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Forest Succession on Alluvial Landforms of the McKenzie River Valley, Oregon

Abstract

Using association tables and a two-dimensional ordination procedure, two topo-edaphic climaxes (associations) have been identified. These are: (1) the *Tsuga heterophylla/Polystichum munitum-Oxalis oregana* association occurring on terraces with fine, sandy loam to silt loam soils derived from silty river alluvium; and (2) the *Tsuga heterophylla/Berberis nervosa-Gaultheria shallon* association occurring on rockier soils with coarser alluvium or glacial outwash. Two early seral associes, each dependent on sedimentation, plus later seral associes, at least one dependent on recent fires, are also identified. A major factor leading to vegetation differences appears to be moisture availability in late summer. (The soils in the *Tsuga heterophylla/Berberis nervosa-Gaultheria shallon* habitat type are shallower, coarser, and rockier than those in the *Tsuga heterophylla/Polystichum munitum-Oxalis oregana* habitat type). This hypothesis is supported by plant-moisture stress-measurements on saplings growing in each of the topo-edaphic associations.

Introduction

Most synecological work on the west slopes of the Oregon Cascades has emphasized the vegetation and environmental characteristics of the mountain slopes. Little or no vegetation study has been done along major drainages where streamflow is sufficient to deposit much alluvial material or to cut terraces large enough for study.

The purposes of this study are to describe and classify forest vegetation occurring on terraces, floodplains, and glacial outwash plains and to determine the successional and environmental relationships of the vegetation units identified.

The study area includes nearly level waterlaid and watercut terraces, floodplains, and glacial outwash plains deposited adjacent to the McKenzie River and one major tributary, Horse Creek. The area includes the McKenzie River Valley from the mouth of Boulder Creek in the east to Quartz Creek in the west (Fig. 1). This region maintains some relatively undisturbed forest vegetation on desired landforms. The average slope of the study area is one degree over the 29 km distance, with elevations from 274 m at Quartz Creek to 560 m at Boulder Creek.

The McKenzie River drainage system was chosen as the study area because it is accessible and contains forests suitable for sampling. The McKenzie River is also close to the H. J. Andrews Experimental Forest where the vegetation is well known (Dyrness, Franklin, and Moir, 1974).

Materials from both the High and the Western Cascades appear in the parent material within the study area. The stratigraphy of the area consists of the Cenozoic Tyee and Umpqua marine deposits successively overlain by the Colestin, Little Butte, and Sardine Formations of volcanic origins (Peck *et al.*, 1964).

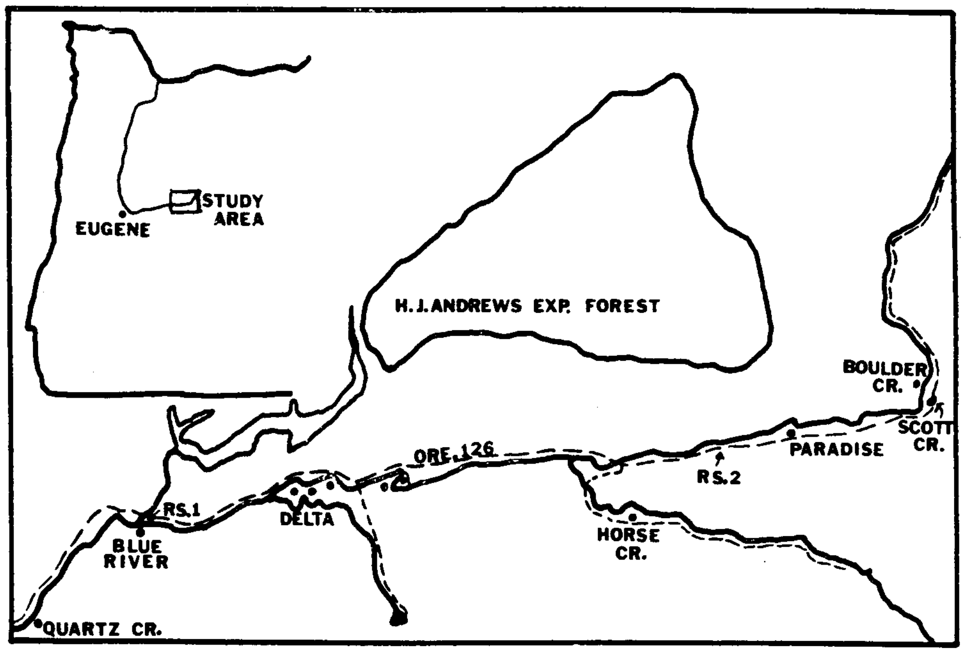

Figure 1. McKenzie River drainage with study sites labeled.

In the past, soils of floodplains and lower terraces have been labeled "alluvial" and have not been extensively studied. The unclassified soils of the lower terraces are primarily sandy loam or loamy sands in highly stratified and well-drained, mixed alluvium.

Climatically, the area has warm, dry summers with cool nights, particularly in the valley bottom. Winters are cool and mild with moderate to high precipitation. Precipitation from 1961 through 1970 averaged 1670 mm at McKenzie Bridge Ranger Station (R.S. 2, Fig. 1) and 1900 mm at Blue River Ranger Station (R.S. 1, Fig. 1) during the same period. Less than 15 percent of the annual precipitation occurs between April 1 and September 31. Snow does not accumulate within the study area, though it does on adjacent slopes and uplands.

Methods

In late spring, 1971, 30 reconnaissance plots were studied using the techniques of Franklin, Dyrness, and Moir (1970). A reconnaissance plot is a circular plot of variable area within which ocular estimates of cover and frequency classes of species are made. Such a plot is located within a relatively uniform stand to avoid ecotones. Data are collected for the same stand characteristics as on an analytic plot, but estimates obviously are not as accurate, and a soil pit description may be included. This kind of plot can be completed in less than two hours, thus allowing many observations in just a few days. Such an approach has often been used to establish basic inventories of plant communities rapidly and inexpensively.

Such reconnaissance plots were used in description of some associes not sampled by analytic plots. During July and August 1971, 54 analytic plots, each 25 x 15 m, as described by Daubenmire (1968), were established on floodplains, terraces, and glacial outwash plains. At each plot the slope was measured with an Abney level, and elevation was estimated from topographic maps and benchmarks. Height above the nearest stream, direction to the nearest substantial canopy opening, and standard soil descriptions were also recorded. Percent-cover of trees and saplings was visually estimated for the whole analytic plot. Cover of seedlings, shrubs, herbs, and mosses was estimated on 50, 20 x 50 cm microplots by the method of Daubenmire (1959).

Increment borings were taken on most plots. Additional age data were obtained from recently felled trees and from stumps near some of the plots.

In August 1972, predawn plant-moisture stress was determined with a pressure chamber (Scholander *et al.,* 1965) for 40 saplings of *Tsuga heterophylla* and *Abies grandis* in each of the two topo-edaphic associations identified earlier in this study.

