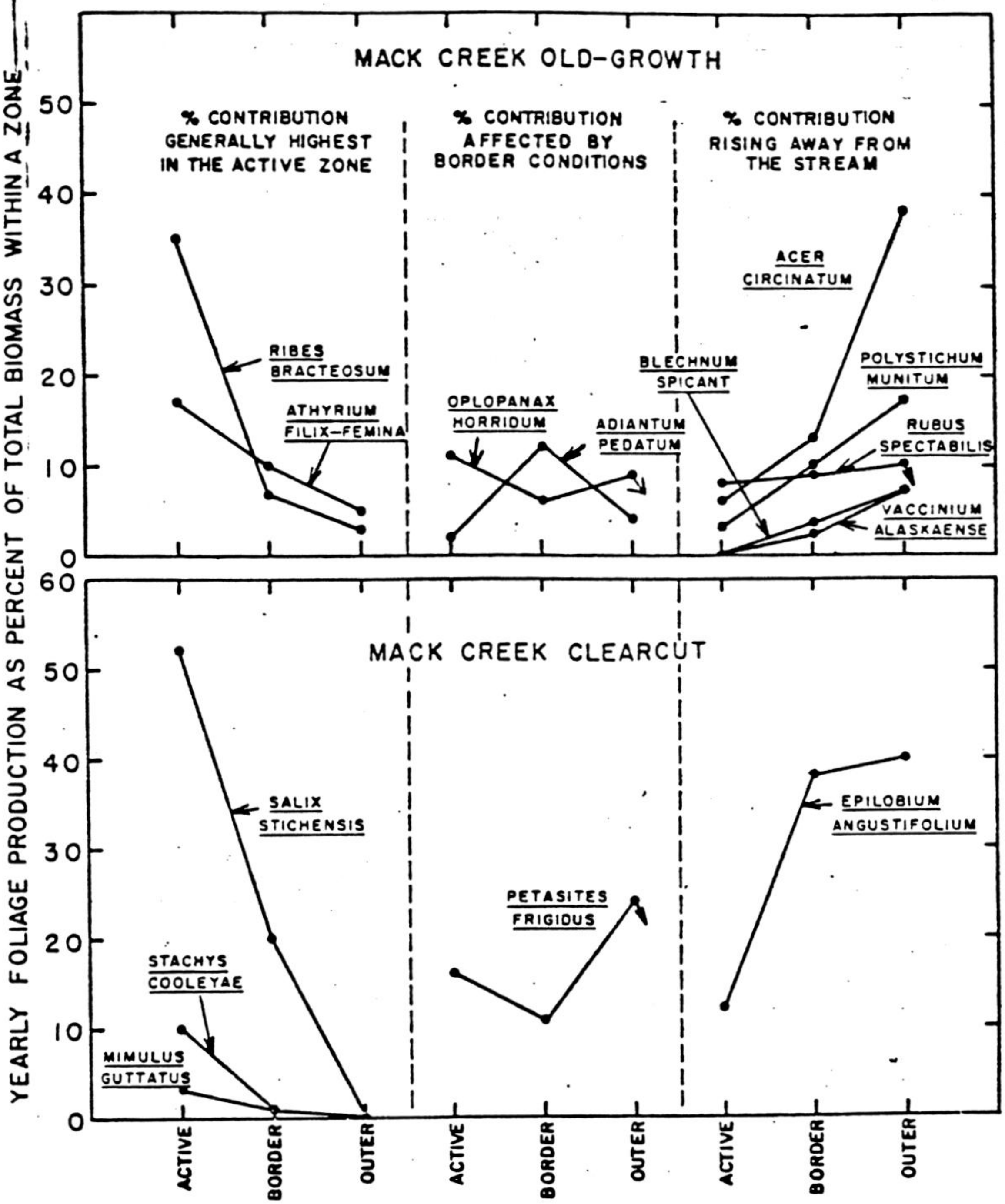


Figure 9. Yearly foliage production of species in different sections of the riparian zones.

432 transects would be needed to estimate the average transect weight ± 10% with 95% reliability.

The range of biomass values in the communities suggests the problem of estimating accurately. In a given community, the highest weight

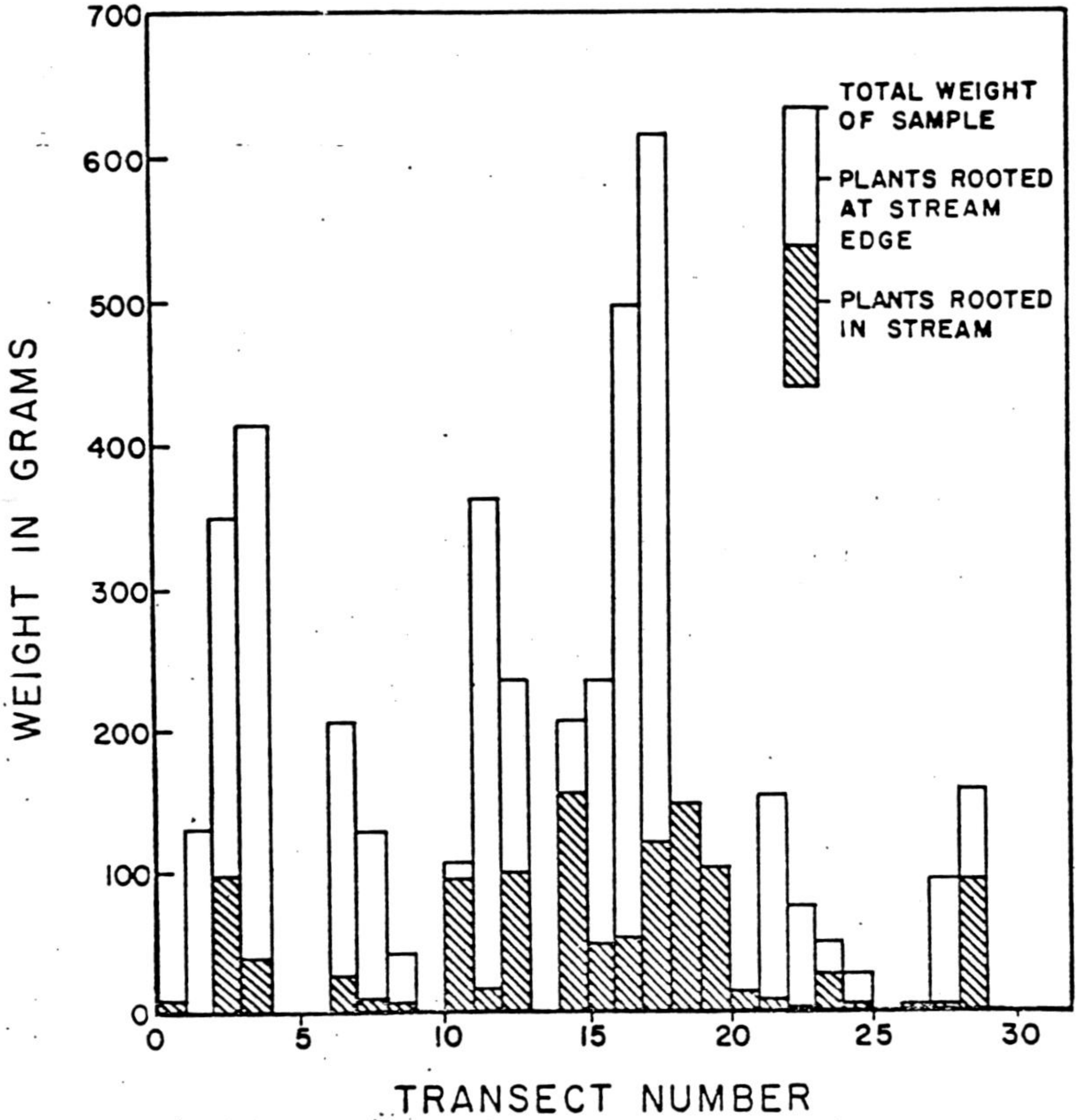


Figure 10. Total of sample weights from active zone transects in Mack Creek old-growth, 1976.

in sampling quadrats is generally twice as high as the average, and the lowest weight is less than half the average (Tables 13 to 22). A measure of variability directly comparable from community to community is the standard error ($S_{\bar{x}}$) of the mean as a percent of the average, where the $S_{\bar{x}}$ is based on the same number of plots. Only communities of medium-size and smaller herbs fall below a standard error of 10%. Quadrat size for herbs is one-tenth the quadrat size for shrubs, therefore increase of quadrat size alone does not appear to reduce variability. Because communities form such a complex mosaic, the ... cannot be increased to much more than 2 m x 2 m and still fit in homogeneous stands. The number of 1-meter-square quadrats that would be needed to estimate average biomass +10% with 95% confidence varies from a low of 61 in the Petasites frigidus/ Brachythecium frigidum community to 453 in the Acer circinatum community. Even acknowledging that larger quadrats should be used with Acer circinatum than with species such as Epilobium angustifolium or Petasites frigidus, variability is still so high for these latter two vegetation types that 360 and 260 quadrats must be sampled, respectively, in order to establish statistical reliability.

AUTUMN PHENOLOGY

The rate and time at which litterfall from terrestrial plants enters the stream determines how it is utilized in and transported from the aquatic system. Materials from terrestrial sources enter the stream throughout the year. Sedell et al. (1974) working in WS 10 near the H. J. Andrews EER report a peak in November, with measurable amounts, largely conifer needles, falling all year. Deciduous leaf fall, primarily from Acer circinatum and Acer macrophyllum, peaked in November and was of little importance from January through August. Because litter traps were used in the WS 10 studies, no herbaceous materials are reported, yet the greatest proportion of vegetation is herbaceous in locales such as young clearcuts.

In this study we monitored the phenology of riparian species, including herbs, throughout the fall, with special attention to senescence and leaf fall, and calculated rates of abscission. Vegetational changes were related to weather and streamflow.

Timing

The greatest leaf fall from deciduous shrubs and trees occurred in October 1977. Virtually no leaves remained on the trees by the first week of November (Figure 11). Alnus rubra and Ribes bracteosum were the first tree and shrub species to lose leaves. Both suffered some slug and insect damage; Ribes was particularly susceptible. Alnus lost leaves earliest on dry sunny locations at low elevations. Maximum leaf fall for most species occurred during mid-October: Ribes bracteosum during the second week, Acer circinatum and Acer macrophyllum during the third week, Rubus spectabilis during the fourth week, and Oplopanax during the last week of October.

Herbaceous senescence began in July with Mimulus guttatus, which was gone by the beginning of September (Figure 11). Most herbs showed some aging by September, but the flowering herbs lost vigor more rapidly after seed set in September and early October. The ferns followed in October and November.

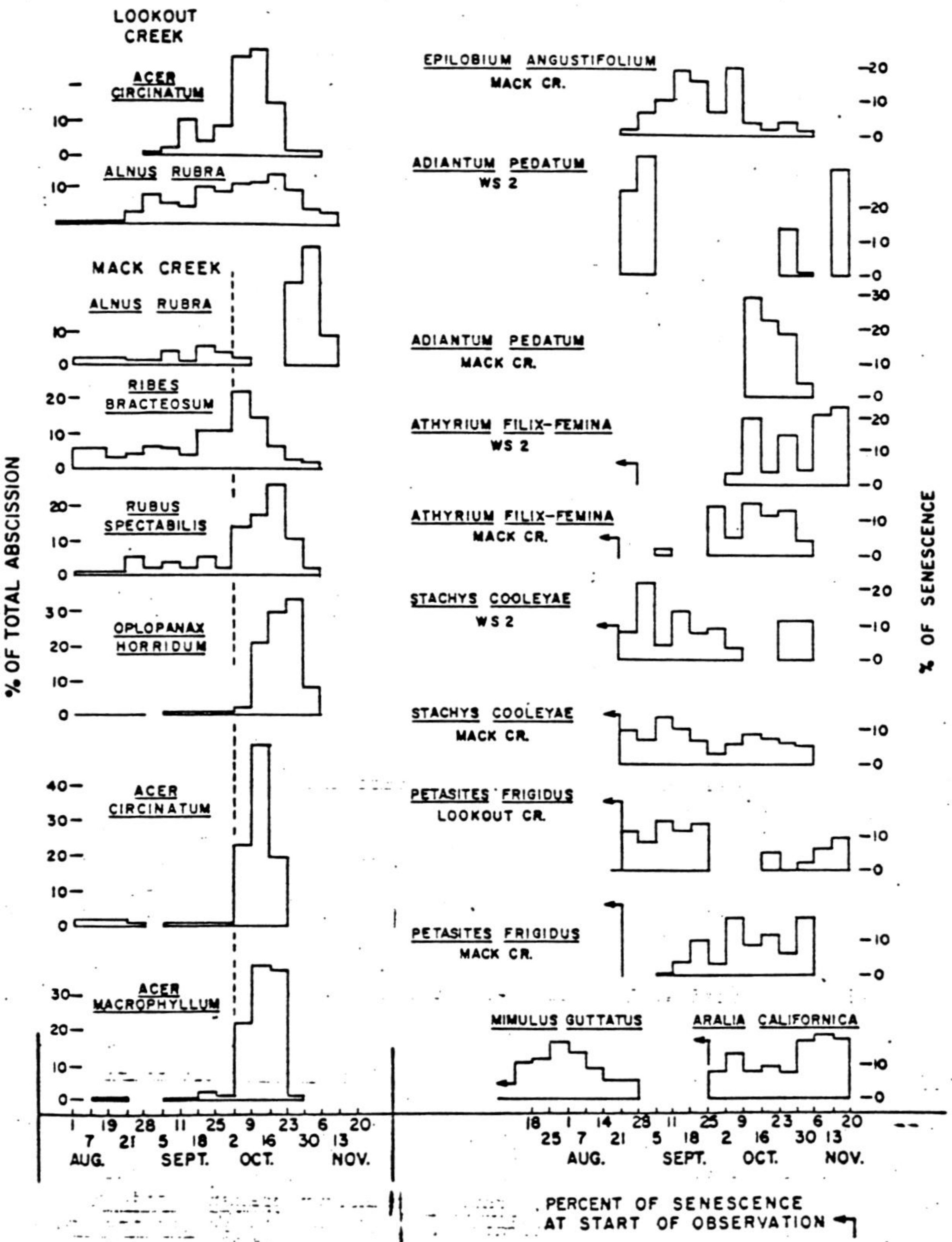


Figure 11. Abscission and senescence recorded weekly on Lookout Creek, Mack Creek, and WS 2.

