Material on Squamish R. floodplain.

ECOLOGY OF WESTERN NORTH AMERICA

EDITED BY

V. J. KRAJINA

VOL. 1.

DEPARTMENT OF BOTANY

UNIVERSITY of BRITISH COLUMBIA

VANCOUVER, B.C., CANADA FEBRUARY 27, 1965

THE COASTAL WESTERN HEMLOCK ZONE ON THE SOUTH-WESTERN BRITISH COLUMBIA MAINLAND

Vegetation - Environmental Patterns and Ecosystem Classification

L a s z l o O r l o c i

NATO Fellow, University College of North Wales,
Bangor, United Kingdom

The Climax Area Pattern

Since the time that Whitford and Craig (1918) described some forest zones ("climatic forest types") from British Columbia, several zonal classifications were proposed, utilizing mainly climatic and vegetational criteria (Table I).

TABLE I. Zonal Classifications with Reference to the South Western British Columbia Mainland

<table>
<tr><th>Whitford and Craig 1918 (Climatic types)</th><th>Halliday 1937 (Sections)</th><th>Rowe 1959 (Sections)</th><th>Krajina 1959, 1964 (Biogeoclimatic units)</th></tr>
<tr><td rowspan="2">Douglas-fir - - Red cedar</td><td>Madrona - Oak transition (C. 1)</td><td>Straits of Georgia (C. 1)</td><td>Coastal Douglas-fir Zone, Garry Oak (Dry) Subzone</td></tr>
<tr><td rowspan="4">Southern Coast (C. 2)</td><td rowspan="3">South Pacific Coast (C. 2)</td><td>Coastal Douglas-fir Zone, Wet Subzone</td></tr>
<tr><td>Red cedar - - Hemlock</td><td>Coastal Western Hemlock Zone, Dry Subzone</td></tr>
<tr><td>Hemlock - - Balsam</td><td>Coastal Western Hemlock Zone, Wet Subzone</td></tr>
<tr><td>The subalpine part of the "subalpine and muskeg type"</td><td>Coastal subalpine</td><td>Mountain Hemlock Zone</td></tr>
<tr><td>Hemlock - Sitka spruce</td><td>Part of the southern and central Coast (C. 1, C. 2) and northern Coast (C. 4)</td><td>Part of the northern Pacific Coast (C. 3), and Queen Charlotte (C. 4)</td><td>Coastal Western Hemlock Zone, Sitka Spruce Subzone (edaphic - ocean spray)</td></tr>
</table>

The zonal classification concept has been broadened and deepened recently in the work of Krajina (1959, 1964) and his students to include climate, soils, and vegetation as the three major criteria for the recognition of biogeoclimatic regions, zones, and subzones.

The Coastal Western Hemlock Zone belongs to a perhumid mesothermal climate (Köppen Cfb) in which the zonal (or mesic) soils are strongly podzolized and western hemlock (Tsuga heterophylla) is the climatic climax tree species.

Two subzones are separated from within the Coastal Western Hemlock Zone: one dry and one wet. These subzones are distinct climax areas and constitute successive segments along a regional climatic gradient, separated on the basis of the climatic climax vegetation and zonal soils. Each subzone is characterized by specific trends of vegetational and soil development which converge to a hypothetical climatic climax (mesic) ecosystem.

Mesic soils are strongly podzolized in the Dry Subzone, characterized by a climatic climax Tsuga heterophylla - Plagiothecium undulatum association.[1] Mesic soils of the Wet Subzone are not only strongly podzolized but also moderately gleyed. In this wettest belt of the region (Table II) the climatic climax community is the Tsuga heterophylla - Abies amabilis - Vaccinium alaskaense - Plagiothecium undulatum association.

TABLE II. Altitudinal Occurrence of Maximum Precipitation at Different Observation Period

Observation period	Long-term averages	1961#	January 1961	July 1961	October 1961
Altitude at which maximum precipitation occurred	2060 ft.	2660 ft.	2390 ft.	4830 ft.	2450 ft.

A random year of the last decade. (After Orloci 1964)

The ecotone of the Dry and Wet Subzones occurs between the 100 and 110 in. isohyets, corresponding approximately to 1200 ft. to 1300 ft. elevations. The division between the Wet Subzone and the Mountain Hemlock Zone lies at a critical altitude (between approximately 3000 ft. and 3200 ft. on slopes, and slightly lower in the valleys). Above these elevations, snow accumulation is considerable during the winter months, but below them snow duration becomes insignificant (vide Peterson 1964, Brooke 1964). A total annual precipitation of 60-70 inches appears to be the critical amount separating the Coastal Douglas-fir Zone from the Coastal Western Hemlock Zone. The differentiating characteristics of the subzones of the Coastal Western Hemlock Zone are shown in Table III.