Data used in vegetation analysis consist of cover and frequency. Since the greatest variation in stands occurred in species coverage values in the shrub and herb layers, these layers were of greatest use for distinguishing plant groupings. Ubiquitous and rare species were removed from consideration in the association-table manipulations. Identification of plant communities was accomplished by shifting rows and columns of the table until groupings of similar species (rows) and similar stands (columns) were evident. Resultant species-stand groupings were then re-ordered in order to follow the hypothetical seral sequence of associes as determined by field observations (see Table 1). Vegetation data were then subjected to computerized analysis using a similarity ordination program, SIMORD (Dick-Peddie and Moir, 1970). This program uses Sorenson's K to determine similarity of stands, identifying communities solely on the basis of the vegetation. We used SIMORD to generate a two-dimensional ordination of stands and, in conjunction with association tables, to establish clusters of similar stands (associes or associations). For this study all 54 stands were subjected to SIMORD using a maximum of 50 species for stand comparisons as dictated by the capacity of the computer used. High fidelity of species to the various associes depicted in the association table was used as the primary criterion for selection of species to be used in SIMORD analysis. In order to obtain more meaningful ordinations by SIMORD analysis, endstands for computer comparisons can be picked through the use of a subprogram of SIMORD, or they may be entered into computations by the investigator. Endstands are those stands picked as ends for the X and the Y axis of the ordination and are chosen to be as dissimilar to each other as possible, yet still representative of recognizable plant communities. Endstands for SIMORD analysis in this study were picked by a combination of computer selection and investigator adjustments of selected stands.

Plant nomenclature in this paper generally follows the following sources: trees, Little (1953); other vascular plants, Hitchcock *et al.,* (1955, 1959, 1961, 1964); and mosses, Lawton (1971). Voucher specimens for the majority of species found in this study are those of Franklin and Dyrness (1971) and are on file at both the Oregon State University Herbarium and the U.S. Forest Service Herbarium in Fort Collins, Colorado. Additional specimens are found in a small herbarium at the H. J. Andrews Experimental Forest headquarters at the Blue River Ranger Station, Blue River, Oregon. Synecological terminology follows Daubenmire (1968), and the glossary of Carpenter (1938) may also be helpful. In many portions of this paper, the

TABLE 1. Cover and constancy for associes and associations on alluvial landforms.

	Alnus rubra associes		*Abies grandis* associes		Tshe/Pomu-Oxor association		Psme/Coco/Pomu associes		Psme/Bene-Gash associes	
	cover* %	const %	cover* %	const %	cover* %	const %	cover* %	const %	cover* %	const %
Overstory Tree Layer										
Alnus rubra	66	100	—	—	—	—	—	—	—	—
Fraxinus latifolia	11	100	—	—	—	—	1	60	—	—
Populus trichocarpa	38	80	—	—	—	—	—	—	—	—
Tsuga heterophylla	—	—	—	—	59	100	2	40	16	71
Libocedrus decurrens	—	—	13	71	—	—	12	90	9	71
Pseudotsuga menziesii	—	—	14	71	23	89	57	100	53	100
Acer macrophyllum	28	80	35	100	23	100	28	90	3	64
Abies grandis	20	80	40	100	2	61	11	90	5	93
Thuja plicata	3	40	9	43	18	78	4	50	35	86
sub-total	166		111		125		115		121	
Tall Shrub Layer										
Ribes lobbii	9	100	—	—	—	—	—	—	—	—
Rubus parviflorus	1	80	—	—	—	—	—	—	—	—
Vaccinium parvifolium	—	—	—	—	1	61	3	80	2	71
Cornus nuttallii	—	—	—	—	4	61	1	50	8	71
Osmoronia cerasiformis	1	100	4	43	—	—	2	70	—	—
Corylus cornuta	20	100	10	100	4	95	30	100	8	85
Acer circinatum	14	100	25	100	11	100	16	90	19	92
Taxus brevifolia	—	—	—	—	—	—	—	—	2	57
Rhamnus purshiana	—	—	—	—	—	—	—	—	T	47
sub-total	45		39		20		52		39	

TABLE 1. Cover and constancy for associes and associations on alluvial landforms. (Continued)

	Alnus rubra associes		*Abies grandis* associes		Tshe/Pomu-Oxor association		Psme/Coco/Pomu associes		Psme/Bene-Gash associes	
	cover* %	const %	cover* %	const %	cover* %	const %	cover* %	const %	cover* %	const %
Low Shrub Layer										
Berberis nervosa	—	—	—	—	8	95	3	80	22	100
Gaultheria shallon	—	—	—	—	1	33	1	30	18	100
Rosa gymnocarpa	—	—	—	—	—	—	1	60	1	85
Symphoricarpos mollis	1	80	1	71	—	—	18	100	2	65
Rubus ursinus	7	100	4	100	2	100	3	100	3	100
sub-total	8		5		11		26		46	
Herb Layer										
Elymus glaucus	1	100	—	—	—	—	—	—	—	—
Equisetum arvense	4	100	—	—	—	—	—	—	—	—
Heracleum lanatum	2	80	—	—	—	—	—	—	—	—
Collomia heterophylla	1	60	—	—	—	—	—	—	—	—
Urtica lyallii	1	40	—	—	—	—	—	—	—	—
Anemone lyallii	T	40	—	—	—	—	—	—	1	50
Stachys cooleyae	2	100	T	43	—	—	—	—	—	—
Carex bolanderii	T	40	1	71	—	—	—	—	—	—
Tolmiea menziesii	2	100	1	86	—	—	—	—	—	—
Petasites frigidus	7	100	1	86	—	—	—	—	—	—
Nemophila parviflora	6	100	1	57	—	—	—	—	—	—
Montia sibirica	12	100	2	86	—	—	—	—	—	—
Prunella vulgaris	—	—	1	57	—	—	—	—	—	—
Agrostis tenuis	—	—	1	57	—	—	—	—	—	—
Hydrophyllum tenuipes	—	—	T	43	—	—	—	—	—	—
Asarum caudatum	—	—	1	57	1	77	—	—	1	36
Trillium ovatum	—	—	—	—	1	55	—	—	1	71
Viola sempervirens	—	—	—	—	1	50	—	—	2	92
Anemone deltoidea	—	—	—	—	1	50	—	—	1	85

TABLE 1. Cover and constancy for associes and associations on alluvial landforms. (Continued)

	Alnus rubra associes		*Abies grandis* associes		Tshe/Pomu-Oxor association		Psme/Coco/Pomu associes		Psme/Bene-Gash associes	
	cover* %	const %	cover* %	const %	cover* %	const %	cover* %	const %	cover* %	const %
Low Shrub Layer										
Berberis nervosa	—	—	—	—	8	95	3	80	22	100
Gaultheria shallon	—	—	—	—	1	33	1	30	18	100
Rosa gymnocarpa	—	—	—	—	—	—	1	60	1	85
Symphoricarpos mollis	1	80	1	71	—	—	18	100	2	65
Rubus ursinus	7	100	4	100	2	100	3	100	3	100
sub-total	8		5		11		26		46	
Herb Layer										
Elymus glaucus	1	100	—	—	—	—	—	—	—	—
Equisetum arvense	4	100	—	—	—	—	—	—	—	—
Heracleum lanatum	2	80	—	—	—	—	—	—	—	—
Collomia heterophylla	1	60	—	—	—	—	—	—	—	—
Urtica lyallii	1	40	—	—	—	—	—	—	—	—
Anemone lyallii	T	40	—	—	—	—	—	—	1	50
Stachys cooleyae	2	100	T	43	—	—	—	—	—	—
Carex bolanderii	T	40	1	71	—	—	—	—	—	—
Tolmiea menziesii	2	100	1	86	—	—	—	—	—	—
Petasites frigidus	7	100	1	86	—	—	—	—	—	—
Nemophila parviflora	6	100	1	57	—	—	—	—	—	—
Montia sibirica	12	100	2	86	—	—	—	—	—	—
Prunella vulgaris	—	—	1	57	—	—	—	—	—	—
Agrostis tenuis	—	—	1	57	—	—	—	—	—	—
Hydrophyllum tenuipes	—	—	T	43	—	—	—	—	—	—
Asarum caudatum	—	—	1	57	1	77	—	—	1	36
Trillium ovatum	—	—	—	—	1	55	—	—	1	71
Viola sempervirens	—	—	—	—	1	50	—	—	2	92
Anemone deltoidea	—	—	—	—	1	50	—	—	1	85