Abscission Rates

Lookout and Mack Creek differ markedly in their leaf-fall patterns (Figure 12). Leaf-fall data from Lookout Creek plot as straight lines on probit paper, but data from Mack Creek do not. Acer circinatum on Lookout Creek began to lose leaves in early September and continued to lose them at a fairly steady high rate for 9 weeks until the leaves were gone by the first week in November. Leaf fall on Mack Creek began at the same time, first at a much slower rate and then more rapidly after October 2. Ninety-four percent of the leaves were lost in 3 weeks. Alnus rubra shows a similar pattern of leaf fall--constant at Lookout Creek, varied at Mack Creek (Figure 12).

Abscission is largely controlled by natural aging, frost, and acceleration due to other weather events such as rain (Carns 1966). Initiation of abscission of Acer circinatum may depend upon day length, since it began within a week at Mack Creek and Lookout Creek and also on two unmonitored upland sites. Once initiated, the steady rate evident on Lookout Creek suggests that aging, a linear process, controls leaf fall. Leaves at Lookout Creek are much older than those at Mack Creek, because on low-elevation, south-facing slopes they develop sooner. This development is apparently responsible for the higher initial leaf fall rate at Lookout Creek. During the week of October 18, an increase in rate at Lookout Creek coincided with first rains after the onset of leaf fall. This mechanical force possibly accelerated susceptible leaves, and heavier rains the next week did not produce similar increases.

Environmental factors probably accelerated leaf fall at Mack Creek, if the slow initial rate was, in fact, due to younger leaves. The first reported frost coincided with the abrupt increase in abscission rate. The weather station temperature did not reach 0°C (Figure 13), but ice crystals were reported in the soil in the adjacent clearcut during the preceeding week (Art McKee, personal communication). Since air temperature probes are well protected from reradiation but not from ground radiation, vegetation quite possibly reached temperatures of 0°C or less. Initial aging is probably a prerequisite for abscission in Acer circinatum, as it is hardy through summer frost. No frost was recorded or reported at Lookout Creek during the abscission period.

All deciduous trees and shrubs from Mack Creek, with the exception of Alnus rubra, have similar patterns (Figure 12). Ribes bracteosum begins abscission earlier than Acer circinatum; although the rate is lower on both slopes, the alteration in rate is noticeable. Ribes seems to respond strongly to aging and is damaged by slugs. Half of the leaves had fallen by first frost, and many of those remaining had lost much of their mass. Acer macrophyllum and Oplopanax horridum have rates of leaf fall almost identical to those of Acer circinatum. Except for initial animal damage, the Acer macrophyllum plot would have fitted over the plot for Acer circinatum.

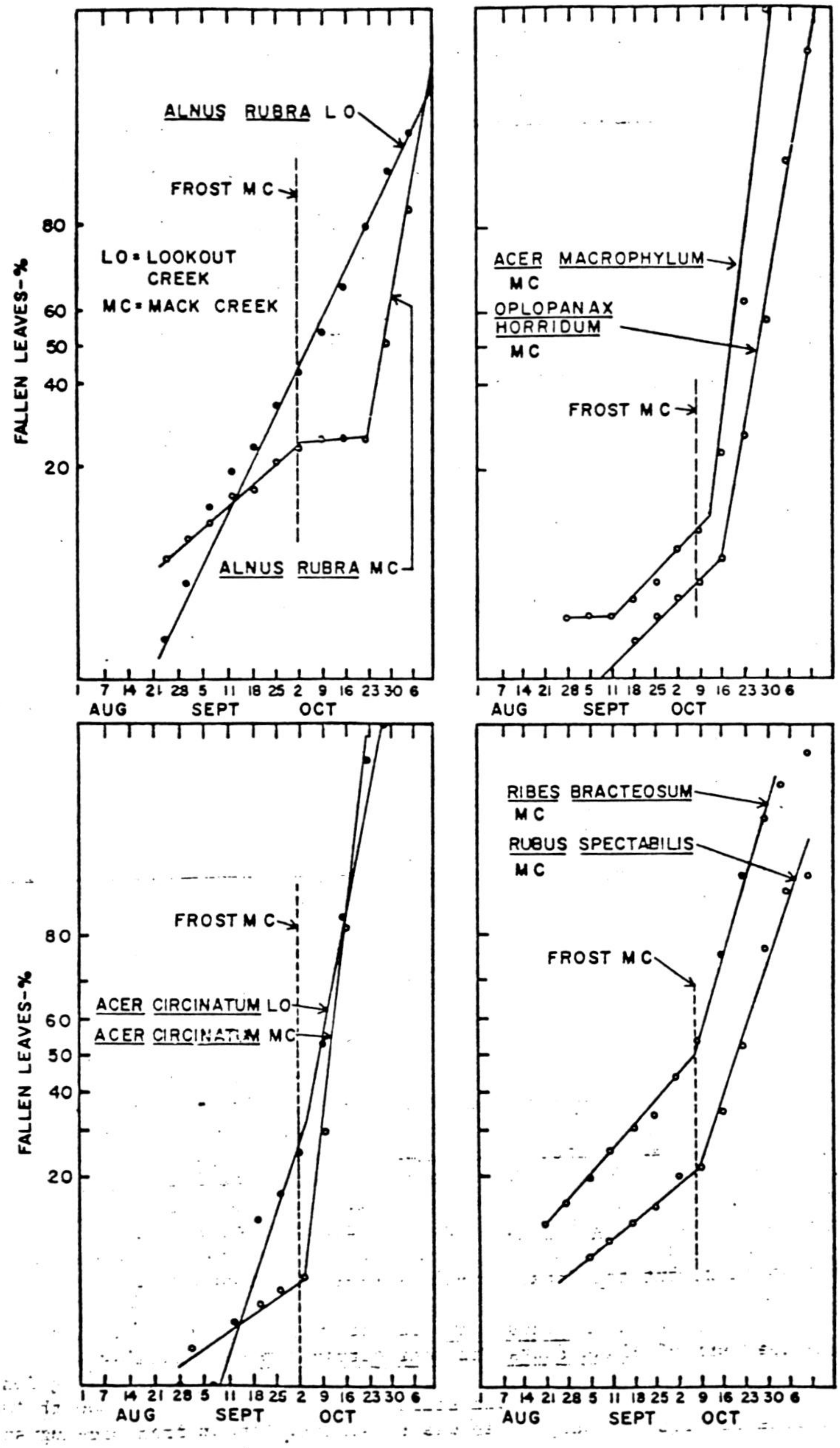


Figure 12. Abscission rates plotted on probit paper for six species at two elevations in 1977.

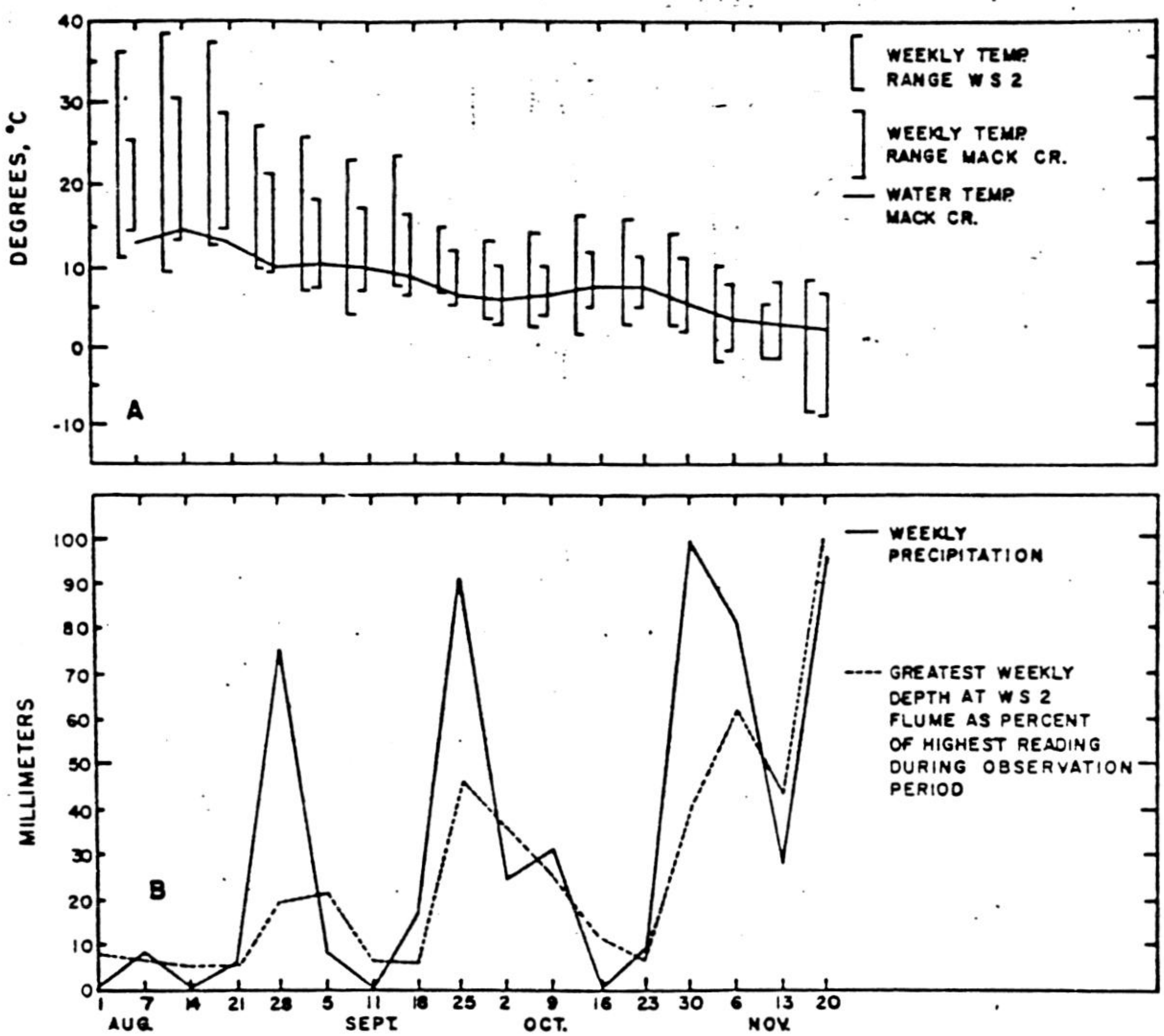


Figure 13. Measurements taken weekly on Mack Creek and WS 2. (A) Air temperature range and water temperature. (B) Precipitation and fluctuation in water depth.

Leaves of Oplopanax horridum deteriorated significantly the week after the first frost, but did not fall. Oplopanax horridum, like Ribes bracteosum, is used by slugs all summer but aging is not readily apparent into the fall. After the first frost, the leaves yellowed and drooped and began to rot on the stem. One week after Acer circinatum, Oplopanax horridum suddenly dropped its leaves. Apparently the process initiated by cold weather is somewhat slower than that in Acer, but the final rates are similar (Figure 12).

A different pattern of Alnus rubra may be weather dependent. The aging pattern of Alnus rubra and Acer circinatum were similar at Lookout Creek, a straight line, but Alnus started earlier, losing its older leaves by midsummer while still developing new ones. Nonetheless, the rate of loss in sunny areas was reasonably linear from mid-August through mid-September. Alnus had a different pattern at Mack Creek where a moderate initial leaf loss of about 25% over a 2-month period ended at the time of first frost. This was followed by 3 weeks with almost no leaf loss and abrupt abscission of the remaining leaves in the following 3 weeks. A heavy insect infestation in the sample trees disappeared after the first frost. We hypothesize that Alnus leaves at Mack Creek abscissed prematurely because of insect damage and probably had not reached a stage of natural senescence. The insects were suppressed by the first frost and abscission ceased. Leaf fall did not begin again until the second frost 3 weeks later, either because leaves were not sufficiently mature or because they are susceptible only to severe frosts. Once leaf fall resumed, however, it proceeded at a high rate.

We were unsuccessful in quantifying Salix leaf fall because a base line could not be established. New leaf formation did not stop until October, by which time older leaves were falling.

Duration of Leaf Fall

Rate of leaf fall is rapid for most of the species. On Lookout Creek, 50% of Acer circinatum and Alnus rubra leaves can be expected to fall during 15- and 20-day periods, respectively (Table 28). If these trees are responding almost entirely to aging at this elevation, prediction of the influx of debris on the stream as a fairly constant function of time should be possible. Frost probably accelerated leaf fall on Mack Creek. There, during the 3 weeks after frost, Acer circinatum lost 94%, Acer macrophyllum 89%, Rubus spectabilis 56%, Oplopanax horridum 52%, and Ribes bracteosum 42% of their leaves. Oplopanax lost an additional 33% during the next week, and Ribes bracteosum had only 47% of its leaves remaining when frost occurred (Table 28). The timing of heavy fall influx of debris at the higher elevation is probably dependent upon temperature and thus much less predictable. Once triggered, however, the process may be similar from year to year.

Table 28. Time required for abscission.

Species	Location	Days required for 50% abscission at median of population	Percent of leaves: Remaining at first frost	Remaining 3 weeks later	Lost
Acer circinatum	Lookout Creek	15	no frost during abscission		
Alnus rubra	Lookout Creek	29	"	" "	"
Acer circinatum	Mack Creek	10	94	0	94
Acer macrophyllum	Mack Creek	10	90	1	89
Alnus rubra	Mack Creek	7	76	74	2
Oplopanax horridum	Mack Creek	13	95	43	52
Ribes bracteosum	Mack Creek	39	47	5	42
Rubus spectabilis	Mack Creek	21	79	23	56

Rate of Senescence in Herbaceous Plants

The senescence of herbaceous plants is more complex than abscission. First, herbaceous plants generally lack sharply defined events, comparable to abscission, which lead to litterfall. They tend to wilt and decay rather slowly. Furthermore, the mechanical action of the stream contributes to breakdown. Second, few general patterns appear in herb senescence. Species appear to respond variously to sun, drought, cold, and natural aging. Maturity, followed by natural decay as a function of growing season, is probably the most common pattern among flowering herbs. Ferns and vegetative herbs appear to respond to environment. Patterns of each herb are considered here individually.

Mimulus guttatus, a delicate, soft, showy herb and one of the first to develop in spring, begins to drop its flowers by July, develops seeds, withers and is 90% down by mid-September (Figure 14). Mimulus aged at roughly the same time and generally at the same rate at both Lookout Creek and Mack Creek. All locations showed a jump in senescence after the first heavy rain in late August, probably because plants were beaten down.