TABLE III. Differentiating Characteristics of the Climax Areas within the Coastal Western Hemlock Zone and the Adjacent Zones on the Southwestern British Columbia Mainland

Climax area	Climatic type	Mean annual temperature (°F)	Annual total precipitation (in.)	Annual total snowfall (in.)	Altitude (ft.)	Zonal soil-forming processes	Climatic climax (mesic) association
Coastal Douglas-fir Zone	Humid (summer dry) mesothermal	over 48	below 65	below 30	0-500	Weak podzolization, very weak laterization, moderate melanization	Pseudotsuga menziesii - Gaultheria shallon - Eurhynchium oreganum
Dry Subzone of the Coastal Western Hemlock Zone	Perhumid mesothermal	46-48	65-110	30-80	0-1200	Strong podzolization	Tsuga heterophylla - Plagiothecium undulatum
Wet Subzone of the Coastal Western Hemlock Zone	Perhumid mesothermal	43-46	over 110	80-200	600-3000	Strong podzolization, moderate gleyzation	Tsuga heterophylla - Abies amabilis - Vaccinium alaskaense - Plagiothecium undulatum
Lower Subzone of the Mountain Hemlock Zone	Perhumid (snowy) microthermal	below 43	over 75	over 200	over 3000	Strong podzolization, strong gleyzation	Tsuga mertensiana - Abies amabilis - Vaccinium alaskaense - Rhytidiopsis robusta

[1] Association is used in the sense of an abstract vegetation type.

TABLE IV. Ecosystem Types of the Rock Outcrop Land Type, Dry Subzone

Associations	Rhacomitrietum canescentis (Rh)	Cladonieto - Polytrichetum (Cl)	Danthonietum spicatae (Da)
Land form	Knoll	Table	Crevice
Relief shape	Convex	Convex	Concave
Slope gradient°	27 (10-40) 9*	16 (10-30) 8*	9 (3-21) 4*
Altitude ft.	620 (250-1000) 9*	610 (250-1000) 8*	740 (250-1200) 4*
Hygrotope	Very dry	Very dry	Very dry
Permeable mineral soil depth (cm.)	1.4 (0.5-3.0) 9*	2.8 (0-5.0) 8*	23.0 (13-33) 4*
pH L-F	4.7 (4.3-5.1) 3*	4.4 (4.3-4.5) 2*	4.5(4.1-4.7) 3*
A	4.4 (4.0-5.0) 3*	4.8 (4.7-4.9) 2*	4.5(4.1-4.6) 3*
B			4.8(4.2-5.5) 3*
C			
Humus form	Raw humus	Raw humus	Duff mull
Characteristic combination of species	Rhacomitrium canescens	Cladonia pacifica Polytrichum piliferum Polytrichum juniperinum Cladonia rangiferina Rhacomitrium canescens Dicranum scoparium Cladonia gracilis	Danthonia spicata Polytrichum piliferum Polytrichum juniperinum Rhacomitrium canescens Cladonia pacifica Cladonia rangiferina Cladonia gracilis

	Polytrichetum communis (Pc)	Gaultherietum shallonis (Ga)	Cladonieto - Pseudotsugetum (LG)
Land form	Crevice	Complex	Upper-slope
Relief shape	Concave	Convex	Convex
Slope gradient°	7 (5-10) 3*	10 (5-21) 8*	25 (8-40) 5*
Altitude ft.	730 (600-1000) 3*	690 (500-1000) 8*	990 (540-1400) 5*
Hygrotope	wet	Dry to moist	Dry
Permeable mineral soil depth (cm.)	21 (7-35) 3*	16 (6-30) 8*	9 (3-13) 5*
pH L-F	4.4	4.7 (4.4-4.9) 5*	3.8 (3.7-4.0) 5*
A	5.0	4.4 (4.1-4.9) 5*	3.6 (3.6-3.7) 3*
B	5.4	5.2 (4.3-5.9) 5*	3.6 (3.6-3.7) 3*
C			
Humus form	Duff mull	Raw humus	Raw humus
Site index[1] Douglas-fir			69 (60-78) 5*
w. hemlock			66 (64-67) 5*
w. redcedar			56 (54-69) 5*
Characteristic combination of species	Polytrichum commune	Gaultheria shallon Danthonia spicata Polytrichum commune Pleurozium schreberi Rhacomitrium canescens Hylocomium splendens Eurhynchium oreganum Cladonia pacifica Cladonia rangiferina Polytrichum piliferum Polytrichum juniperinum	Pseudotsuga menziesii Gaultheria shallon Eurhynchium oreganum Hylocomium splendens Cladonia pacifica Cladonia rangiferina Rhacomitrium canescens Polytrichum piliferum Pleurozium schreberi

* The number of measurements.

1) Site index in ft. per 100 years in all tables.

The climax area pattern fluctuates as a consequence of regional climatic changes. Hansen (1947) has described two major changes in the climate which occurred in the region since the last glaciation. A warm climate prevailed 8000 to 4000 years ago in which the Coastal Douglas-fir Zone reached its maximum distribution. A return to a cool climate resulted in the migration of the Coastal Western Hemlock Zone and the Mountain Hemlock Zone to their present geographic positions.

Ecosystem Classification

It seemed appropriate to separate land types from within each subzone on the basis of the origin and general type of the parent materials as the second step in stratification. These land types are natural units and they constitute qualitatively and quantitatively distinct segments of the vegetation and ecotopes.