TABLE 1. Cover and constancy for associes and associations on alluvial landforms. (Continued)

	Alnus rubra associes		*Abies grandis* associes		Tshe/Pomu-Oxor association		Psme/Coco/Pomu associes		Psme/Bene-Gash associes	
	cover* %	const %	cover* %	const %	cover* %	const %	cover* %	const %	cover* %	const %
Herb Layer cont.										
Adiantum pedatum	—	—	—	—	1	39	—	—	—	—
Linnaea borealis	—	—	—	—	1	66	1	50	6	100
Coptis laciniata	—	—	—	—	—	—	1	50	—	—
Whipplea modesta	—	—	—	—	—	—	1	40	—	—
Polystichum lonchitis	—	—	—	—	—	—	T	40	—	—
Clintonia uniflora	—	—	—	—	—	—	—	—	2	65
Pyrola asarifolia	—	—	—	—	—	—	—	—	1	57
Listera caurina	—	—	—	—	—	—	—	—	1	57
Achlys triphylla	—	—	—	—	—	—	—	—	1	50
Chimaphila umbellata	—	—	—	—	—	—	—	—	1	43
Chimaphila menziesii	—	—	—	—	—	—	—	—	T	43
Pyrola picta	—	—	—	—	—	—	—	—	T	36
Tiarella unifoliata	T	40	1	57	1	83	—	—	—	—
Adenocaulon bicolor	1	60	—	—	1	61	6	100	T	36
Synthyris reniformis	1	60	—	—	—	—	3	80	1	50
Goodyera oblongifolia	—	—	—	—	—	—	1	80	1	92
Pteridium aquilinum	—	—	—	—	1	33	1	60	1	57
Osmorhiza chilensis	1	80	1	86	—	—	1	60	—	—
Stachys palustris	1	100	1	43	—	—	1	50	—	—
Thalictrum occidentale	1	60	1	57	—	—	2	80	—	—
Trientalis latifolia	T	40	1	57	—	—	1	80	2	100
Fragaria vesca	—	—	T	43	—	—	1	90	—	—
Bromus vulgaris	—	—	1	71	T	33	1	100	—	—
Smilacina stellata	—	—	1	43	1	39	3	90	1	71
Disporum hookeri	—	—	1	71	T	44	T	40	1	65
Oxalis oregana	6	100	32	100	26	95	10	90	—	—
Polystichum munitum	1	40	15	100	22	100	26	100	1	36
Circaea alpina	4	100	8	100	T	33	2	70	—	—

TABLE 1. Cover and constancy for associes and associations on alluvial landforms. (Continued)

	Alnus rubra associes		*Abies grandis* associes		Tshe/Pomu-Oxor association		Psme/Coco/Pomu associes		Psme/Bene-Gash associes	
	cover* %	const %	cover* %	const %	cover* %	const %	cover* %	const %	cover* %	const %
Herb Layer contd.										
Galium triflorum	6	100	3	100	2	100	3	100	1	65
Galium bifolium	1	100	1	100	1	89	1	100	T	43
Viola glabella	1	80	1	86	T	33	1	100	—	—
Vancouveria hexandra	T	40	1	57	7	89	6	100	1	71
sub-total	62		78		68		73		28	
Moss Layer										
Isothecium stoloniferum	—	—	—	—	1	38	—	—	1	36
Plagimnium insigne	—	—	8	100	5	71	2	70	—	—
Leucolepis menziesii	—	—	7	86	3	66	1	50	—	—
Rhytidiadelphus triquetrus	—	—	4	100	10	100	15	100	9	100
Eurhynchium oreganum	—	—	4	86	14	100	14	80	23	100
Dicranum fuscescens	—	—	4	71	1	38	1	80	T	36
Hylocomium splendens	—	—	1	57	8	77	7	80	7	92
Hypnum circinale	—	—	1	43	1	33	1	40	1	36
sub-total	00		26		43		41		41	
Total Cover	281		259		267		307		275	

*Covers of .5 percent or less are given a T. All other covers are rounded to nearest whole number.

vegetation groupings identified are referred to as "communities." This is a general term denoting relatively homogeneous and repetitious groupings of species. A community capable of reproducing itself is an "association." The collective area that supports, or is capable of supporting, a given association is a "habitat type." Portions of a habitat type may be temporarily occupied by one or more "associes," the seral communities which will develop into a particular association.

A soil profile was described for a pit near the center of each plot, and a sample was collected from each horizon. Soil samples were subjected to moist color determination, air-drying for 72 hours, dry color determination, and seiving to 2 mm. Volumes and weights of gravels and finer fractions were recorded. Subsamples of the soil material less than 2 mm were removed for textural analysis using the hydrometer method (Day, 1956). Ten-gram subsamples were used to determine pH.

Results and Discussion

We found eight plant communities on alluvial landforms. They included: two apparent topo-edaphic climaxes (associations), the *Tsuga heterophylla/Polystichum munitum-Oxalis oregana* (Tshe/Pomu-Oxor) association and the *Tsuga heterophylla/Berberis nervosa-Gaultheria shallon* (Tshe/Bene-Gash) association; two early seral associes which may develop into either association (the *Salix* associes and the *Alnus rubra* associes); one early seral associes of uncertain relationships (the *Populus trichocarpa* associes); two later seral associes leading to the Tshe/Pomu-Oxor association (the *Abies grandis* associes and the *Pseudotsuga menziesii/Corylus cornuta/Polystichum munitum* (Psme/Coco/Pomu)) associes; and one late seral associes leading to the Tshe/Bene-Gash association (the *Pseudotsuga menziesii/Berberis nervosa-Gaultheria shallon*, Psme/Bene-Gash, associes). The hypothetical successional relationship of the above communities is shown in Figure 2 and diagrammatically in Figure 3. Species composition of five communities is given in Table 1. The *Salix* and the *Populus trichocarpa* associes were sampled only by reconnaissance plots; their general characteristics are summarized in the text. Results from the computer ordinations based on herbs, herbs plus shrubs, shrubs plus trees, or trees alone showed no evidence counter to the arrangement of specific stands or species listed in the association-table clusters (Fig. 4).