Aralia californica has a pattern similar to Mimulus guttatus, although many of the stems do not flower (Figure 14). Aging first appeared as browning on the lower leaves and continues steadily until leaves and most of the stem become soft and decayed and finally collapse on the substrate. Senescence in Aralia californica is relatively late, the first noticeable withering about mid-September. Decadence continues at a steady rate until about November 9, when a frost rapidly accelerated failure of the remaining 20%.

Patterns of senescence in Epilobium angustifolium, a tall vigorous fireweed, are similar to those for Mimulus guttatus. Flowering is followed by browning after little apparent environmental stimulus (Figure 14). At Mack Creek, visible deterioration began in early September and continued until early October. Epilobium angustifolium is a stiff herb, however, and unlike Mimulus guttatus, remains brown and upright. Epilobium angustifolium stems occasionally tipped into the creek, but the greatest proportion of stems were still standing on November 6. Very high water or snow is required to bring them down; hence this species enters the stream system quite late.

Stachys cooleyae is a mint which stands 0.5 to 1.5 m tall. An apparent change in rate in September is an artifact of the rating system, which gave considerable importance to flower drop. After flowering, the lower leaves begin to wither, but senescence proceeds slowly and many stems were bent into the water while still green and functioning. Evidence of water action can be seen in late September and early October where senescence is positively associated with water level. All Stachys cooleyae were bent and killed by high water at the end of October.

The Petasites frigidus plant is a vigorous clump of leafy stems with flowers born early in the spring on separate stalks. It was the

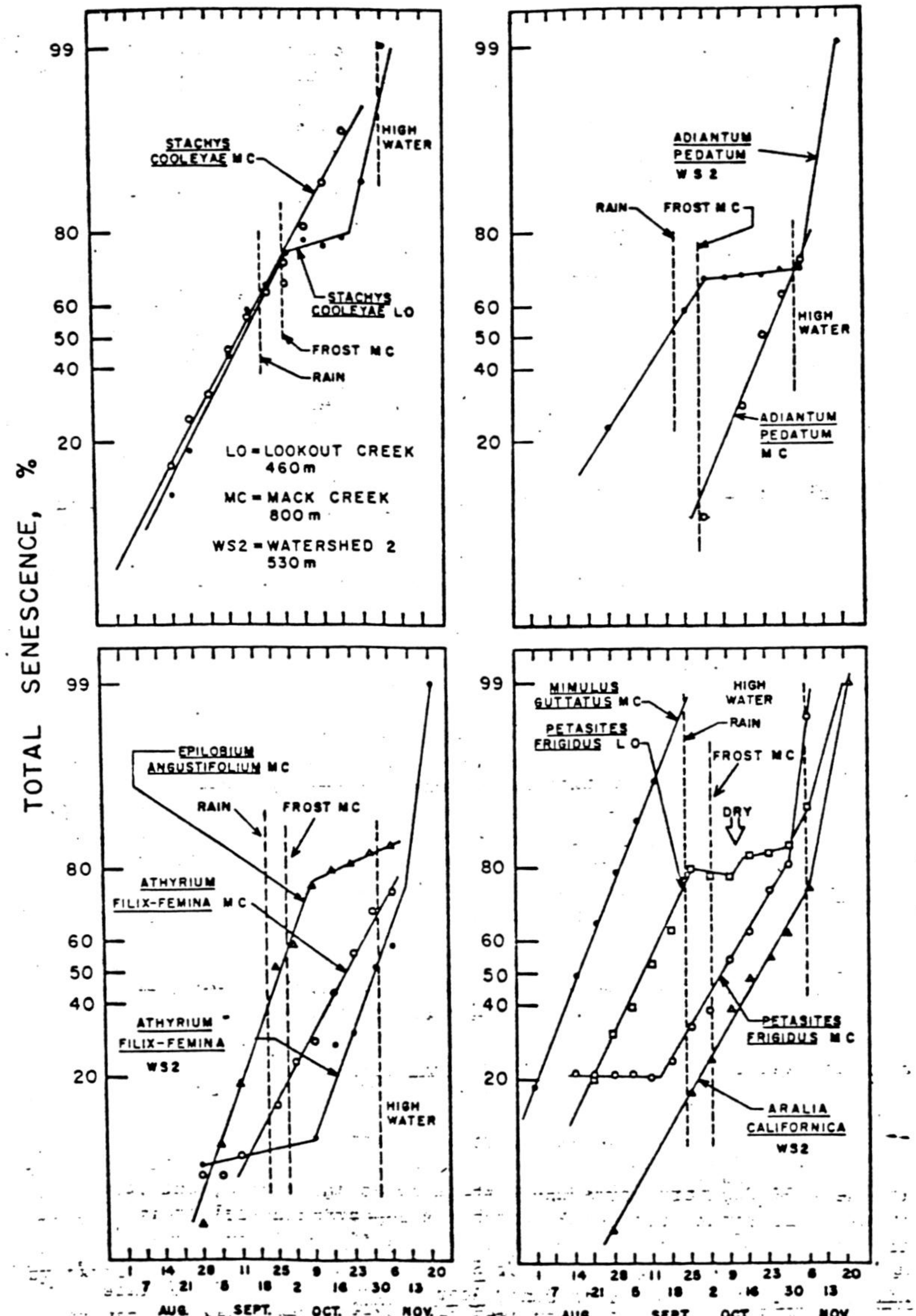


Figure 14. Senescence rates plotted on probit paper for five herbs and two ferns from three elevations in 1977.

second species to show signs of decay on Lookout Creek (Figure 14) but remained vigorous for 6 more weeks on Mack Creek. Plants showing the most distress were on sunny gravel bars. Moisture stress would seem impossible at these locations. It appears that sunlight and reflected radiation from the gravel cause premature aging.

Petasites decline at Lookout Creek continued at a relatively steady rate until cool rainy weather apparently rejuvenated the plants. Senescence continued slowly into November when high water covered all plants. At the cooler Mack Creek site, Petasites frigidus remained vigorous until the first frosts of fall. Again, cool weather preceeding frost seemed to revive wilted plants. Later, after frost initiated decline, withering and leaf fall proceeded at a relatively even rate. When Petasites frigidus is vigorous it can withstand strong water flow, but because it grows in the stream channel, wilted or decayed leaves are subject to water action as soon as they drop.

Adiantum pedatum, the maidenhair fern, declined from drought at WS 2 (Figure 14). Deterioration almost stopped after heavy rains and did not begin again until a heavy frost at the end of the observation period. On Mack Creek, Adiantum pedatum was observed in two locations. On an exposed cliff, deterioration began abruptly at first frost in early October and continued at a steady rate. Many fronds were still up at last observation, although badly yellowed. Fronds under shrubs or trees at stream edge did not show any deterioration during the observation period.

Athyrium filix-femina is a large fern of wet habitats. It began to senesce in early October at Mack Creek (Figure 14), apparently as a result of frosts. Senescence proceeded at a fairly steady rate, and only about 25% of fronds remained above the ground by early November. Because the plants often grow on very low spots, they have immediate contact with the water even before the fronds are dead. On WS 2, Athyrium senesced 2 weeks later but at the same rate as on Mack Creek. All fronds were down by November 21.

Herbaceous species senesce at variable rates and appear to respond to a number of environmental influences. Early rains probably slow the decline of Petasites frigidus while hurrying the decline of other species. An early sharp frost damages Aralia californica severely, and high water adversely affects Stachys cooleyae.

Other Sources of Litter

The heavy influx of leaves and herbage comes in October, but other types of detritus from shrubs and herbs appear much earlier in the growing season. Flowers and seeds of Petasites frigidus appear in May and June, large quantities of Salix catkins in May through July, Mimulus guttatus flowers in June, Acer macrophyllum seeds in late summer, and Ribes bracteosum fruits in August. This detritus can be important because maximum water temperatures and minimal stream flows in August cause organic materials introduced to streams to become concentrated and to decompose rapidly.

Total weight of fruit and flower parts may be low, but the nutrient content is high. Flower parts have been shown to contain 2.5 times the nitrogen contained in leaves from a hardwood forest, and seed kernels contain 1.2 times as much (Cromack and Monk 1975). In a *Quercus* forest, flowers contained almost 3 times the nitrogen of autumn leaves (Carlisle et al. 1966). The C/N ratio of flowers and fruits is commonly favorable. Further investigation of this potentially important nutrient source seems desirable.

SUMMARY

Sixteen understory plant communities in the riparian zones of small streams have been identified and stand tables constructed for pioneer communities on gravel and rock, for rhyzomatous communities, for well-developed herbaceous and shrub communities on flood plains and terraces, and for some topographic climax communities. Clans on a clear-cut section have been ordered in space from instream to bank. They reach maturity at different times during the summer.

Distribution of communities within the riparian zone was extremely heterogeneous. The *Acer circinatum* community was the only community found on all streams surveyed, but its range of cover was wide (2% to 45%) and never consistent. The *Rubus spectabilis*/*Ribes bracteosum* community was common, particularly in the active zone, but was missing from three segments. Stream segments with bedrock substrates had high herbaceous cover but low shrub cover.

Annual foliar biomass production was estimated for riparian vegetation along three stream segments. Distribution of communities and species controlled detrital input. WS 2, a recently scoured stream, had lowest overall mass followed by the Mack Creek old-growth stream segment, which has considerable shrub cover, and the Mack Creek clear-cut segment, where vigorous herbaceous clans and young *Salix sitchensis* dominate.

Yearly foliar production by communities was least among small herbaceous communities which averaged from 5 to 21 g/m^2. Medium-size-herb communities averaged from 12 to 85 g/m^2 and large-herb communities from 78 to 277 g/m^2. Herbaceous communities occurred most often in the active zone and contributed detritus directly to the stream. Communities dominated by shrubs ranged from 28 to 88 g/m^2.

The variance of biomass samples was extremely high, but the number of samples needed to estimate averages is accurately calculated. It ranges from a low of 61-m^2 quadrats for the *Petasites frigidus*/*Brachythecium frigidum* community to 763 1-m-wide transects for estimating total foliage at stream edge in old-growth. The latter number may be reduced by stratifying by community.

Each zone was characterized by different species. *Ribes bracteosum*, *Athyrium filix-femina*, *Aralia californica* and *Salix sitchensis* were

most productive in the active zone; Adiantum pedatum was most productive in the border zone; and Acer circinatum and Polystichun munitum most productive in the outer zone.

Abscission and fall senescence were monitored for thirteen riparian species. Deciduous leaf fall commenced as a function of age in August, but the rate increased abruptly after frost in early October. All leaves had fallen by the first week in November. Herbaceous species responded to aging and a number of environmental influences, chiefly frost and water action. Senescence began in August, and most species had collapsed by the first week of November.

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APPENDIX

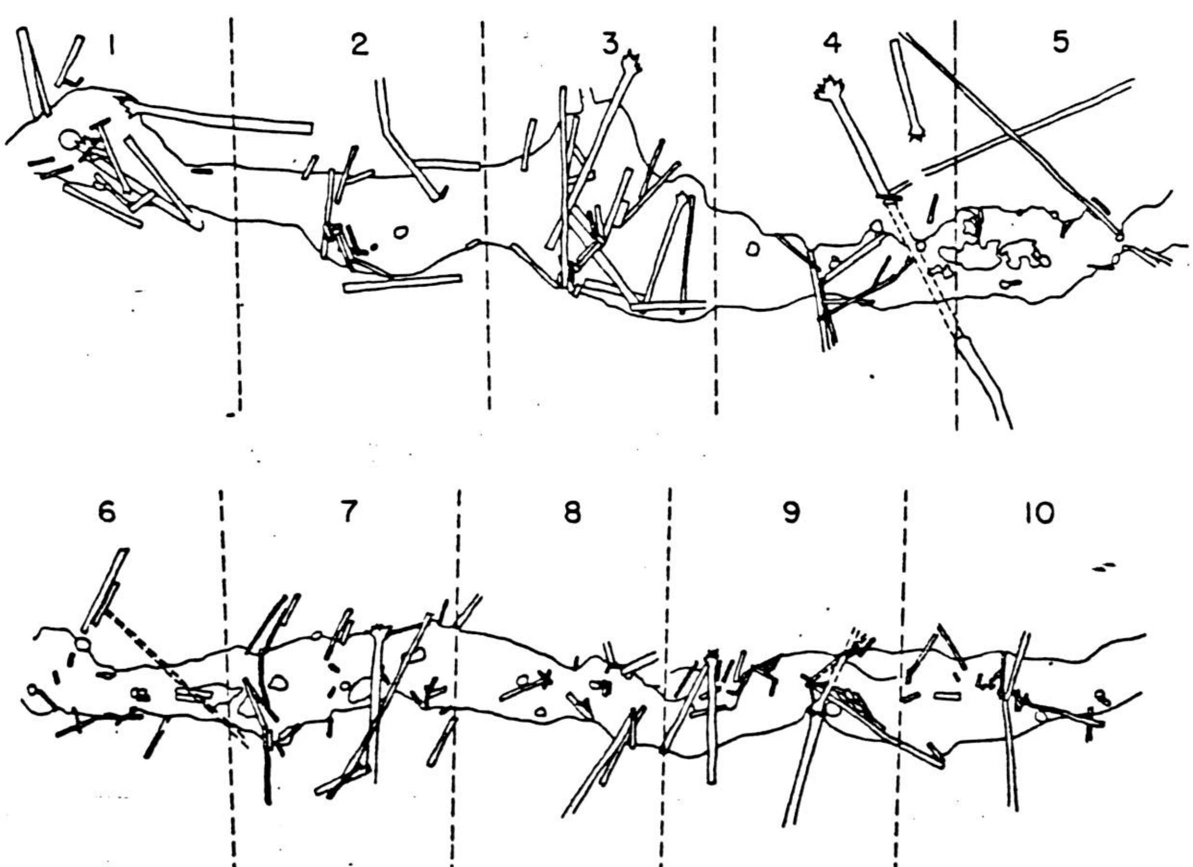
Maps of Riparian Communities in Mack Creek Old-Growth

Communities of the 290 m sample segment in the riparian zone of Mack Creek old-growth were mapped in the summer of 1976. The maps follow here in two series of 10 maps each. They are contiguous and may be placed side by side to form a continuous map. The first series (A1-A10) illustrates the distribution of shrub and herbaceous communities. The second (B1-B10) is a repetition of the first and shows the distribution of midheight cover of large shrubs and small trees.

On the first series of maps, all slopes are indicated in degrees and abrupt changes in slope by dotted lines. Riparian zones are often characterized by steep banks and cliffs covered by several communities. With conventional foreshortening and horizontal projection, communities on dry upper slopes appear superimposed upon those close to the water. Also, the area occupied by a given community is severely distorted, therefore all surface areas are treated as flat.