Ecosystem types[2] of the Rock Outcrop Land Type, Dry Subzone

The rock outcrop land type includes localities which lack continuous soil cover, and in which the ground surface is a complex of peaks, knolls, and crevices. The patterns of these different habitat types closely coincide with the different plant associations. The peaks are characterized by a loosely integrated association of the crustose and foliose lichens. The knolls and the side slopes of the peaks are colonized by a bryophytic association in which Rhacomitrium canescens dominates. The community of fruticose lichens and some bryophytes is transitional between the Rhacomitrium canescens and the Gaultheria shallon associations. The dry crevices are indicated by Danthonia spicata, lichens, and bryophytes. Wet crevices, on the other hand, are marked by Polytrichum commune.

The Gaultheria shallon association is specific to a thick raw humus on lithic soils along the forest edge. The side slopes and depressions where soil development is the most advanced are occupied by a lithosolic forest. This is the only forest association in the Coastal Western Hemlock Zone in which Douglas-fir (Pseudotsuga menziesii) can be self-perpetuating without fire or logging. The ecosystem types of the rock outcrop land type are described in Table IV.

Ecosystem types of the Glacial Drift Land Type

The glacial drift land type includes all localities of glacial deposits except those of the swampy habitats. Glacial deposits originated on the southwestern British Columbia mainland during the Seymour, Semiamu, Vashon, and Capilano glaciations (Armstrong 1956, 1957). The Seymour sediments are more than 30,000 years old. The Capilano sediments are approximately 11,000 years old.

Two major environmental gradients were identified through ordination techniques within the glacial drift land type as the underlying causes of variations in the floristic structure among individual ecosystems: a soil-moisture gradient, and a local climatic gradient.

Three distinct associations occur along the soil-moisture gradient of the Dry Subzone: Gaultheria of xeric habitats, Plagiothecium of mesic habitats, and Polystichum of hygric habitats. The occurrence or absence of Mahonia nervosa signifies the warm or cool exposures respectively within the Gaultheria and the Plagiothecium associations. Utilizing the occurrence or absence of Mahonia nervosa, the Gaultheria and the Plagiothecium associations are segmented into the Gaultheria-Mahonia, orthic Gaultheria, Plagiothecium - Mahonia, and the orthic Plagiothecium ecosystem types. The orthic and Mahonia variations constitute successive segments along a local climatic gradient from cool to warm aspects. The Polystichum association is divided among two ecosystem types: the orthic Polystichum, possessing melanized soils, and many nitrophilous species and the degraded Polystichum of well podzolized soils, characterized by raw humus inhabiting plants. A brief description of these ecosystem types is given in Table V.

The xeric, mesic, and hygric segments of the soil moisture gradient within the Wet Subzone are characterized respectively by the Vaccinium - Gaultheria, the Vaccinium - Plagiothecium, and the Blechnum associations. The Vaccinium - Gaultheria association consists of two distinct ecosystem types: the orthic Vaccinium - Gaultheria of shallow glacial tills, and the lithosolic Vaccinium - Gaultheria of lithic (AeC) soils (Lesko 1961). The Vaccinium - Plagiothecium consists of an orthic and a hygric segment. The latter is transitional between the mesic and wet habitats. The influence of a local climatic gradient is apparent within the Blechnum association. The orthic Blechnum ecosystem type is characteristic for low elevations in the Wet Subzone. The Blechnum - Streptopus ecosystem type, on the other hand, occurs at the higher elevations in the Wet Subzone and also in the Mountain Hemlock Zone (Peterson 1964). The ecosystem types of the Wet Subzone are described in Table VI.

---

[2] Ecosystem type includes a multitude of individual ecosystems among which variations in floristic structure are independent of the environmental variations.