Early Seral Communities

Three early seral communities (the *Salix, Alnus rubra,* and *Populus trichocarpa* associes) apparently have the capability to develop into either of the associations, although the seral relationship of the *Populus* community is not very clear.

The *Salix* associes is usually the first seral stage to occupy areas of recent alluvium. No analytic plots were placed within this associes because of its limited extent.

The *Salix* associes occurs on floodplains with large stones and cobbles, exposed and little sand or finer particles. This associes is not common within the study area at this time, probably because of recent moderation of stream flow by upstream reservoirs, and is short-lived where it does occur. Moisture is probably seldom limiting, as the water table is usually within the root zone of the common plants. High insolation is augmented by reflection from the river. Surface temperatures vary more than in other communities due to the lack of a well-developed tree canopy. During summer nights, dew and fog from the river probably help some species that occur here to recover from moisture stress.

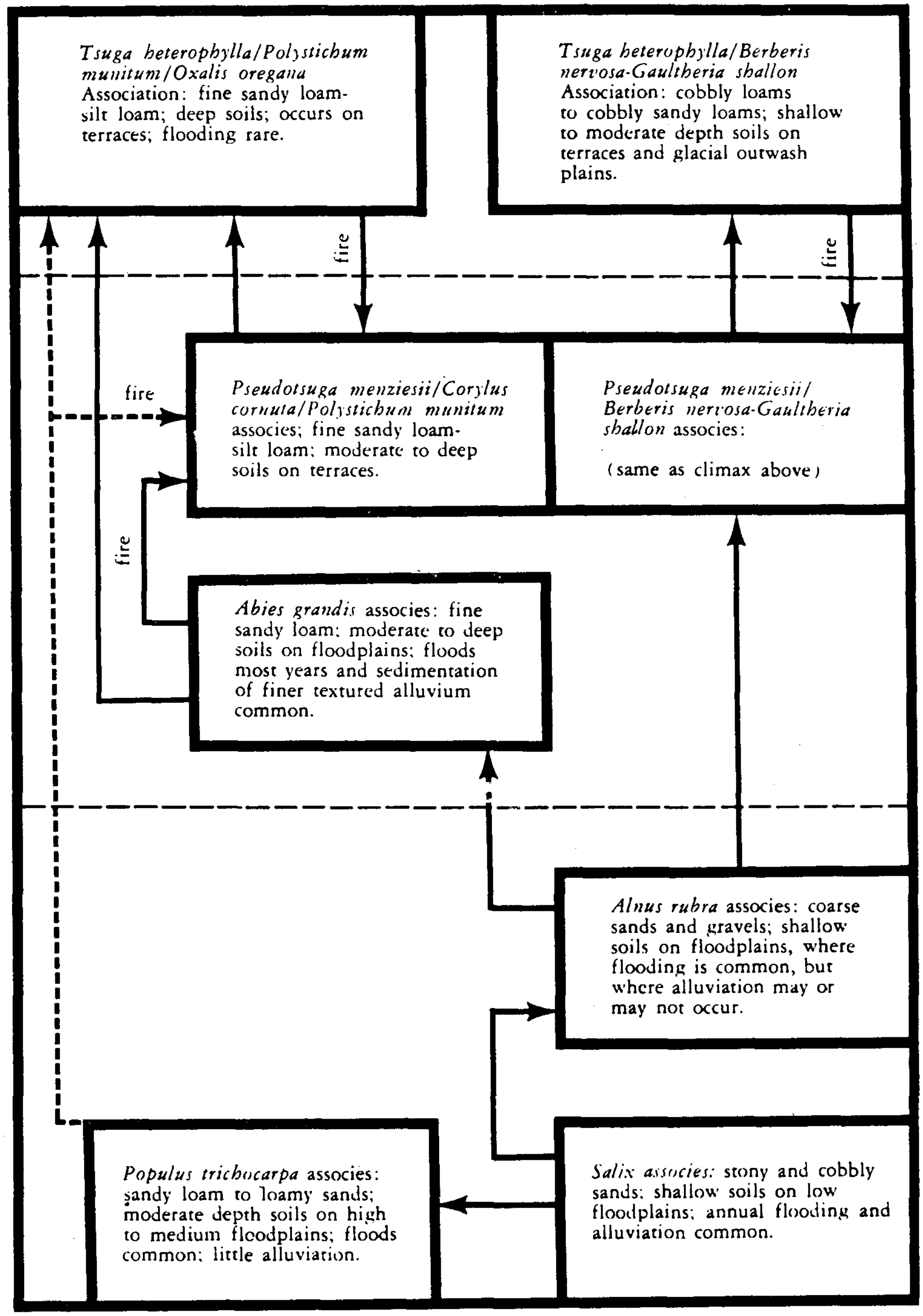

Figure 2. Hypothetical seral relationship of communities on alluvial landforms along the McKenzie River, Oregon.

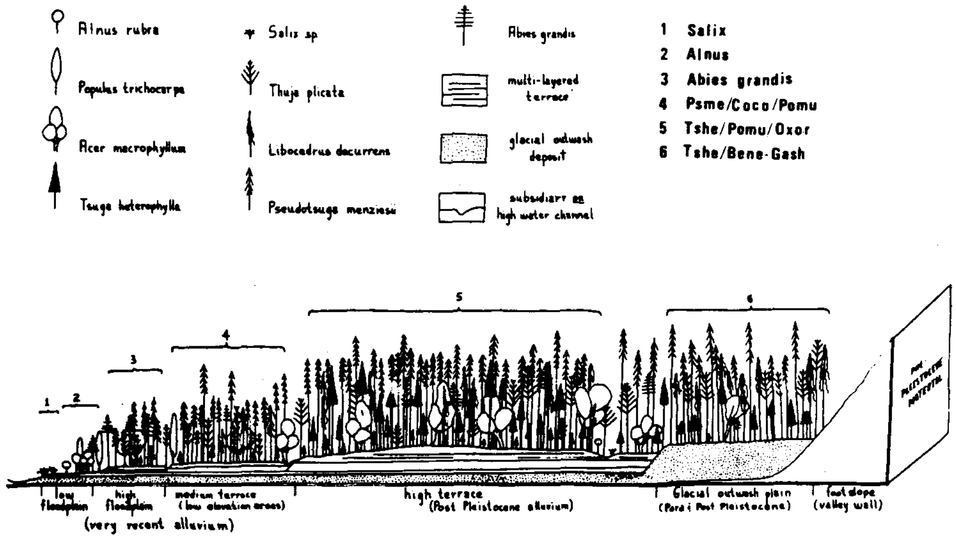

Figure 3. Diagramatic cross-section of forest communities of floodplains, terraces, and glacial-outwash plains on the McKenzie River, Oregon.