Stream channel portions of the maps are taken from a series by George Lienkaemper, U.S. Forest Service, Forest Sciences Laboratory, Corvallis, OR 97331.

Map Overview



Symbols

———	STREAM EDGE
-----	ABRUPT CHANGE IN SLOPE
— — —	THE BREAK
+	REFERENCE POINTS
10°	SLOPE
←	WATER FLOW
	LOGS AND WOODY DEBRIS
(R)	ROCK
●	*ACER MACROPHYLLUM*
⊕	*THUJA PLICATA*
△	*TSUGA HETEROPHYLLA*
○	*PSEUDOTSUGA MENZIESII*
38 └DBH,cm	
□	SNAG

SERIES A—KEY

SHRUBS

RUBUS SPECTABILIS / RIBES BRACTEOSUM

OPLOPANAX HORRIDUM

VACCINIUM ALASKAENSE, V. PARVIFOLIUM

HERBS

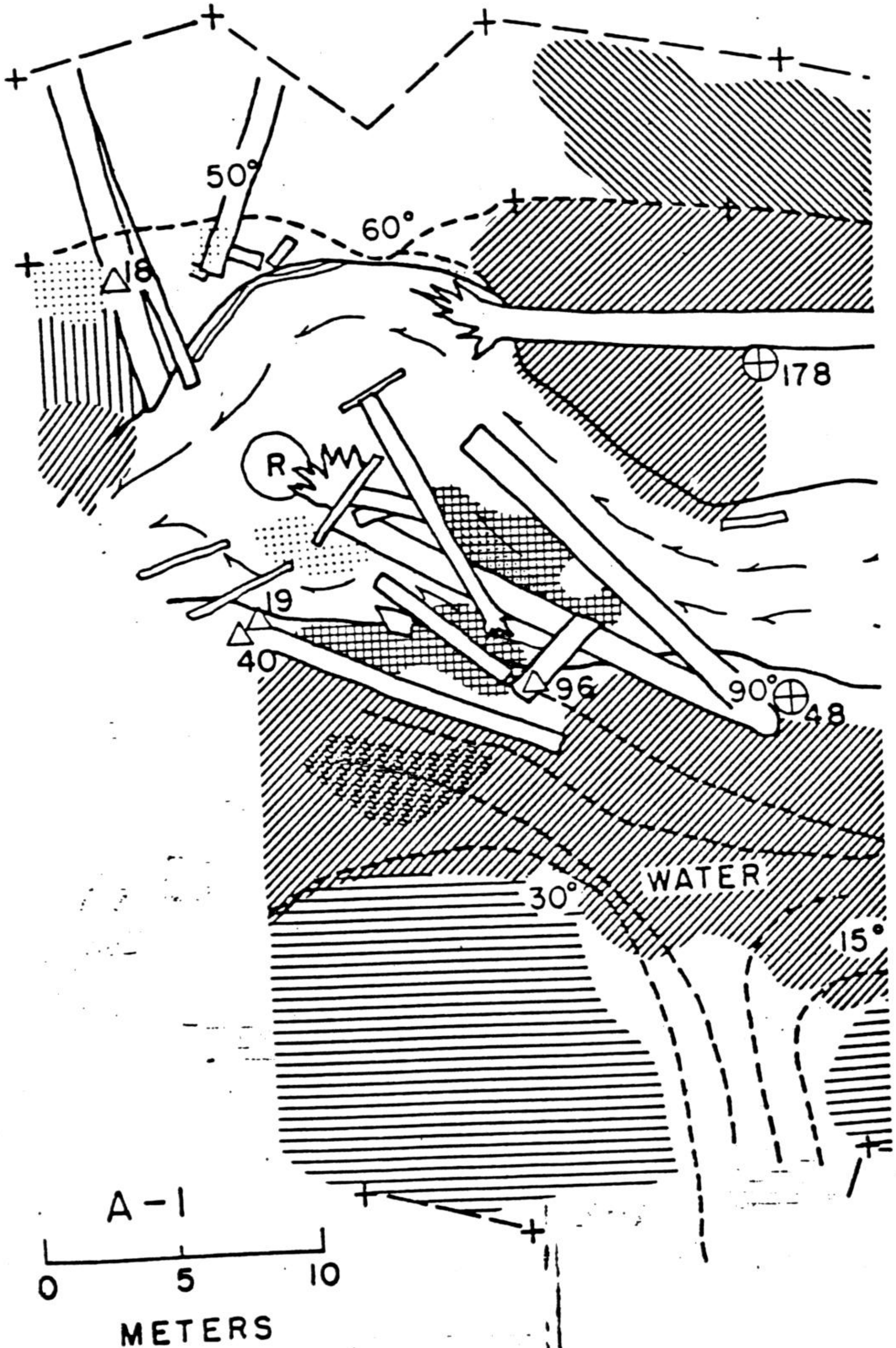
INVASIVE SMALL HERBS:
MONTIA SIBIRICA, CIRCAEA ALPINA
GALIUM TRIFLORUM

TOLMIEA MENZIESII

TALL HERBS:
ATHYRIUM FILIX-FEMINA, PETASITES
FRIGIDUS, ADIANTUM PEDATUM

POLYSTICHUM MUNITUM, BLECHNUM SPICANT

SPARSE FOREST HERBS:
CLINTONIA UNIFLORA, SMILACINA
STELLATA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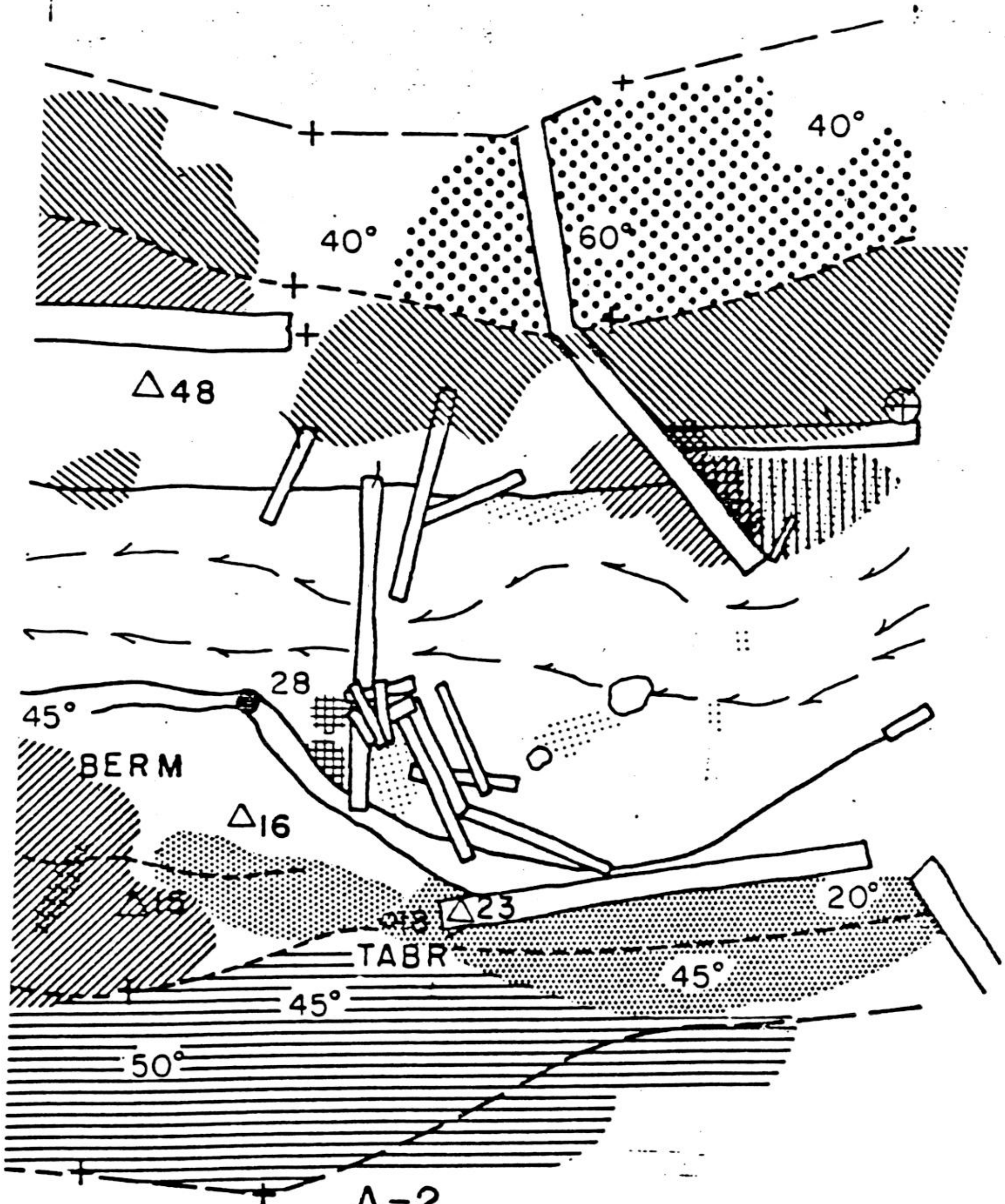

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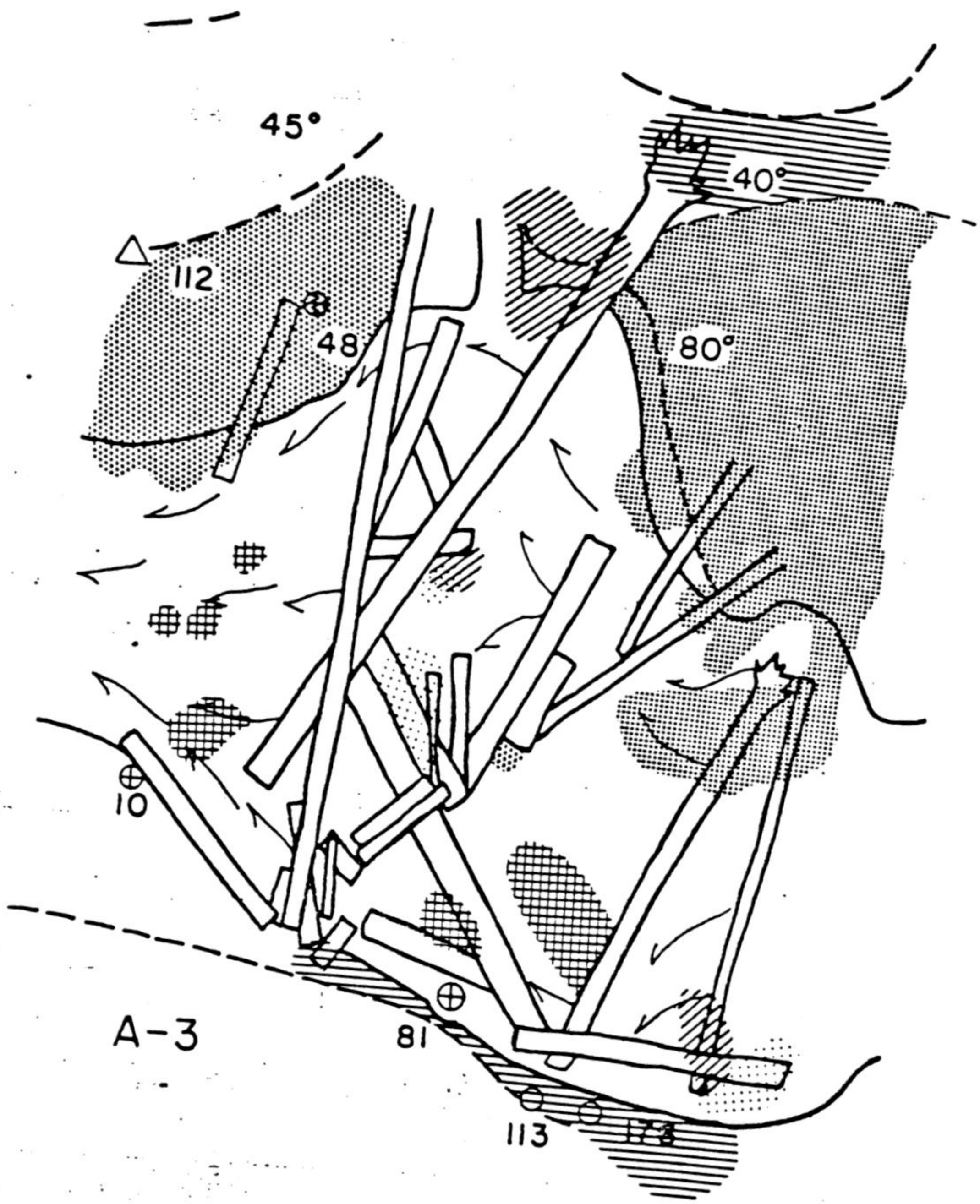
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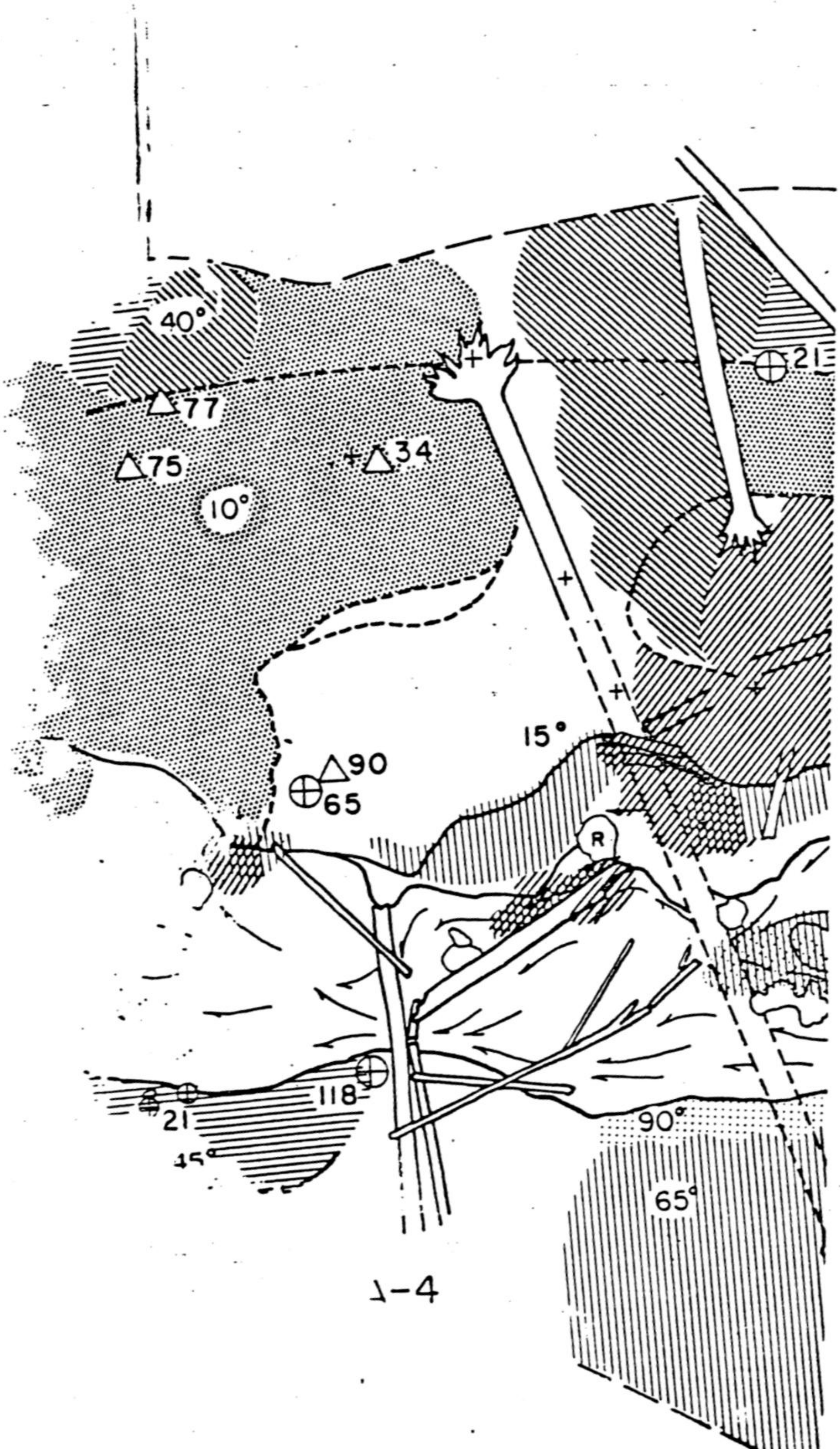