TABLE V. Ecosystem Types of the Glacial Drift Land Type, Dry Subzone

Associations		Gaultherieto - Pseudotsugetum		Tsugetum heterophyllae	
Ecosystem type		Orthic Gaultheria (OG)	Gaultheria-Mahonia (G-M)	Orthic Plagiothecium (OPl)	Plagiothecium-Mahonia (Pl-M)
Land form		Upper-slope	Upper-slope	Middle-slope	Middle-slope
Relief shape		Convex to straight	Convex to straight	Straight (to convex)	Straight *
Slope gradient°		12 (3-25) 8*	31 (18-40) 5*	6 (1-17) 14*	18 (1-31) 4
Altitude ft.		1030 (750-1640) 8*	750 (450-900) 5*	780 (200-1050) 14*	540 (360-880) 4*
Hygrotope		Moderately dry (to mesic)	Moderately dry (to mesic)	Mesic (to mod. dry or moist)	Mesic (to moderately dry)
Stoniness (%)		40 (25-60) 4*	60 (40-80) 2*	31 (1-60) 7*	2
Permeable mineral soil depth (cm.)		62 (40-85) 4*	98+	71+	125+
Endo-humus depth (cm.)	A_h	Nil	Nil	Nil	Nil
Eluviated horizon depth (cm.)	A_e	8 (3-18) 4*	7 (5-8) 2*	5 (1-13) 7*	5
pH	L-F	4.0 (3.4-4.5) 4*	4.3	4.1 (3.4-4.5) 5*	4.0
	A	4.0 (3.7-4.3) 4*	4.4	4.2 (3.8-4.7) 5*	4.1
	B	5.2 (5.0-5.5) 4*	5.7	5.4 (5.3-5.6) 5*	5.5
	C	5.6 (5.5-5.7) 4*	?	5.7	5.5
Humus form		Raw humus	Raw humus	Raw humus	Raw humus
Site index	Douglas-fir	109 (96-127) 8*	93 (78-109) 5*	142 (114-157) 14*	138 (117-155) 4*
	western hemlock	102 (90-126) 8*	86 (73-91) 5*	121 (83-143) 14*	109 (99-122) 4*
	western redcedar	84 (76-107) 8*	73 (70-78) 5*	88 (70-132) 14*	84 (76-91) 4*
Characteristic combination of species		Tsuga heterophylla Pseudotsuga menziesii Gaultheria shallon Eurhynchium oreganum Hylocomium splendens Plagiothecium undulatum	Tsuga heterophylla Pseudotsuga menziesii Gaultheria shallon Mahonia nervosa Eurhynchium oreganum Hylocomium splendens Plagiothecium undulatum	Tsuga heterophylla Pseudotsuga menziesii Plagiothecium undulatum Rhytidiadelphus loreus Hylocomium splendens Eurhynchium oreganum	Tsuga heterophylla Pseudotsuga menziesii Mahonia nervosa Plagiothecium undulatum Hylocomium splendens Eurhynchium oreganum

* The number of measurements.

TABLE V. (continued)

Associations	Tsugetum heterophyllae	Polysticheto - Thujetum plicatae	
Ecosystem type	Eurhynchium-Mahonia (E-M)	Orthic Polystichum (OPo)	Degraded Polystichum (DPo)
Land form	Middle-slope	Lower-slope	Lower-slope
Relief shape	Straight	Concave	Concave
Slope gradient°	22 (2-33) 4*	18 (6-35) 12*	16 (3-40) 15*
Altitude ft.	820 (450-950) 4*	860 (430-1200) 12*	840 (460-1740) 15*
Hygrotope	Mesic (to moist)	Moist (to wet)	Moist (to wet)
Stoniness (%)	45 (40-50) 2*	31 (5-50) 10*	37 (0-75) 10*
Permeable mineral soil depth (cm.)	45+	60+	60+
Endo-humus depth (cm.) Ah	Nil	9 (3-15) 10*	Nil
Eluviated horizon depth (cm.) Ae	8 (0-15) 2*	Nil	3 (0-15) 10*
pH L-F	4.0 2*	4.3 (3.7-5.5) 9*	4.3 (3.4-5.7) 7*
A	4.0 2*	4.4 (3.7-5.2) 9*	4.2 (3.5-5.0) 7*
B	5.3 (5.0-5.6) 2*	5.2 (4.7-5.6) 9*	5.3 (5.1-5.5) 7*
C	?	5.5 (4.8-5.8) 9*	5.7 (5.3-6.0) 7*
Humus form	Raw humus	Duff mull	Raw humus
Site index Douglas-fir	131(121-141) 4*	168 (145-192) 12*	163 (143-180) 15*
western hemlock	103(95-118) 4*	136 (109-157) 12*	132 (102-180) 15*
western redcedar	98(90-108) 4*	121 (90-165) 12*	118 (96-170) 15*
Characteristic combination of species	Tsuga heterophylla Pseudotsuga menziesii Mahonia nervosa Eurhynchium oreganum Hylocomium splendens Plagiothecium undulatum	Thuja plicata Tsuga heterophylla Pseudotsuga menziesii Rubus spectabilis Sambucus pubens Acer circinatum Polystichum munitum Tiarella trifoliata Dryopteris austriaca Athyrium filix-femina Mnium insigne Blechnum spicant	Tsuga heterophylla Thuja plicata Pseudotsuga menziesii Acer circinatum Polystichum munitum Dryopteris austriaca Hylocomium splendens Plagiothecium undulatum Eurhynchium oreganum Rhytidiadelphus loreus

Note: Data were compiled from the field notes of Lesko (1961), Orloci (1961), and Eis (1962). pH was measured by Lesko (1961).

* The number of measurements.