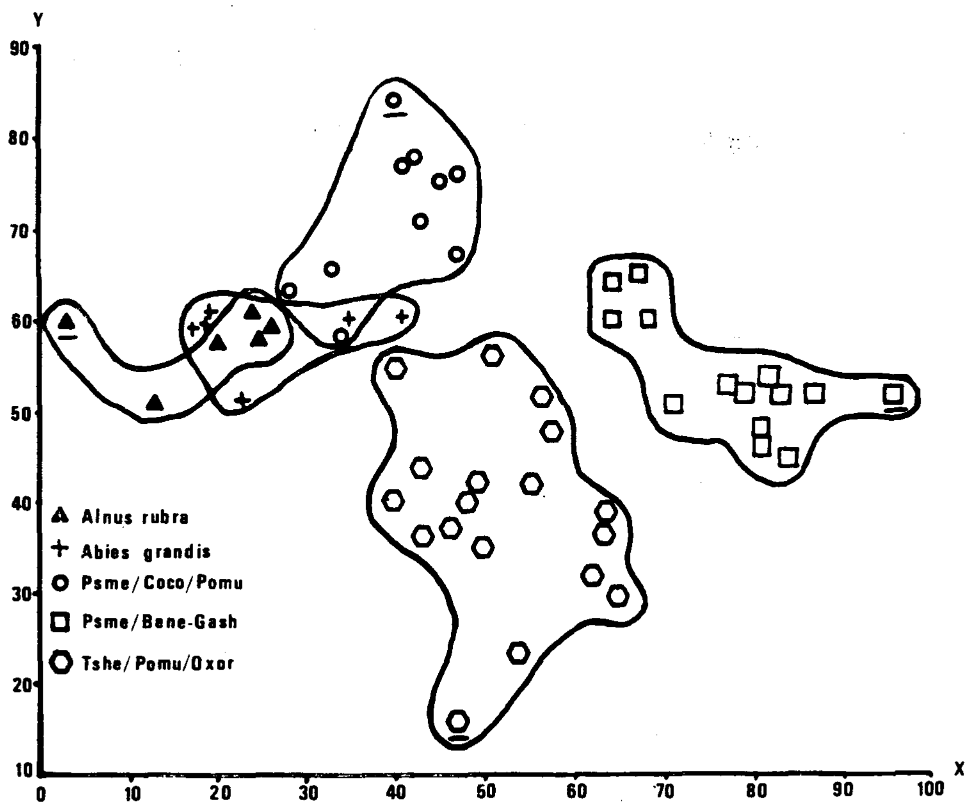

Figure 4. Similarity ordination of stands based on cover percentages of the 50 shrub and herb species with the most indicator significance and endstands (underscored) subjectively picked by investigator.

This associes includes the dominant *Salix* spp. and several herbaceous or shrub species dispersed widely between the stones and cobbles. These species include *Gilia capitata, Cytisus scoparius, Chrysanthemum leucanthemum, Anaphalis margaritacea, Cirsium vulgare, Hieraceum albiflorum, Epilobium paniculatum, E. augustifolium,* and *E. watsonii.*

The next steps in seral development of the vegetation result from further sedimentation during winter flooding. As the elevation of the terrace increases, the texture of the sediment generally becomes finer, although it varies considerably with the conditions during its deposition.

Establishment of *Alnus rubra* usually follows the deposition of 20-30 cm of coarse to fine gravelly sand over areas occupied by the *Salix* associes. The *Alnus rubra* associes may be immediately adjacent to the river but generally occurs in a narrow band separated from the river by the *Salix* associes. The *Alnus rubra* associes is more extensive and of longer duration than the *Salix* associes.

Alnus rubra is the dominant tree, though *Acer macrophyllum* germinates and survives in large numbers in this seral stage. *Acer macrophyllum* is found in canopy openings in older stands of this associes as well. Sediment from subsequent flooding and a concurrent increase in canopy density create conditions suitable for shrubs such as *Acer circinatum.* Open areas are occupied by *Corylus cornuta* and *Osmaronia cerasiformis. Ribes lobbii* is a common tall shrub that is found only within this associes. The only common elements of the low shrub layer are *Rubus ursinus* and *Symphoricarpos mollis.* The herb layer is diverse, with 44 species, but is dominated by *Montia sibirica, Nemophila parviflora, Petasites frigidus, Galium triflorum,* and *Oxalis oregana* (Table 1).

Total soil depth over stones and cobbles ranges from 20-60 cm. Additional vegetative development helps to stabilize the soils. This soil development is also augmented by organic matter from the plants. The sandy soils and a water table below the root zone of the herbs would be expected to cause severe moisture stress during the summer. However, wilting was only observed in larger openings during the hottest days. A generally dense tree-canopy (Table 1) and common fog and dew during summer months probably ameliorate the water-supply problem considerably. Drip from the plants may account for moist soil in the top 12 cm of profiles in shaded areas; soils of the same texture at 18-30 cm in the same profile were noticeably drier when sampled in mid-August.

Flooding in the *Alnus rubra* associes areas is an annual event. Since the establishment of reservoirs, flooding normally occurs in late winter or early spring while most species of trees on floodplains are dormant. Therefore, submersion of root systems may not be fatal. However, if deposition of sediments is extensive, seedlings as well as some larger trees may die because of oxygen deficits in buried root zones. Mechanical action by flood-carried debris may also cause injury, death, or removal of trees of any age. *Pseudotsuga menziesii* seedlings may die from flooding during any season (Brink, 1954). Minore (1968) reports death of young *Pseudotsuga menziesii* from effects of flooding. *Thuja plicata* has been observed to become very chlorotic but to survive floods during the growing season (Brink, 1954). Flooding accompanied by siltation kills all size classes of *P. menziesii* and *Abies grandis* growing with redwood on alluvial flats in northern California (Stone and Vasey, 1968).

Flooding is only one reason why conifers are not important in the tree layer of the *Alnus rubra* associes. Biotic interaction also seems to be a very important reason. The presence of the fast-growing *Alnus rubra* reduces the success of conifers during the first 20-25 years (Fowells, 1965). The acidity (pH 4.0 to 4.95) of surface soils in young stands of this associes may exclude some species from the area.

In most cases soils from young stands of the *A. rubra* associes have surface horizons that are as much as 75 percent gravels by weight. Ninety-four percent of the 2 mm fraction is sand. Gravels decrease while stones and cobbles increase with increasing depth in most profiles. Older stands occur on deeper soils having no particles greater than 2 mm diameter in the rooting zone. Surface soils, however, still contain 80-90 percent sand, 5-10 percent silt, and 2-5 percent clay.

In most areas the *A. rubra* associes is replaced within 30-50 years. If little elevation of the floodplain occurs by either sedimentation or down-cutting of the river, the *A. rubra* may be replaced by *Populus trichocarpa,* another fast growing species. Where additional sediments, usually of increasingly finer textures, are deposited, *Abies grandis* may replace *A. rubra* within 30-70 years. The rate of the replacement of *Alnus rubra* by *Abies grandis* varies and apparently depends on the rate of sediment accumulation. Thus, in some stands *Populus trichocarpa* may be important in depressions, with *Abies grandis* on higher ground.

Early seral stages of the two habitat types are quite similar. Differences are that the overlying, fine textured soils are less common, and that there are more coarse fragments in the soils of the Tshe/Bene-Gash habitat type. Also the development of the low shrub layer of the *A. rubra* associes is markedly different with *Berberis nervosa* and *Gaultheria shallon* appearing in the *A. rubra* associes of the Tshe/Bene-Gash habitat type, while very little of these two species is found in the *A. rubra* associes of the Tshe/Pomu-Oxor habitat type, on the finer-textured sediments.