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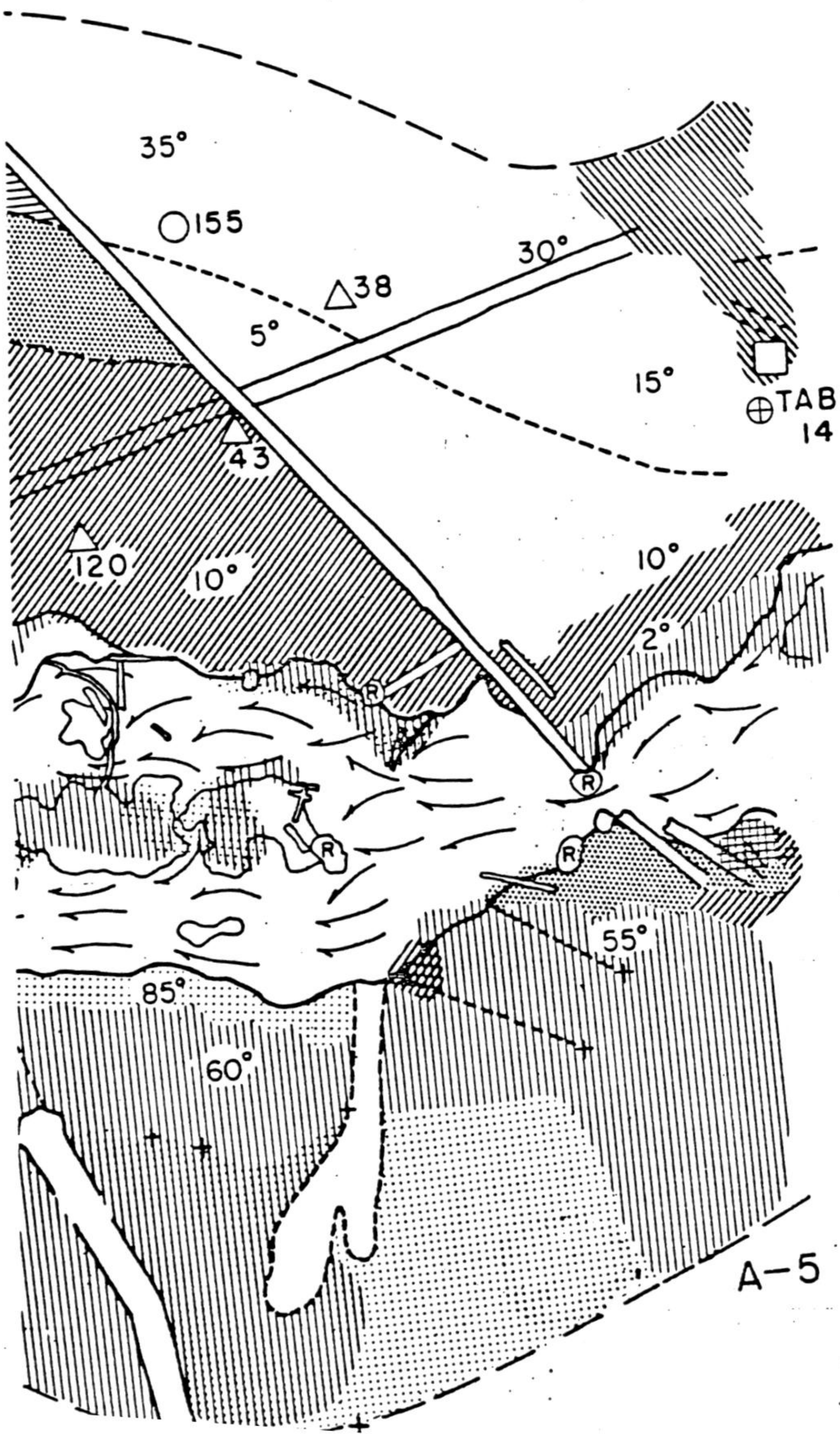
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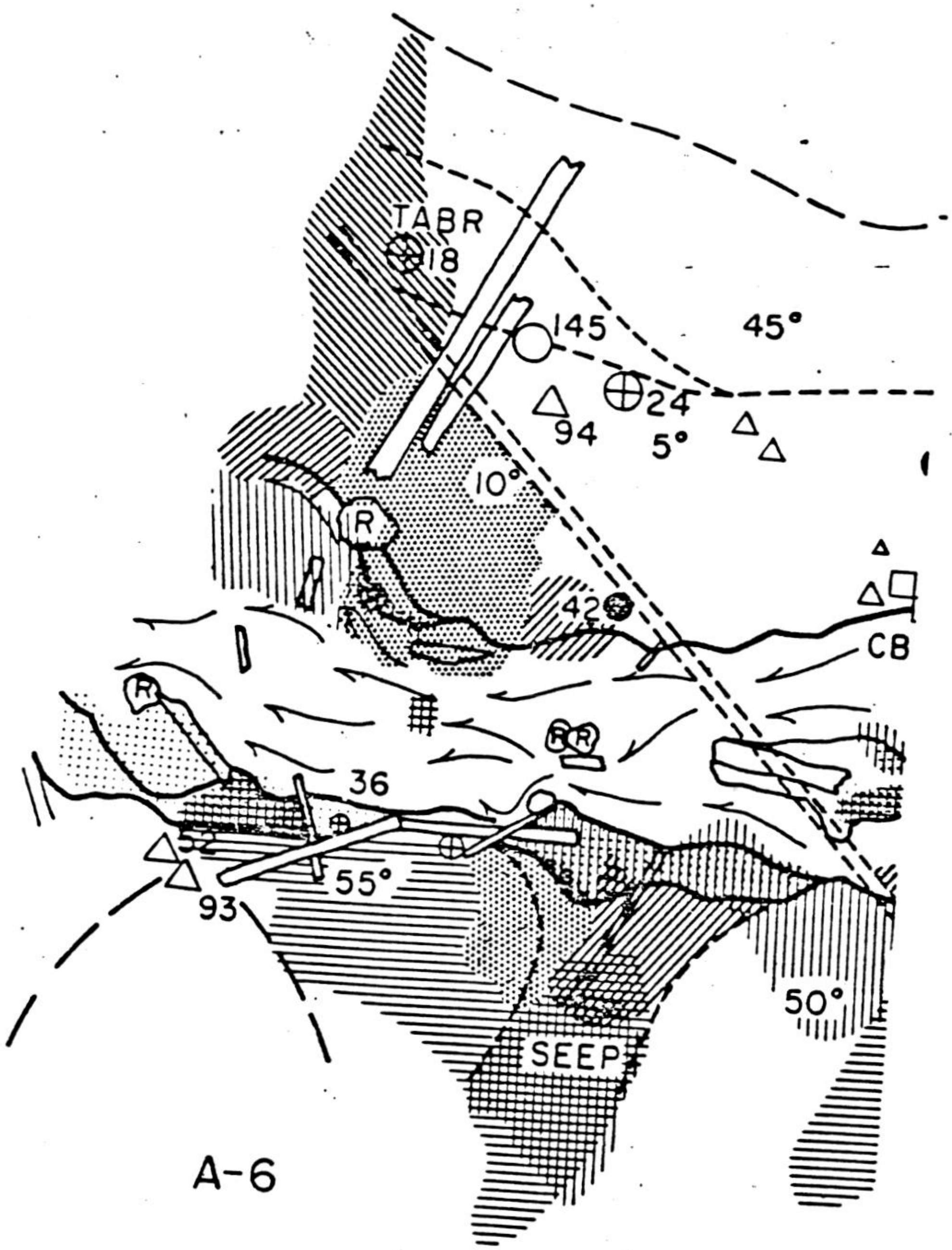

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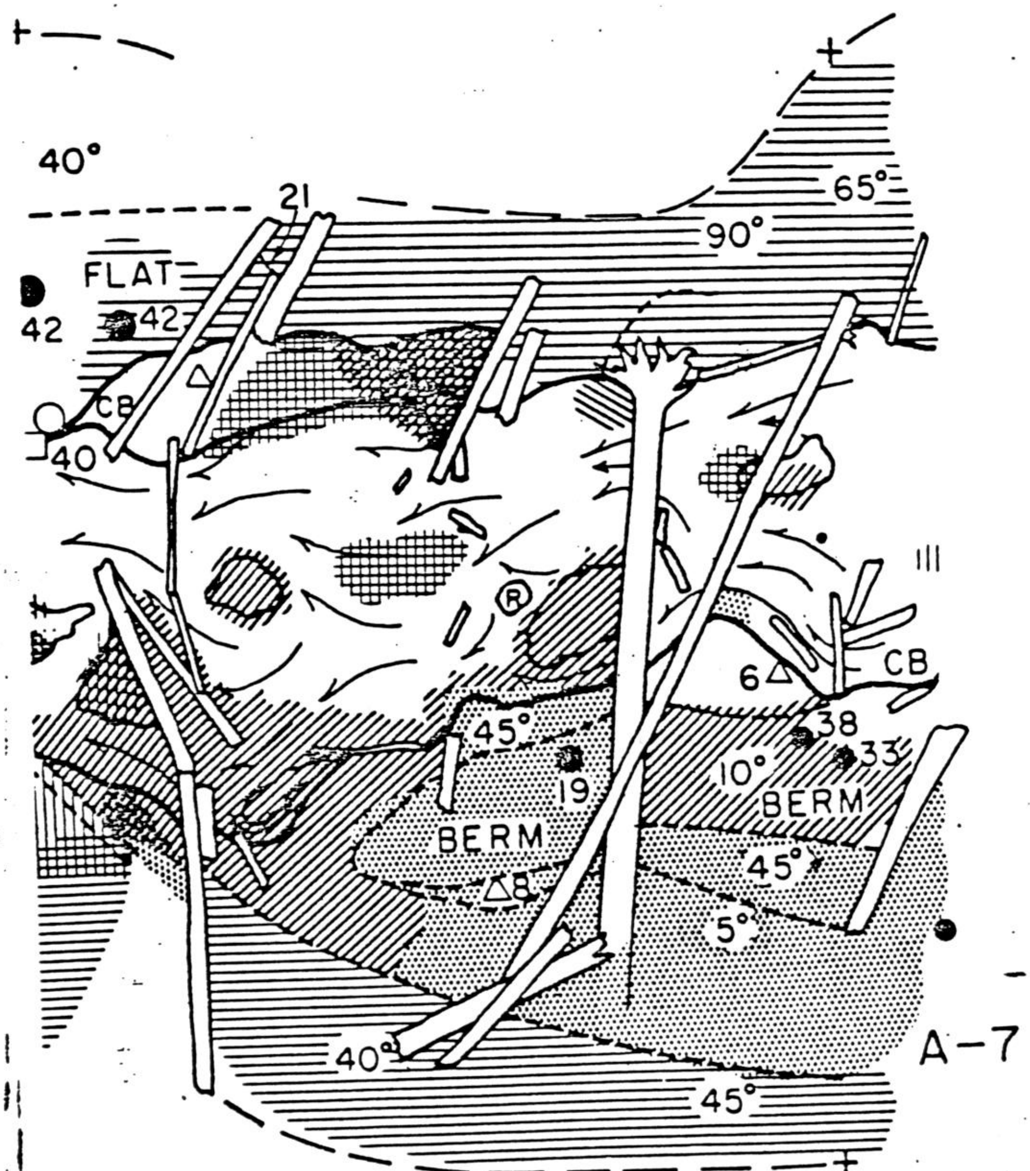
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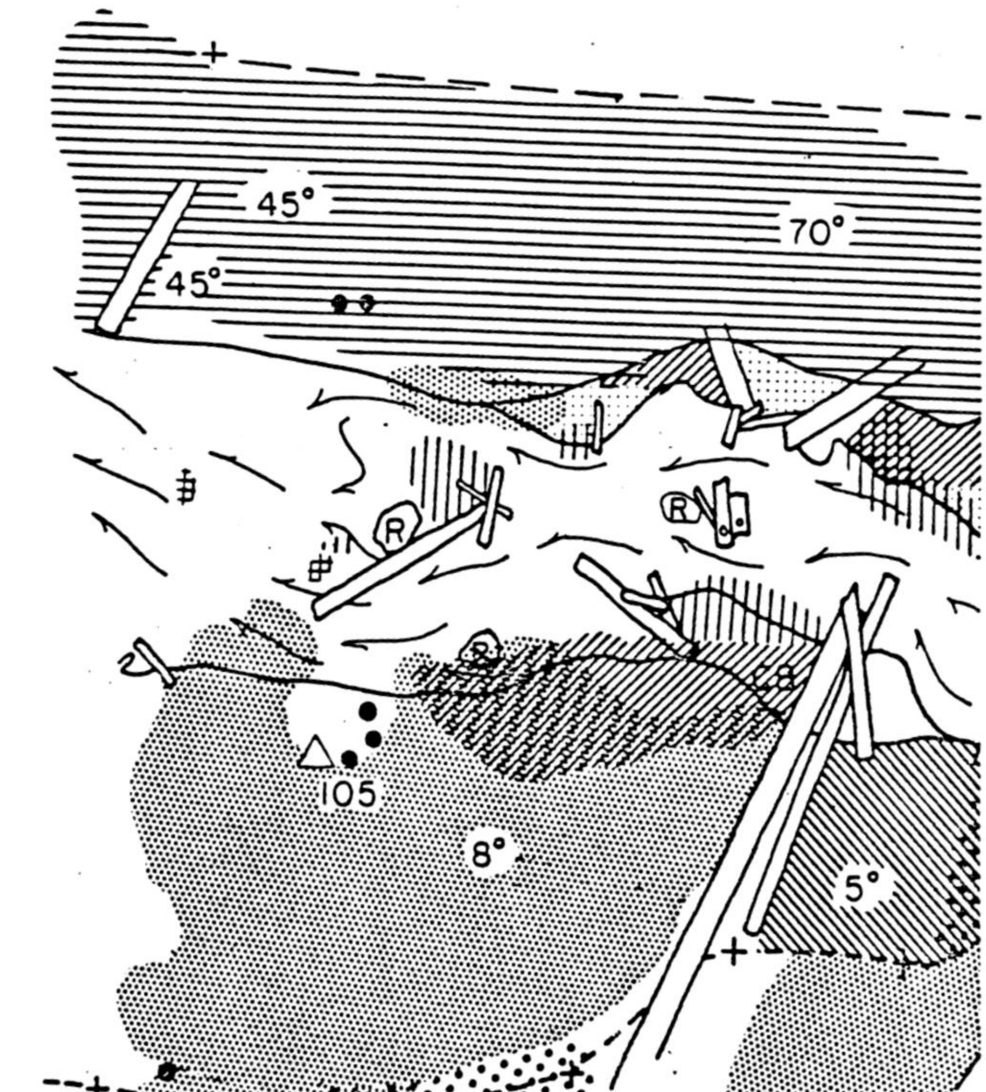