TABLE VI. Ecosystem Types of the Glacial Drift Land Type, Wet Subzone

Associations		Gaultherieto - Tsugetum heterophyllae		Abieteto - Tsugetum heterophyllae	
Ecosystem type		Orthic Vaccinium - Gaultheria (OV-G)	Lithosolic Vaccinium - Gaultheria (LV-G)	Orthic Vaccinium - Plagiothecium (OV-Pl)	Hygric Vaccinium - Plagiothecium (HV-Pl)
Land form		Upper-slope	Upper-slope of hilltop	Middle-slope	Middle-slope
Relief shape		Convex	Convex	Straight	Straight to slightly concave
Slope gradient°		11 (8-16) 3*	7 (0-10) 5*	16 (5-30) 5*	10 (0-18) 14*
Altitude (ft.)		1730 (1450-2000) 3*	1510 (590-1800) 5*	1680 (690-2330) 5*	1100 (550-2100) 14*
Hygrotope		Dry	Dry	Mesic	Moist
Stoniness (%)		7 (5-10) 3*	2 (0-10) 5*	55 (40-80) 5*	16 (0-50) 14*
Permeable mineral soil depth (cm.)		18 (15-21) 3*	10 (4-15) 5*	127 (90-145) 5*	40+
Endo-humus depth (cm.)	Ah	Nil	Nil	Nil	Nil
Eluviated horizon depth (cm.)	Ae	9 (7-10) 3*	10 (4-15) 5*	3 (2-5) 5*	2 (0-8) 14*
pH	L-F	3.4 (3.3-3.5) 2*	3.7 (3.5-4.0) 2*	3.8 (3.5-4.1) 5*	3.6 (3.3-3.9) 11*
	A	3.5 (3.4-3.5) 2*	3.6 (3.4-3.7) 2*	3.9 (3.8-4.1) 5*	3.8 (3.6-4.6) 11*
	B	4.3 (4.0-4.6) 2*	Nil	5.2 (5.0-5.7) 5*	5.2 (4.7-5.4) 11*
	C	?	?		5.4 (4.9-5.7) 11*
Humus form		Raw humus	Raw humus	Raw humus	Raw humus
Site index	Douglas-fir	75 (70-79) 3*	69 (60-80) 5*	123	127 (118-135) 14*
	western hemlock	62 (53-69) 3*	56 (39-75) 5*	104 (91-116) 5*	106 (88-134) 14*
	western redcedar	65 (48-84) 3*	53 (38-81) 5*	100 (85-113) 5*	108 (85-129) 14*
	amabilis fir	59	40	94 (78-117) 5*	85 (73-129) 14*
	yellow cedar	44	67	Nil	Nil
Characteristic combination of species		Tsuga heterophylla Thuja plicata Pseudotsuga menziesii Pinus monticola Chamaecyparis nootkatensis Vaccinium alaskaense Gaultheria shallon Rhytidiopsis robusta Hylocomium splendens Plagiothecium undulatum	Tsuga heterophylla Thuja plicata Pseudotsuga menziesii Pinus monticola Chamaecyparis nootkatensis Vaccinium alaskaense Gaultheria shallon Pleurozium schreberi Rhytidiopsis robusta Hylocomium splendens Plagiothecium undulatum	Tsuga heterophylla Thuja plicata Abies amabilis Vaccinium alaskaense Blechnum spicant Clintonia uniflora Plagiothecium undulatum Rhytidiadelphus loreus Rhytidiopsis robusta	Tsuga heterophylla Thuja plicata Abies amabilis Vaccinium alaskaense (Acer circinatum) Blechnum spicant Tiarella trifoliata Dryopteris austriaca (Athyrium filix-femina) (Streptopus amplexifolius) Plagiothecium undulatum Rhytidiadelphus loreus

* The number of measurements.

TABLE VI. (continued)

Associations		Blechneto - Tsugetum heterophyllae	
Ecosystem type		Orthic Blechnum (OB)	Blechnum - Streptopus (B-S)
Land form		Lower-slope	Lower-slope
Relief shape		Concave	Concave
Slope gradient°		7 (2-10) 13*	8 (5-14) 5*
Altitude (ft.)		1370 (570-2730) 13*	2810 (2650-2950) 5*
Hygrotope		Wet	Wet
Stoniness (%)		29 (0-60) 12*	34 (25-50) 4*
Permeable mineral soil depth		35+	18+
Endo-humus depth (cm.)		1 (0-15) 12*	Nil
Eluviated horizon depth (cm.)		5 (0-13) 12*	6 (0-13) 4*
pH	L-F	3.8 (3.2-4.4) 6*	3.2
	A	3.8 (3.5-4.1) 6*	?
	B	4.8 (4.3-5.1) 6*	4.2
	C	5.2	5.7
Humus form		Raw humus	Greasy raw humus
Site index	Douglas-fir	125 (96-149) 13*	?
	western hemlock	118 (96-136) 13*	108 (97-123) 5*
	western redcedar	107 (85-149) 13*	112
	amabilis fir	115 (77-141) 13*	109 (92-122) 5*
	yellow cedar	Nil	Nil
Characteristic combination of species		Tsuga heterophylla Thuja plicata Abies amabilis Vaccinium ovalifolium Vaccinium alaskaense Rubus spectabilis Sambucus pubens (Oplopanax horridus) Blechnum spicant Tiarella trifoliata Athyrium filix-femina Streptopus amplexifolius Dryopteris austriaca (Lysichitum americanum) (Polystichum munitum) Rhytidiadelphus loreus Hylocomium splendens (Pellia sp.) (Conocephalum conicum) (Eurhynchium stokesii)	Tsuga heterophylla Thuja plicata Abies amabilis Vaccinium ovalifolium Vaccinium alaskaense Rubus spectabilis Sambucus pubens (Oplopanax horridus) Blechnum spicant Tiarella trifoliata Streptopus amplexifolius Athyrium filix-femina Rubus pedatus Streptopus roseus Dryopteris austriaca Cornus canadensis (Lysichitum americanum) Rhytidiadelphus loreus Rhytidiopsis robusta Plagiothecium undulatum

Note: Data were compiled from the field notes of Lesko (1961), Orloci (1961), and Eis (1962).