The *Populus trichocarpa* associes occurs in the Blue River region of the study area (Fig. 1). It is a vegetation unit of uncertain seral status. As indicated in Figure 2, this associes does not clearly lead to either of the two associations hypothesized within the study area. It may represent a lower seral stage of an entirely different habitat type. Several reconnaissance plots serve as the basis for the description of this associes.

The *Populus trichocarpa* associes occurs where water tables remain close to the surface and where flooding is not normally accompanied by massive sedimentation such as that occurring between the *A. rubra* and *Abies grandis* associes. A natural levee usually occurs between the *Populus* stands and the river. Behind the levee there is a slight depression and then a gentle rise or level plain occupied by the *Populus trichocarpa* associes.

Progression from the river towards the *Populus* associes stands shows a *Salix* associes at streamside and an *A. rubra* associes occupying the levee. Then, there is usually a rapid transition to the *Populus trichocarpa* associes.

The overstory of this associes is dominated by large *Populus trichocarpa* over smaller *Acer macrophyllum, Pseudotsuga menziesii, Abies grandis, Libocedrus decurrens,* large *Taxus brevifolia,* and in some cases even a few *Tsuga heterophylla* and *Thuja plicata* seedlings or saplings. The tall shrub layer is poorly developed with a few *Acer circinatum* in the shaded areas and *Corylus cornuta* in the open areas, giving the associes a park-like appearance. The low shrub layer is even more sparse with only an occasional *Symphoricarpos mollis, Rosa gymnocarpa,* or *Rubus ursinus.*

The great diversity within both the tree layer and the herb layer of this associes indicates that it may be a part of the seral development of the Tshe/Pomu-Oxor association. The herb layer usually contains large amounts of many species that are otherwise common to one or more of the early seral stages discussed above, as well as to the *Abies grandis* associes which follows. However, only in this associes do all of these species develop so abundantly together. Dominants of the herb layer include *Polystichum munitum, Oxalis oregana, Petasites frigidus, Heracleum lanatum, Circaea alpina,* and *Montia sibirica.*

In older stands *Populus* is being replaced by *Libocedrus decurrens* and *Abies grandis.* In most stands a few small *Pseudotsuga menziesii* are filling the gaps vacated by fallen *Populus.* There is no evidence of past fires within the areas observed. The broken line in Figure 2 indicates the hypothetical relationship of the *Populus trichocarpa* associes as a possible early stage of the Tshe/Pomu-Oxor association that is dependent upon a decline in water table itself rather than on sedimentary increase in elevation above the flood level, as found in the *Abies grandis* associes discussed below.

Tsuga heterophylla/Polystichum munitum-Oxalis oregana Habitat Type

Late Seral Communities. The first associes that is exclusively a part of the Tshe/Pomu-Oxor habitat type is the *Abies grandis* associes. The *Abies grandis* associes has been sampled in the Delta and Blue Rivers regions (Fig. 1). It occurs in areas which were previously occupied by the *Alnus rubra* associes but which have been sufficiently elevated so that extensive flooding occurs only during [illegible] periods of high precipitation.

Many of the species in the *Alnus rubra* associes are also present in the *Abies grandis* associes. However, the relative importance of the species changes (Table 1). The overstory tree layer is dominated by *Abies grandis* between 50 and 100 years old. In very young stands young *Abies grandis* seedlings and saplings grow in dense clumps until a few more hardy individuals become dominant. *Pseudotsuga menziesii* and *Libocedrus decurrens* are both common in most stands, while *Thuja plicata* is present only as seedlings and saplings in some stands. *Populus trichocarpa* and *Fraxinus latifolia,* common in the *Alnus rubra* associes, are rarely found in the *Abies grandis* associes. *Acer macrophyllum* remains as a canopy-dominant carried over from the *Alnus rubra* associes, until it is overtopped by *Abies grandis.*

The tall shrub layer is dominated by *Acer circinatum* and *Corylus cornuta* and also includes saplings of *Tsuga heterophylla.* The low shrub layer is dominated by *Rubus ursinus* and patches of *Symphoricarpos mollis.* The herb layer is quite diverse, and is dominated by *Oxalis oregana* and *Polystichum munitum* (Table 1).

The most significant vegetative change from the *Alnus rubra* to the *Abies grandis* associes is in the moss layer. Whereas there are essentially no mosses in the *Alnus rubra* associes, in the *Abies grandis* associes there are seven species of mosses that are common to most stands (Table 1). Reductions in deciduous litterfall as well as reduction of the herbaceous and shrub cover, concurrent with the development of a dense tree-canopy, may allow the development of a moss layer.

The moisture-holding capacity of the soils in the *Abies grandis* associes is greater than the *Alnus rubra* associes, due to the finer sediments deposited on those high floodplains as well as to the normal processes of soil development.

Within the area studied, all stands of this associes are sheltered to the south by more mature forest but are often open to the north, toward the river. The floodplain associes and their substrate may be of recent origin. They are commonly still within meander or flood range, and most stands show little evidence of fire. Ages of the oldest trees sampled were less than 120 years.

Soils of this associes are typically 50-60 percent sand, 30-40 percent silt, and 5-10 percent clay within the rooting zone. These sandy loams usually overlie loamy sands, sands or gravels.

Pseudotsuga menziesii/Corylus cornuta/Polystichum munitum (Psme/Coco/Pomu) associes. This associes is restriced to the limits of relatively recent burns (100-200 years ago). Such stands are on medium to high terraces located at the Blue River and Delta regions (Fig. 1).

The tree-canopy of the Psme/Coco/Pomu associes is less dense than that of most associes, due primarily to the immaturity of the trees and the sparse development of the lower tree layers. This associes is dominated by even-aged *Pseudotsuga menziesii,* with an average cover of 57 percent. *Acer macrophyllum* is the second most important tree species. *Abies grandis* and *Libocedrus decurrens* are common in medium-size classes of most stands, and *Thuja plicata* is present in half of the sampled stands. However, *Abies grandis* and *Libocedrus decurrens* do not appear to reach the canopy in this associes. Both begin to degenerate at young ages, 65-75 years for *Abies grandis* and 45-65 years for *Libocedrus decurrens.*

The tall shrub layer is more dense than that in any other community studied: dominants include *Corylus cornuta* and *Acer circinatum* (Table 1). Where the canopy is open, *Corylus cornuta* replaces *Acer circinatum* as the dominant. This pattern is the reverse of that in areas where fire disturbance is not as recent and where the canopy is more dense. *Symphoricarpos mollis* dominates the low shrub layer. The herb layer of this associes, with 39 species, is dominated by *Polystichum munitum* with 26 percent cover. Average moss cover is 41 percent: the layer is dominated by *Rhytidiadelphus triquetrus* and *Eurhynchium oreganum.*

The Psme/Coco-Pomu associes occurs on soils about 1 m deep. They have well-drained, silt loam surface soils over coarse subsoils and may be either stone free or stony below 20 cm. The terrain is typically level. The only exception to this is where high water channels cross the terraces.