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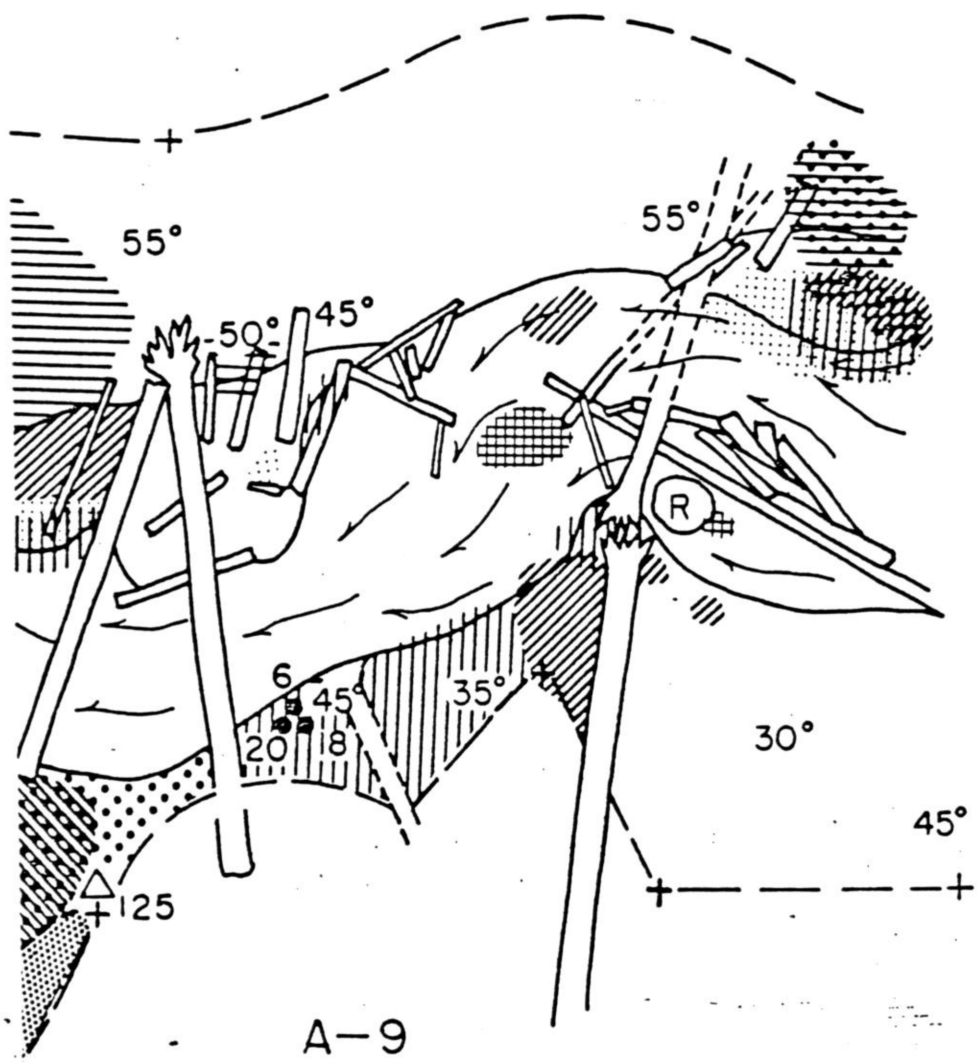

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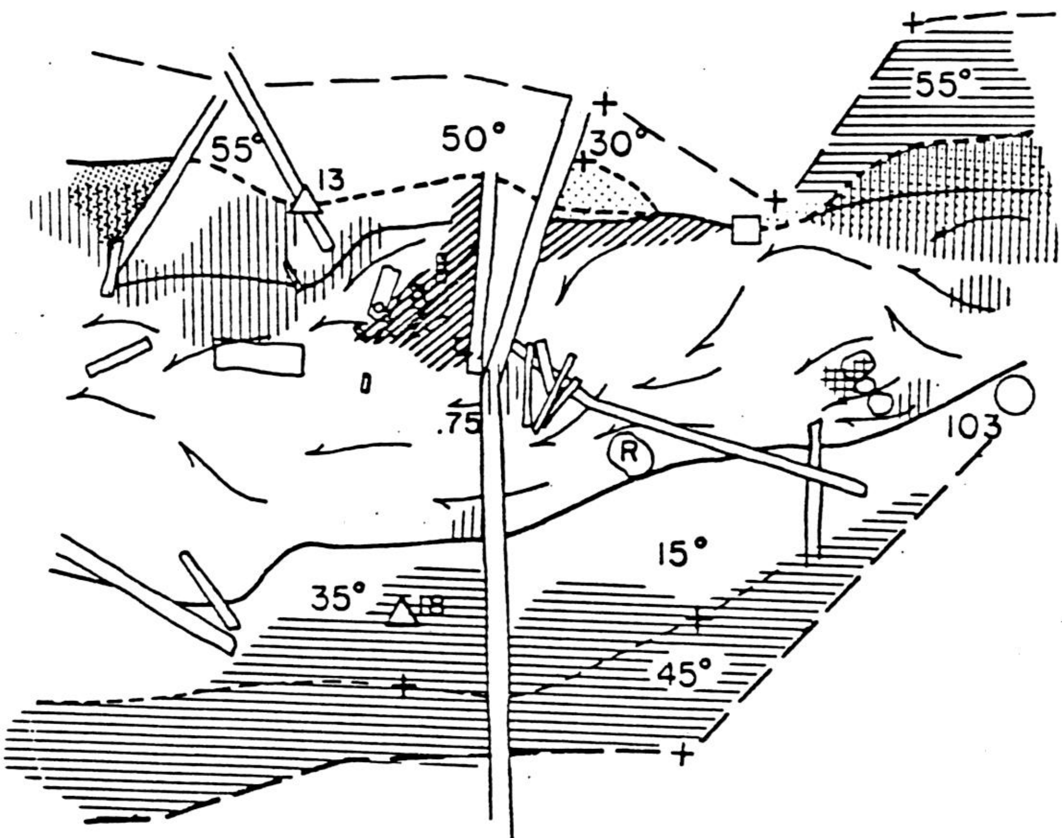


A—10

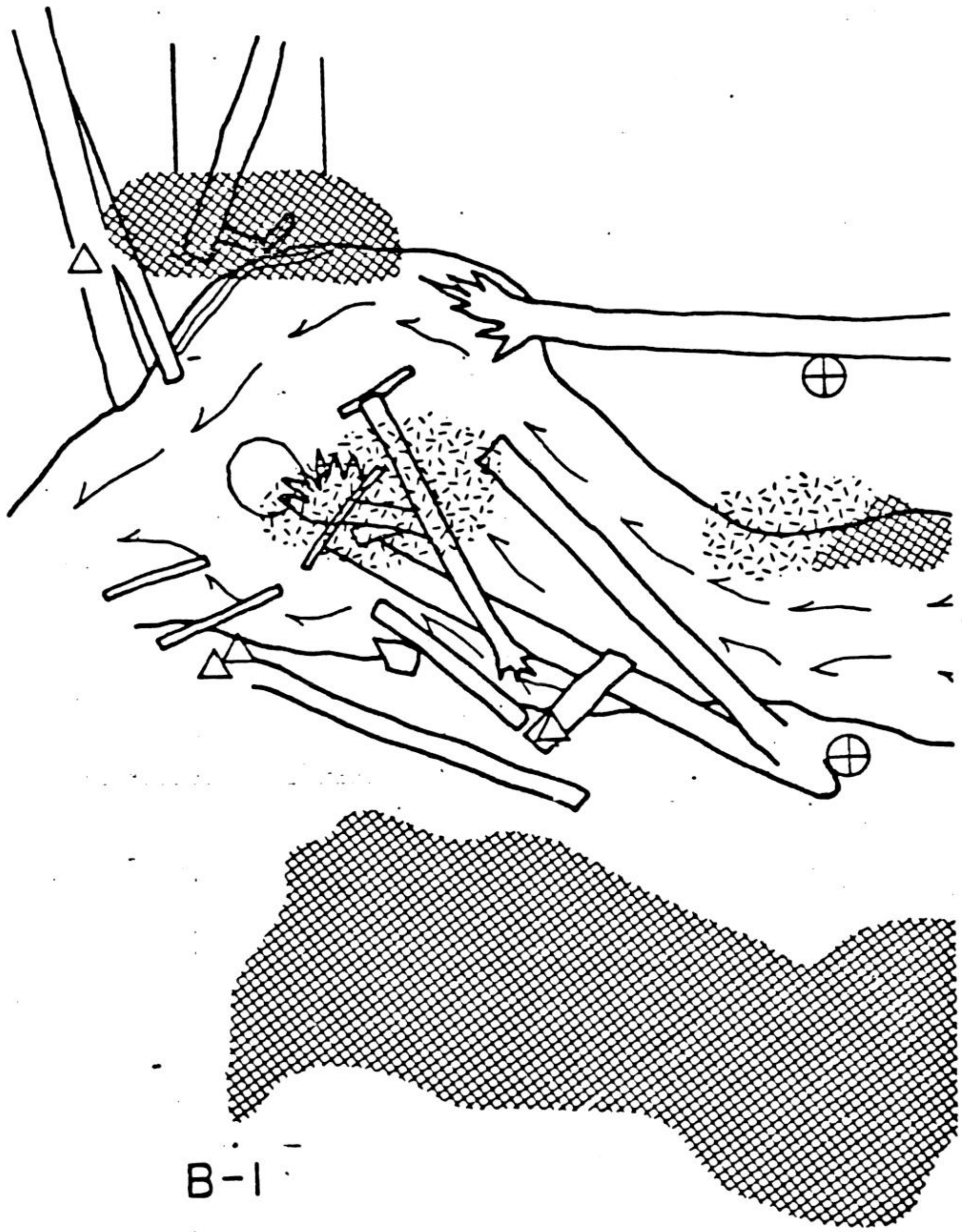
SERIES B — KEY

LARGE SHRUBS AND SMALL TREES
(foliage less than 3m high)

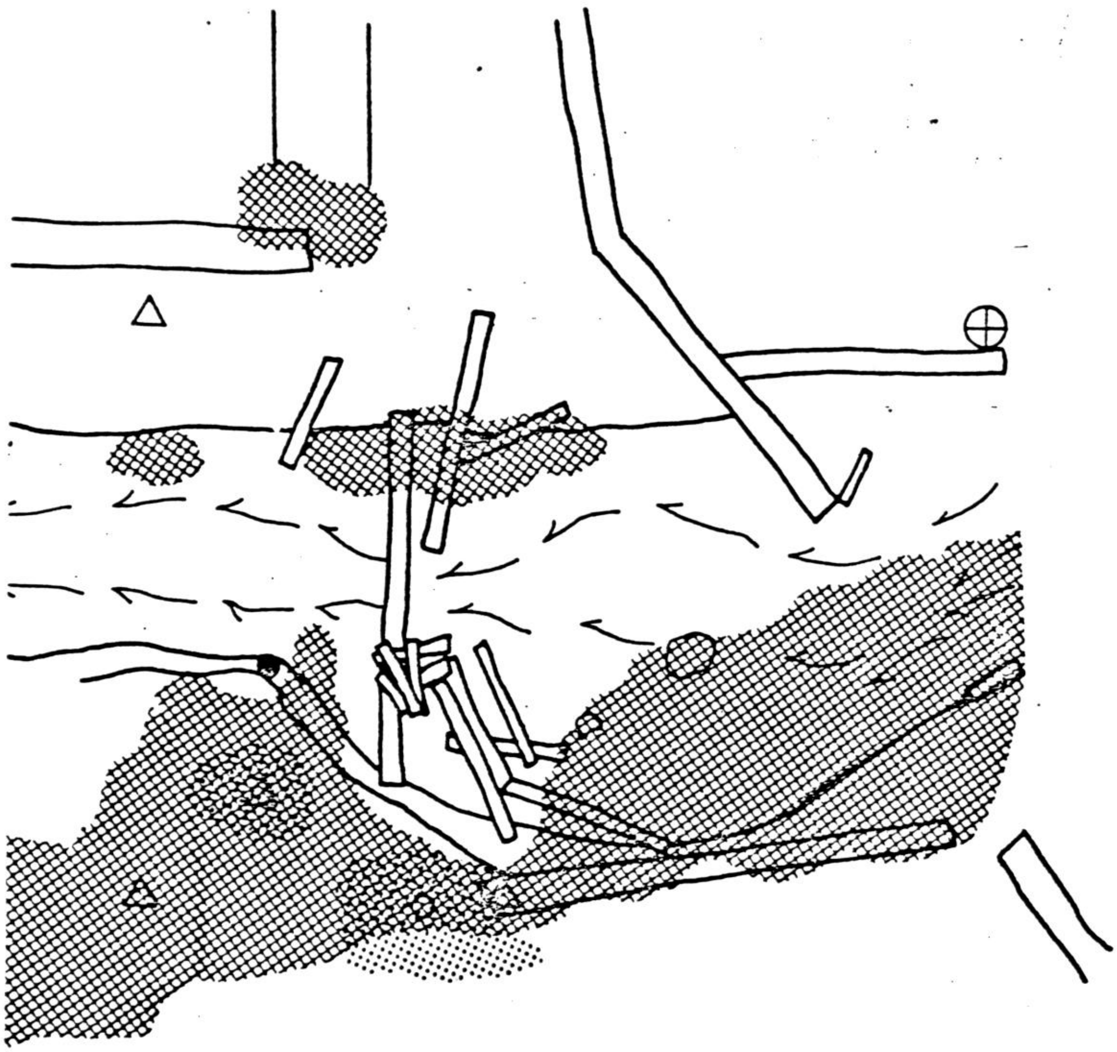
ACER CIRCINATUM (and CORNUS NUTTALLII)