* The number of measurements.

Ecosystem types of the Spring-Water Swamp Land Type

After water infiltrates the soils on the slope, it begins to move laterally under gravitational pressure over the impervious layer. If the impervious layer outcrops on the slope, then the overlying water comes to the surface at this point, saturates the soils downslope, and a spring-water swamp is formed. Two pedogenically distinct types of spring-water swamps are encountered in the Coastal Western Hemlock Zone: one on waterlogged mineral soils, and the other on waterlogged woody peats. Swamps with mineral soils are confined mainly to slopes, while woody peats occur in the depressions. The ecosystem types of the spring-water swamp land type are described in Table VII. It should be mentioned that the Vaccinium - Lysichitum type is characteristic for localities with intensive water movement. The Lysichitum - Coptis type, however, is confined to the margins of high moors with stagnant water, but exposed to run-off water or seepage from the adjacent slopes.

Ecosystem type of the Ravine Alluvium Land Type

In the glossary of geology and related sciences (American Geological Institute 1962), a ravine is defined as a "depression worn out by running water, larger than a gully and smaller than a valley". This term is applied in the present work to narrow valley-like depressions which were cut by running water in the glacial drift substratum, and

TABLE VII. Ecosystem Types of the Spring-water Swamp and Ravine Alluvium Land Type

Associations		Lysichiteto - Thujetum plicatae	Copteto - Thujetum plicatae	Oplopanaceto - Thujetum plicatae
Ecosystem type		Vaccinium-Lysichitum (V-Ly)	Lysichitum-Coptis (Ly-C)	Oplopanax-Adiantum (O-A)
Land form		Lower-slope and outwash terrace	Depression	Ravine
Relief shape		Concave	Straight	Concave
Slope gradient°		2 (0-10) 10*	0	6 (4-10) 5*
Altitude ft.		880 (700-160) 10*	820 (700-1000) 3*	906 (480-1800) 5*
Hygrotope		swampy	swampy	swampy
Ground water table		Near surface, moving	Near surface, stagnant.	Near surface, intermittent overflow
pH	O (organic)	4.3 (3.0-4.9) 7*		5.5
	C	5.3 (4.6-6.1) 7*		5.8
Humus form		Anmoor or peat anmoor	Peat anmoor	Anmoor or mull
Site index	Douglas-fir			136 (130-150) 5*
	western hemlock	102 (88-130) 10*	98 (80-129) 3*	137 (84-160) 5*
	western redcedar	101 (76-125) 10*	79 (70-98) 3*	121 (100-44) 5*
Characteristic combination of species		Thuja plicata (Picea sitchensis) Vaccinium alaskaense Rubus spectabilis Lysichitum americanum Blechnum spicant Dryopteris austriaca Tiarella trifoliata Athyrium filix-femina Conocephalum conicum Mnium punctatum Eurhynchium stokesii Pellia sp. Sphagnum squarrosum	Thuja plicata Pinus monticola Menziesia ferruginea Rubus spectabilis Vaccinium alaskaense Sambucus pubens Lysichitum americanum Coptis asplenifolia Coptis trifolia Mnium punctatum Sphagnum squarrosum	Thuja plicata Oplopanax horridus Ribes bracteosum Rubus spectabilis Vaccinium alaskaense Lysichitum americanum Adiantum pedatum Athyrium filix-femina Blechnum spicant Viola glabella Circaea alpina Gymnocarpium dryopteris Tiarella trifoliata Dryopteris austriaca Eurhynchium stokesii Conocephalum conicum Pellia sp. Sphagnum squarrosum Mnium punctatum Mnium menziesii

* The number of measurements.

which usually contain permanent or semi-permanent streamlets or creeks.

The Thuja plicata - Oplopanax horridus association which characterizes the ravine alluvium land type is remarkably uniform throughout both subzones, constituting a single ecosystem type. It extends into the Mountain hemlock zone where Thuja plicata is replaced by Chamaecyparis nootkatensis. A brief description is given in Table VII.

Ecosystem types of the Squamish Flood-Plain Land Type

Variations in floristic structure among the flood-plain ecosystem types are attributed mainly to differences in overflow and post-flood drainage. Overflow is directly related to a fluctuation of the stream water level, and is therefore indirectly controlled by the climatic elements of the drainage area. Post-flood drainage reflects how rapidly the flood water is removed from an area when the water level of the stream starts to fall. In this connection, the differences are most marked between the benches along the active channel and the scars, between soils which contain a gravel horizon close to the soil surface, and soils which do not contain such a horizon, and so forth.

The terrain of a flood-plain grows by deposition of sediments from intermittent overflow. As the surface grows higher, overflow becomes less frequent. A similar reduction of overflow frequencies can occur as a consequence of downcutting in the river bed.

The bench height gradient coincides with a definite sequence of plant communities. Variations can occur at any particular bench height as a consequence of differences in post-flood drainage and soil quality. The ecosystem types of the Squamish flood-plain land type are described in Table VIII. Scars and oxbow lakes are not discussed.