Mueller-Dombois (1965) concluded that dominant plants following clearcutting of *Pseudotsuga menziesii* and *Tsuga heterophylla* may be divided into three groups: 1) forest plants characteristic of the original vegetation; 2) semitolerant forest weeds present in the original vegetation but never as dominants; and 3) intolerant weeds rare in forest stands. These same classes can be applied to burned-over areas. The Psme/Coco/Pomu stands are old enough to no longer contain members of the class 3 above. However, species such as *Symphoricarpos mollis, Synthyris reniformis, Adenocaulon bicolor, Fragaria vesca,* and *Whipplea modesta* fit well in class 2, and they occur in unusually large amounts in this associes. Other common to abundant species, including *Polystichum munitum, Vancouveria hexandra,* and *Oxalis oregana* fit well in class 1. In many cases, species common to both climax and seral stages appear to be growing with less vigor in the seral stage. The *Polystichum munitum* growing in this associes was chlorotic and thin-leaved as compared to that growing in most stands within the Tshe/Pomu-Oxor association.

Soils of the Psme/Coco/Pomu associes contained 40-60 percent sand, 40-60 percent silt, and 5-10 percent clay within horizons of the rooting zone.

Within 150-200 years this associes takes on the appearance of the Tshe/Pomu-Oxor association. Tree-age data for the stands in this associes indicate a range of ages from 75-95 years to 165-200 years. All stands have occasional large *Pseudotsuga menziesii* stems over 350 years old, which have fire scars.

Tsuga heterophylla /Polystichum munitum-Oxalis oregana (Tshe/Pomu-Oxor) association. The Tshe/Pomu-Oxor association is the most extensive community in the study area. It was sampled in timber 200-500 years old, by 18 plots, located at Quartz Creek, Blue River, Delta, Horse Creek, and Boulder Creek (Fig. 1). There is evidence that most areas of this association have been through one or more cycles of secondary succession following fire.

The tree-canopy is dominated by *Pseudotsuga menziesii* in near-climax stands and by *Tsuga heterophylla* in the oldest stands. *Tsuga heterophylla* is a tolerant species and will replace itself. This condition combined with a multilayered tree-canopy results in tree coverage exceeding 100 percent. In near-climax stands *Pseudotsuga menziesii* almost forms a closed canopy; in the oldest stands death of *Pseudotsuga* has created gaps that are only partially filled by *Tsuga heterophylla. Abies grandis* occurs in over 50 percent of the stands, but only occasionally does it become part of the upper canopy.

The tree layer varies apparently in response to moisture and topographic factors. In mesic areas *Thuja plicata* is an understory dominant prior to *Tsuga heterophylla.* This may be because of the greater tolerance of *Thuja plicata* for an open canopy (Krajina, 1965). *Thuja plicata* in western Montana is a strong competitor in open areas of early seral stands, but it is dominated by *Tsuga heterophylla* in later seral stages (Habeck, 1968).

On wetter sites, *Thuja plicata* is codominant in the tree canopy. Fine-textured soils at Horse Creek and Quartz Creek show evidence of poor internal drainage when compared to those of other stands in this association. The five stands at Horse Creek and Quartz Creek have 18 percent cover for *Tsuga heterophylla* and 42 percent for *Thuja plicata,* whereas stands outside of the above two locations average 74 percent cover for *Tsuga heterophylla* and 10 percent for *Thuja plicata.* These facts agree with Habeck's (1968) findings, that where both *Tsuga heterophylla* and *Thuja plicata* occur, *Thuja* dominates more hygric areas and *Tsuga* dominates the better-drained areas.

Both shrub layers of the Tshe/Pomu-Oxor association are sparse (Table 1). Tall shrubs are dominated by *Acer circinatum,* occurring in all stands and averaging 11 percent cover. Major shrub species are *Berberis nervosa* and *Rubus ursinus.* The herb layer consists of 47 species, dominated by *Polystichum munitum* and *Oxalis oregana* with 22 percent and 26 percent cover respectively. *Vancouveria hexandra* is the only herb of importance from the standpoint of cover (Table 1). The moss layer is well-developed; the layer is dominated by *Rhytidiadelphus triquetrus* and *Eurhynchium oreganum.*

The Tshe/Pomu-Oxor association occurs on terraces with deep, well-drained to moderately well-drained surface soils overlying coarser subsoils. Most profiles are stone free. The terrain is commonly hummocky, especially in the oldest stands where windthrow and dead-tree fall, with resultant pits and root balls, are common. The stands are usually not flooded, even in years of high stream-flow.

After about 450-550 years a transition begins as the old *Pseudotsuga menziesii* dies. This process may be accelerated by the relative instability of some alluvial substrates. As the trees fall out of the canopy, *Tsuga heterophylla,* suppressed beneath them for 200 years or more, becomes more vigorous and fills the canopy gaps.

The texture of the root-zone soils of this association is variable. It ranges from 14.7-33 percent sand, 45-68 percent silt, and 16-22 percent clay at Horse Creek; 38-46 percent sand, 42-38 percent silt, and 14-18 percent clay at Quartz Creek; to 52-93 percent sand, 3-43 percent silt, and 2-4 percent clay at some of the more xeric Delta region stands.

Tsuga heterophylla/Berberis nervosa-Gaultheria shallon (Tshe/Bene-Gash) Habitat Type

Late Seral Communities. The Tshe/Bene-Gash habitat type is less common than the Tshe/Pomu-Oxor habitat type and occurs on coarser, shallower soils. The successional sequence leading to the Tshe/Bene-Gash association is represented primarily in the study area by late seral examples. Early seral stages are not extensive at higher elevations, probably because less river disturbance occurs there than at lower elevations. Stands sampled begin with the Psme/Bene-Gash associes, assumed to follow (probably after burning) the *Alnus rubra* associes. This latter associes occurs on shallower soils that receive little sedimentation but that may be elevated above normal flood level by other means prior to massive alluviation such as that occurring within the Tshe/Pomu-Oxor habitat type.

Pseudotsuga menziesii/Berberis nervosa-Gaultheria shallon (Psme/Bene-Gash) associes. The Psme/Bene-Gash associes occurs on terraces and glacial outwash plains at Boulder Creek, Scott Creek, Paradise C. G., and the Blue River regions of the study area (Fig 1).

The tree canopy is dominated by *Pseudotsuga menziesii.* In most stands *Thuja plicata* is more important than *Tsuga heterophylla* in the understory. *Libocedrus decurrens* is also found in the larger size classes of most stands. *Acer macrophyllum* and *Abies grandis* also occupy the extremes of the moisture gradient, although the growth rates of the trees at either end of the gradient vary markedly.

The shrub layer is dominated by *Acer circinatum, Berberis nervosa,* and *Gaultheria shallon* (Table 1). The fairly open nature of the tree canopy and the coarse-textured soils allow the development of more light-tolerant, schlerophyllous shrubs rather than the delicate herbs common in shady, moist habitats. Coarse-textured soils within this associes often support patches of *Symphoricarpos mollis.* The patchiness of the shrub layer apparently results from patterns of interception of precipitation, soil texture, and shading.

The herb layer is perhaps the most distinctive stratum. Ten of its 42 species were found only in this associes. Many of these species are more common to the uplands flanking the study area. *Linnaea borealis* is the most abundant herb, occurring in all stands, but with an average cover of only 6 percent. The moss layer is well-developed, especially in some older stands. *Eurhynchium oreganum* is the dominant species of the moss layer while *Hylocomium splendens* and *Rhytidiadelphus triquetrus* are important locally.