ACER MACROPHYLLUM

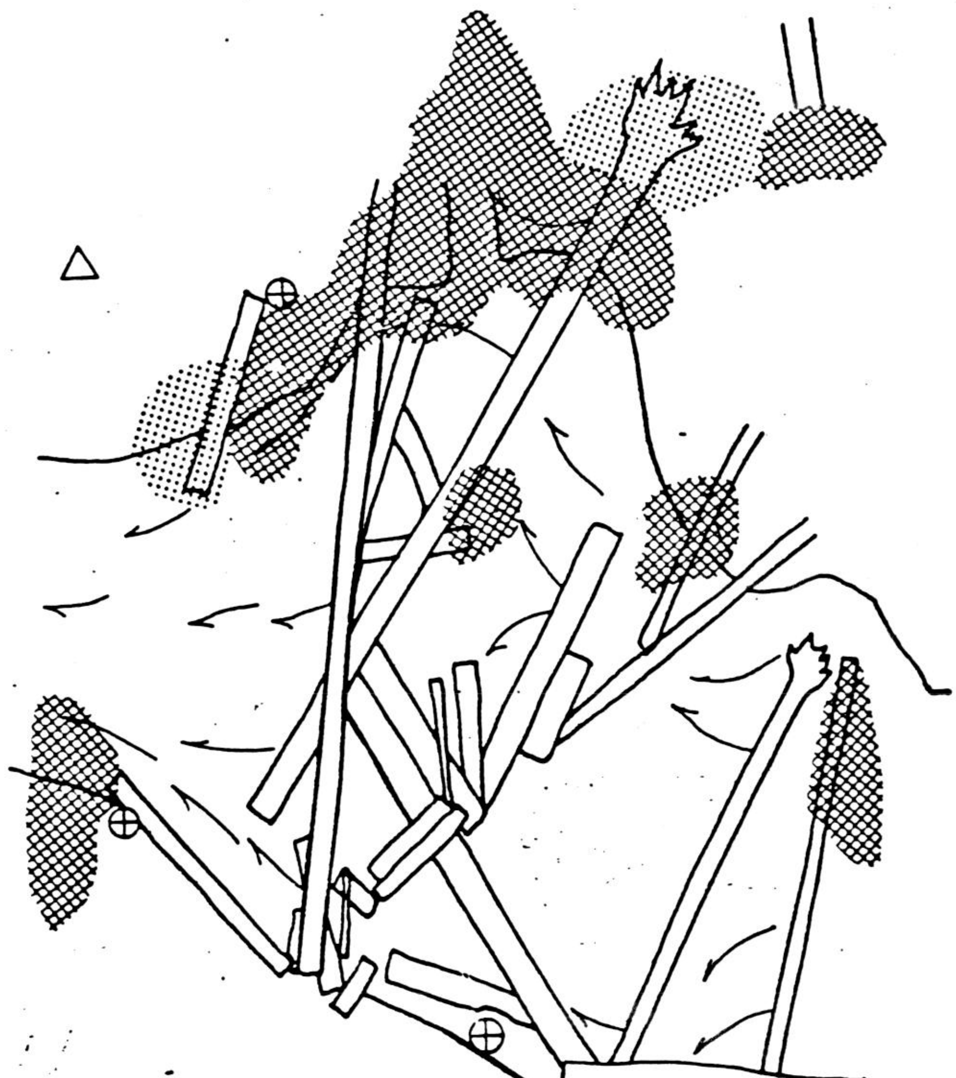
LOW EVERGREEN FOLIAGE



B-1



B-2



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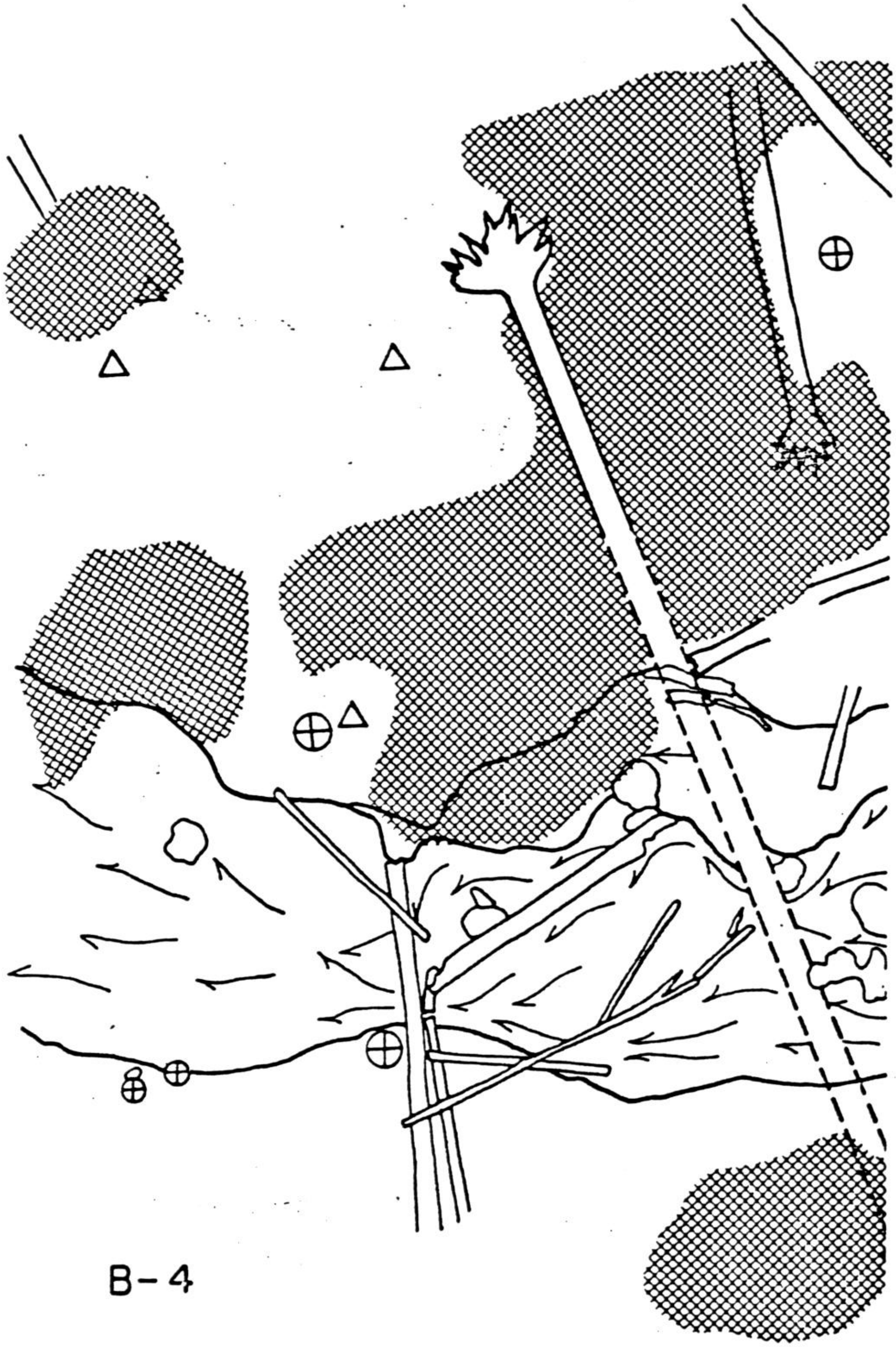