Plant communities are most specific in their ecotopic requirements in all land types which were considered in this paper. This makes it possible to utilize the plant communities as indicators of the different ecotopes.

Development of Ecosystems

Development implies vegetational and environmental ecosystem changes which result in a successional (time) sequence of plant communities and ecotopes at any particular point of the landscape. Developmental trends in time can be anticipated on the basis of present plant community distribution in space along existing environmental (ecotopical) gradients. The successional sequence, so defined, necessarily pertains only to plant communities and ecotopes which presently exist in the general region. It should be mentioned that a successional sequence of plant communities and ecotopes does not necessarily coincide with their geographic sequence.

Each individual plant community is visualized as the product of development that can be produced in a particular habitat. Any further plant community development requires a habitat change. In this way, each individual community represents a habitat "climax" ("permanent community" sensu Braun-Blanquet 1932). A geographic pattern of the habitat climax communities ("climax pattern" sensu Whittaker 1953) appears as a cross-section across individual developmental lines, evolving at different points of the landscape.

Lesko (1961) has recognized within the Coastal Western Hemlock Zone distinct trends in soil developments that converge to mesic podzols. These podzols have a thick raw humus surface horizon, a prominent eluviated horizon (Ae) and a cemented illuvial horizon rich in humus and iron oxides (Bfhc). The lower part of the B horizon is gleyed in the Wet Subzone, but gleization is absent from these soils in the Dry Subzone.

The convergence in plant community development to a climatic climax status is the consequence of a trend in habitat change towards a mesic condition. The concept of successional convergence implied in the present work can be understood at two levels of generalization: a universal establishment of a particular dominance type appropriate to the forest climate, and the establishment of a mesic state of environment and vegetation through a sequence in time of many different plant associations at a given point of the landscape. While a trend of successional convergence is recognized, it does not mean that development must go through the complete successional sequence in every locality of the landscape. In some localities, development is very slow and it would require substantial physiographic changes to move toward a mesic status. In a mountainous terrain substantial physiographic change, however, may involve a period of time far exceeding that required for substantial soil or climatic changes. The climax pattern therefore, may change geographically in such a way, that the developmental lines evolving at the different points of the landscape may be re-oriented several times before a climatic climax state ecosystem would develop in certain localities. No distinction is made between climax and seral communities in a sense that one is more stable than the other. The climax community itself is a changing entity, and therefore in successional convergence, as Cowles (1901) pointed out, one variable approaches another variable rather than a constant.

The direction in plant community development depends on the nature of the environmental gradient produced in a locality by environmental changes in time. For example, a change to a warmer and drier climate could result in successions as indicated by the horizontal arrow from right to left in Table X. This succession could lead, for example, to the establishment of plant communities which characterize the Coastal Douglas-fir Zone in place of those which occur at present in the Coastal Western Hemlock Zone.

TABLE VIII. Ecosystem Types of the Squamish Flood-plain Land Type, Benches

Associations	Hygrohypneto - Scoulerietum (H-S)	Equisetetum arvensis (E)	Scoulerieto - Salicetum (S-S)	Saliceto - Populetum (S-P)
Bench height (ft.)	6.5 (5-8) 4*	12 (11-13) 3*	10	11.9 (10-13.5) 8*
Days of overflow per year	146 (102-190) 4*	10 (4-18) 3*	42	15 (3-42) 8*
Depth to first gravel horizon (cm.)	0	44 (33-60) 3*	0	32 (0-95) 8*
Stand age (years)	--	--	?	4 (2-7) 8*
Characteristic combination of species	Scouleria aquatica Hygrohypnum ochraceum	Equisetum arvense	Salix sitchensis Alnus rubra Populus trichocarpa Elymus glaucus Scouleria aquatica	Populus trichocarpa Salix sitchensis Alnus rubra Salix lasiandra Equisetum arvense

Associations Ecosystem type	Lonicereto - Populetum Lonicera - Rubus type (L-R)	Oplopanaceto - Piceetum Ribes - Oplopanax type (R-O)	Symphoricarpeto - Piceetum Symphoricarpos type (S)
Bench height (ft.)	15.5 (14-17.5) 10*	19.6 (18-21.5) 4*	19.2 (18-21) 5*
Days of overflow per year	2 (up to 3) 10*	less than 1	less than 1
Depth to first gravel horizon (cm.)	104 (50-120) 10*	125+	69 (60-85) 5*
Stand age (years)	19 (14-45) 10*	66 (25-89) 4*	40 (27-55) 5*
Characteristic combination of species	Populus trichocarpa Alnus rubra Picea sitchensis (Thuja plicata) Salix sitchensis Lonicera involucrata Rubus spectabilis Maianthemum dilatatum Osmorhiza chilensis Equisetum arvense	Picea sitchensis Populus trichocarpa (Alnus rubra) (Acer macrophyllum) Thuja plicata Oplopanax horridus Ribes bracteosum Rubus spectabilis Athyrium filix-femina (Dryopteris filix-mas) (Polystichum andersonii) Polystichum munitum Maianthemum dilatatum Osmorhiza chilensis Tiarella trifoliata Dryopteris austriaca Disporum oreganum Mnium insigne	Picea sitchensis (Acer macrophyllum) Thuja plicata Populus trichocarpa Symphoricarpos rivularis Disporum oreganum Polystichum munitum Athyrium filix-femina (Dryopteris filix-mas) Dryopteris austriaca Osmorhiza chilensis Mnium insigne

* The number of measurements.