Soils here are generally shallow with many stones and cobbles. The associes also occurs on glacial-outwash plains typified by shallow, stony or cobbly loams, or cobbly, sandy loams. Texture of the fine fraction is similar to that of soils within the Tshe/Pomu-Oxor association, but the amount of coarse fragments is much higher. This results in a lower soil moisture-holding capacity within the total profile, which may be important in determining species composition. Textural analysis of the soils of the rooting zone showed them to contain 40-80 percent sand, 9-48 percent silt, and 2-12 percent clay.

The Tshe/Bene-Gash association will follow this associes at an age of about 450-500 years. Most Psme/Bene-Gash stands studied have undergone secondary succession after fire at least once. The development of climax stands in this drier habitat type is probably much less likely than in the Tshe/Pomu-Oxor habitat type.

Tsuga heterophylla/Berberis nervosa-Gaultheria shallon (Tshe/Bene-Gash) association. This association was only sampled by one plot, which has been included with the Psme/Bene-Gash associes in Table 1 and in the above discussion. The Tshe/Bene-Gash association develops as the Psme/Bene-Gash associes becomes more mesic with maturity and thus supports more *Tsuga heterophylla* in reproductive size classes.

The tree layer differs from that of the Psme/Bene-Gash associes in that *Tsuga heterophylla* dominates rather than *Pseudotsuga menziesii.* The shrub layers are both noticeably less dense, while herbaceous cover increases during transition into the Tshe/Bene-Gash association. In areas of rocky, shallow soils the ground may be devoid of vascular plants and may support a dense mat of bryophytes. The moss layer is well-developed in most areas and covers nearly 100 percent of the shallow stony areas occurring in either the Psme/Bene-Gash or the Tshe/Bene-Gash stages of this habitat type.

Regional Vegetation

Alluvial landforms support vegetation different from that of adjacent uplands. The Tshe/Pomu-Oxor association of alluvial landforms is analogous to the Tshe/Pomu-Oxor community of the H. J. Andrews Experimental Forest (Dyrness, Franklin, and Moir, 1974). The tree layers of the two associations differ in that *Acer macrophyllum* and *Tsuga heterophylla* are more abundant in the alluvial areas. There is more *Corylus cornuta* and *Cornus nuttallii* in the tall shrub layer of the alluvial association. The low shrub layers of the two associations differ in that *Berberis nervosa* and *Gaultheria shallon* are both more common in the upland association than on the alluvial landforms. There is very little difference between the herb layers and the moss layers of the two associations.

The Psme/Bene-Gash association of alluvial landforms, although not really similar to any community described for the H. J. Andrews Experimental Forest, most closely resembles the Psme-Tshe/Corylus community of Dyrness, Franklin, and Moir (1947). Their *Corylus* community occurs on steep slopes and includes *Pinus lambertiana* in addition to the tree species also common to the alluvial association. The shrub layers of the two communities are similar in total cover, but *Gaultheria shallon,* which is dominant in the upland community, is joined in dominance by *Berberis nervosa* on the alluvial landforms. The herb layers and moss layers on alluvial landforms (Psme/Bene-Gash associes) contain species that reflect a slightly more mesic habitat than those common to the upland *Corylus* community.

Areas similar to the *Salix, Alnus rubra, Abies grandis,* Psme/Coco-Pomu and Psme/Bene-Gash associes and the Tshe/Pomu-Oxor associations have also been observed along the South Santiam River, at Blue River, and at Lookout Creek (within the H. J. Andrews Experimental Forest). Reconnaissance plots in these areas reveal stands very similar to the associes and associations described above.

Soil Stoniness and pH

In addition to studying the results of textural analysis of the 2-mm soil fraction from each of the vegetation units above, we also studied gravels, cobbles and stones occurring within rooting zones.

Whereas some gravels were common in most pedons, stones and cobbles were present only in two stands of the Tshe/Pomu-Oxor habitat type. In contrast, stands of the Tshe/Bene-Gash habitat type contained 5-25 percent gravel, 3-20 percent cobbles, and 1-35 percent stones in all horizons of the rooting zone. Moisture availability in soils of the same textural type (within the 2-mm, seived fraction only) varied greatly depending on the coarse fragment content of the pedon.

Soil reaction of surface soils within different vegetation units is given in Table 2. The only noticeable difference occurs between the young *Alnus rubra* associes stands and any of the later successional stages. High acidity is common to the younger *Alnus rubra* stands but is apparently ameliorated in older stands. No significant differences were found between other successional stages.

Plant Moisture Stress

Excluding the few *Abies grandis* saplings that were sampled, pressure-chamber measurements of plant moisture stress were made on 72 saplings of *Tsuga heterophylla* (Table 3). There are differences of up to 2-4 bars among trees within the same stand or among different stands within the same habitat type. However, moisture stress of saplings growing within the two topo-edaphic climaxes is significantly different and this fact further emphasizes the difference in moisture availability to plants growing on the two very different substrate types. Moisture stress was measured late in August at a time when maximum values were anticipated by investigators.

TABLE 2. Average pH values of surface horizons of alluvial landforms occurring in the McKenzie River Valley.

	Vegetation Units					
	A. rubra associes		*A. grandis* associes	Psme/Coco/ Pomu associes	Tshe/Pomu Oxor association	Psme/Bene-Gash associes
	young	old				
average pH range	4.0-4.9	5.6-5.8	5.5-6.0	5.3-6.2	5.3-6.4	5.0-6.1

TABLE 3. Predawn plant moisture stress of *Tsuga heterophylla* saplings growing in different vegetation units occupying alluvial landforms of the McKenzie River Delta. Data were collected in mid-August 1972.

Hatitat Type	Tshe/Bene-Gash Habitat Type			Tshe/Pomu-Oxor Habitat Type		
Community	Psme/Bene-Gash Associes		Tshe/Bene-Gash Association	Tshe/Pomu-Oxor Association		Psme/Coco/Pomu Associes
Plot Location	Boulder Creek	Scott Creek	Paradise Camp Ground	Horse Creek	Delta	Delta
# trees	12	10	16	16	8	10
average stress (bars)*	24.8	22.9	22.5	7.4	7.8	11.9

*One bar = 14.5 psi pressure.

Conclusions

The major factors responsible for distribution of plants and vegetation units on floodplains, terraces, and glacial-outwash plains along the McKenzie River appear to be edaphic. A major effect is apparently that of moisture availability to plants. In the early stages of succession, the plant communities change as finer-textured sediments are deposited by successive flooding. Finer soil-texture and increased depth to water table are highly correlated with plant-community distribution within the study area. After floodplains are elevated beyond normal flood level, communities develop towards climax, unless they are interrupted by severe flooding or by fire.

Most stands of both habitat types included in this study have been burned at least once in the past. In addition to vegetation responses to the edaphic factors, stand composition appears to be regulated in some cases by effects of elevation, increased insolation close to the river, and proximity to upland plant-communities. However, the amount and texture of sediment deposited during flooding of early associes seems to play the dominant role in determining which habitat type, Tshe/Bene-Gash or Tshe/Pomu-Oxor, will ultimately develop in any given area.

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