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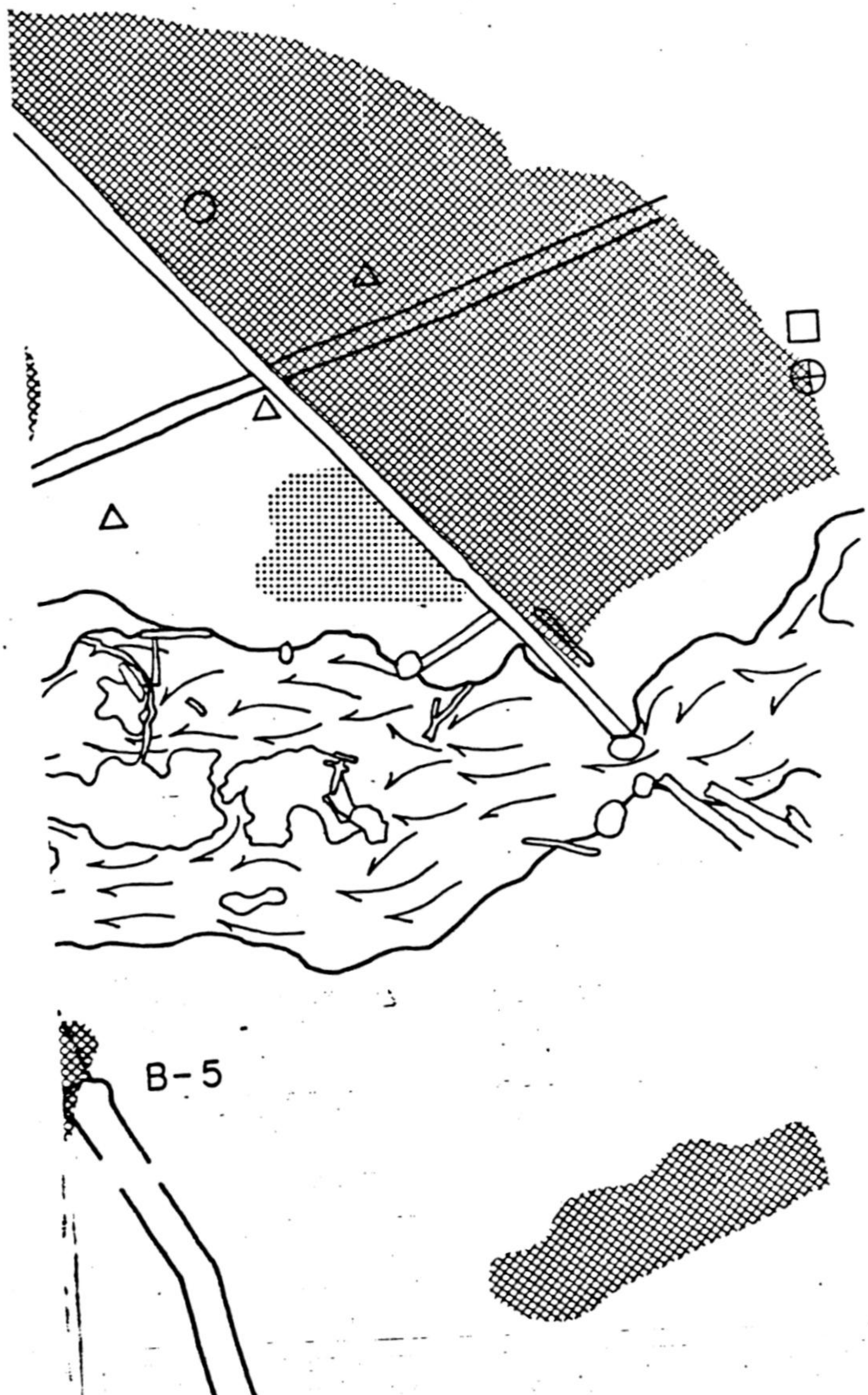
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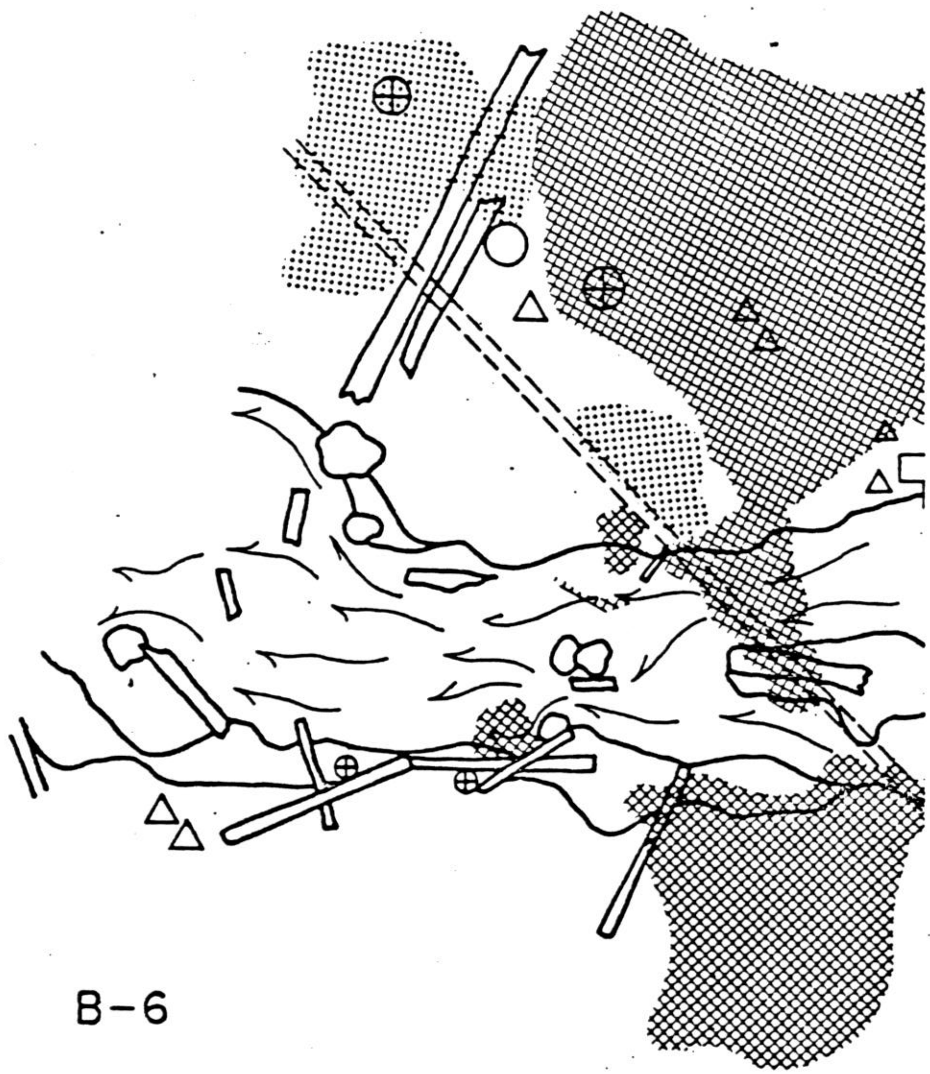
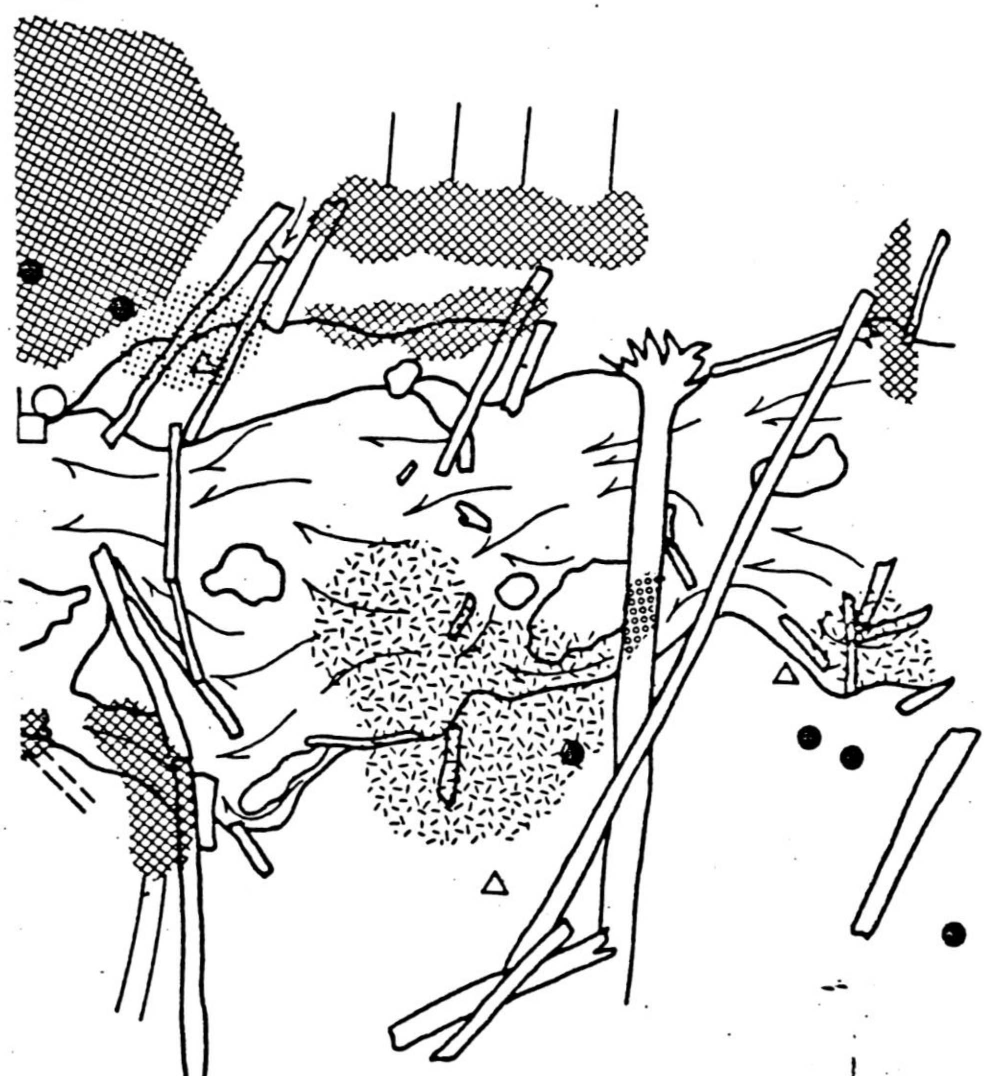
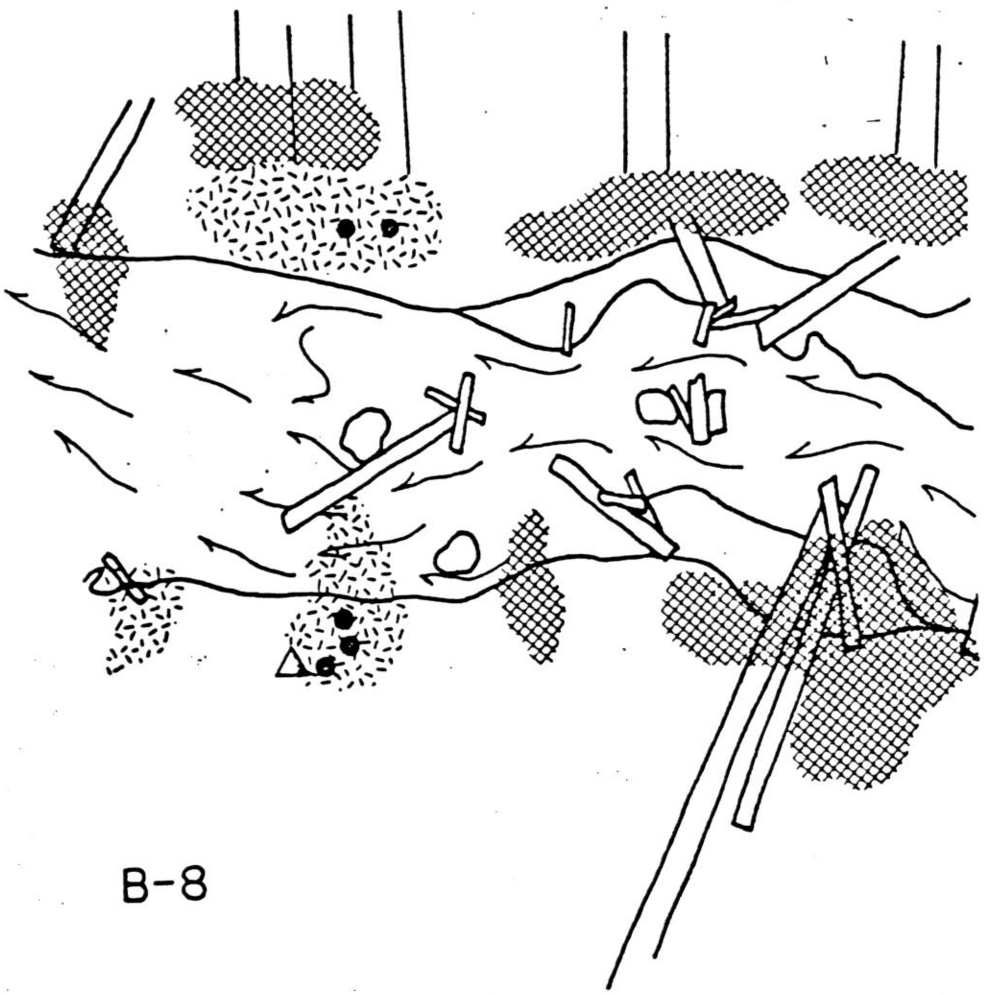


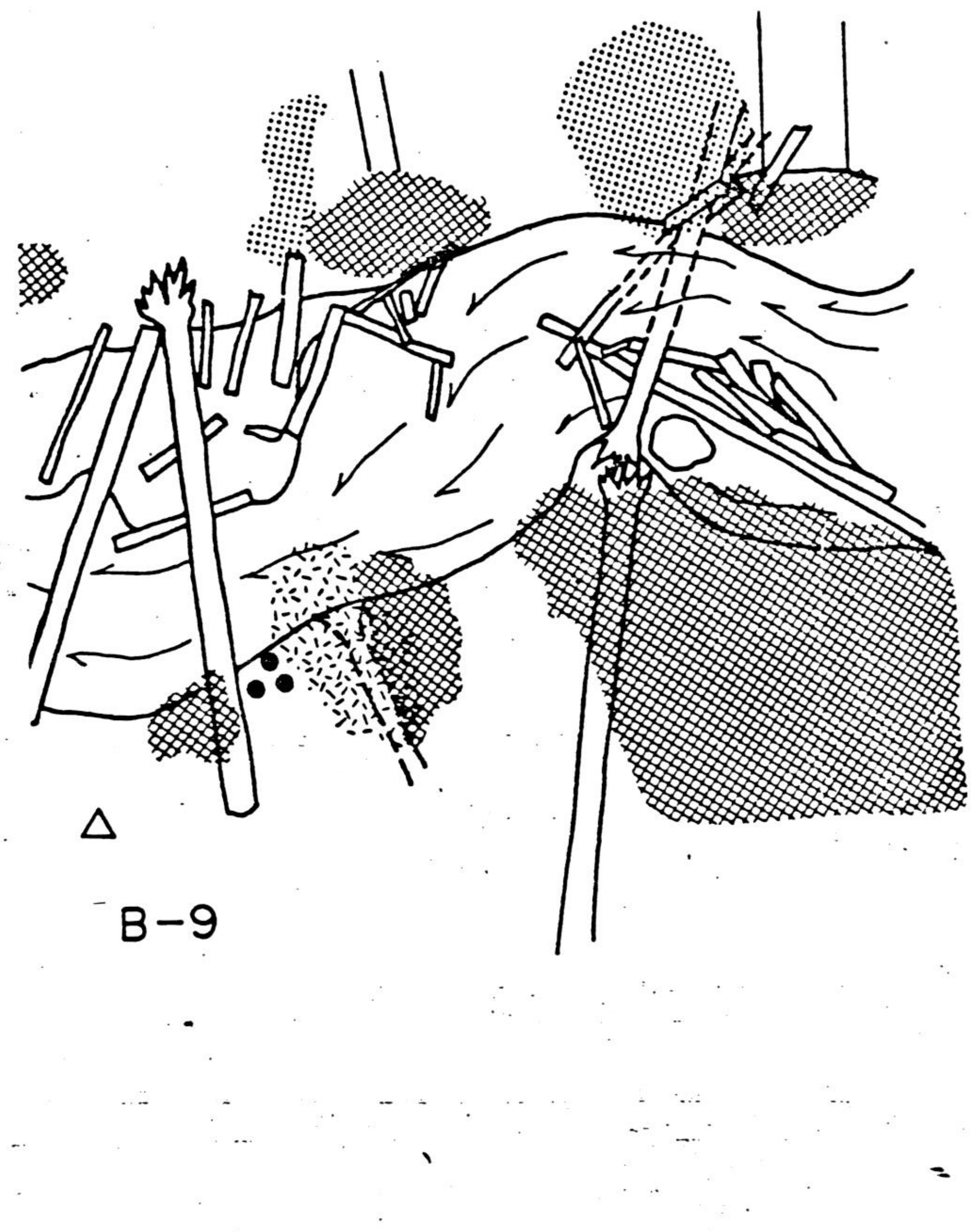
B-6



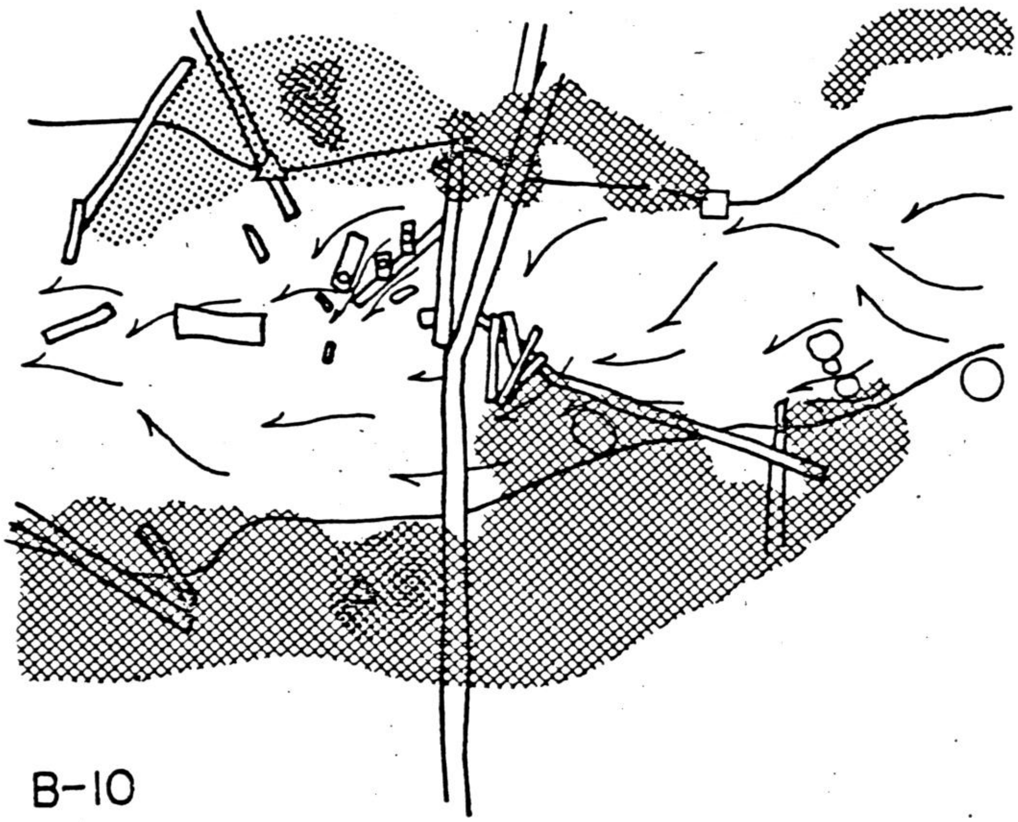
B-7



B-8



B-9



B-10