Primary successions on Rock Outcrops (Dry Subzone)

Since the loosened particles are immediately removed by wind, water, and gravity from the peaks and the steep knolls of rock outcrops, no essential endogenic development can occur in their ecosystems, and, therefore, the pioneer stages can be greatly prolonged. The shade, litter, and root action of the arboreal vegetation, which usually surrounds the pioneer communities, however, can accelerate development in them far beyond their endogenic potentials.

Development binds the pioneer communities into a common complex with Gaultheria shallon. At this stage of development, organic matter accumulates more rapidly than in any one of the preceding stages, and raw humus (or root mor) is formed. Accumulation of raw humus and the root action of Gaultheria shallon cause the destruction of the pioneer community fragments, and promote an environmental uniformity.

The decomposition of the rock surface perhaps is accelerated under the Gaultheria association. The weathering products are well protected against erosion, they accumulate, become bleached, and form a soil horizon which is ash-gray in colour. The soil profile, hence, consists of a thick root mor underlain by an eluvial (Ae) horizon and the parent rock. This soil type was described by Lesko (1961) as an Eluviated Lithosol.

Establishment of Douglas-fir (Pseudotsuga menziesii) leads to the development of a lithosolic forest. At this stage of development, the disintegration of the remnants of the pioneer lichen and bryophytic communities is nearly completed by a combination of shading and root action. Roots concentrate in the crevices, thereby occupying the space of the extra soil which had accumulated there and which conditioned the floristic structure of the Danthonia spicata and the Polytrichum commune associations. The sequence of primary successions on rock outcrops is shown in Table IX.

Successions in some forest ecosystems

Glacial till soils are very unstable on steep slopes. They are easily removed by erosion when the continuity of the vegetation is interrupted, especially after fires. The trend indicates a possibility of complete removal of glacial till soils from the steep and convex slopes, and a subsequent expansion of the lithosolic forest (LG) and other rock outcrop communities. Accumulation of the weathering products is very slow and the erosion potential in this perhumid climate is great. Materials which are removed from the upper slopes are deposited on the lower slopes or carried further by the streams. These deposits increase soil depth and alter the soil-moisture regime. In this way, aggradation is a significant source of development on the lower slopes.

Glacial drift is a relatively young and little altered material in the Coastal regions of British Columbia. Therefore, soils originating from glacial drift can change a great deal in a relatively short period of time. The perhumid mesothermal climate supports raw humus accumulation, leaching, and subsequent ortstein development. The ortstein layer may develop at various depths in the soil profile. This inevitably reduces the effective soil depth and alters the soil-moisture regime. In some habitats, seepage may rise in the soil profile and succession may proceed towards the hygro- or hydro-phytic communities. Ortstein development may also bring about a shift toward xeric conditions in those soils which are intensively drained and lack seepage.

Seepage will contribute to changes in the soils by causing sedimentation of fine materials in the soil profile which, in turn, reduce aeration and impede drainage. Seepage water, enriched by nutrients, affects the floristic composition of the plant communities and consequently may also influence humus quality. This rich seepage water can promote fast decomposition of the organic matter, thereby affecting soil and plant community development. Successions in the forest ecosystems of the Coastal Western Hemlock Zone, except those of the flood plains, are indicated in Table X.

Successions on the Squamish flood plain

While the meander cuts away the bank where the turbulence of water is greatest, it deposits sediments along the opposite bank where turbulence is least. This causes migration of the meander and builds up a new terrain that is open to plant colonization. Additional deposits of sediments will raise the surface of the terrain above a critical level suitable to plant colonization.

Different successional trends (see Table XI) evolve on the different initia. Equisetum arvense is the first species to establish itself on loose sand. By its production of long rhizomes, Equisetum arvense efficiently stabilizes sand and promotes aggradation. Scouleria aquatica and Hygrohypnum ochraceum form an initial community on stabilized boulders. Scouleria and Hygrohypnum are attached firmly to the substratum and resist a strong current and long summer overflow. Accumulation of a tiny horizon of silt from the withdrawing flood on gravel benches may provide a suitable seed-bed for the establishment of Salix sitchensis, S. lasiandra, S. scouleriana, Alnus rubra, and Populus trichocarpa. Successful establishment of the trees, however, requires the coincidence of several factors. The bench should be slightly higher than the average summer water level, the flood should have retreated leaving a moist nutritive surface soil behind at the time of seed dissemination, and germination should be followed by a long flood-free period for successful development of the seedlings.

A surface which is vegetated will aggrade faster than one without vegetation. This will initiate a process of differentiation of levels on a flood plain. Topographic forms which were produced by an even aggradation under stands of vegetation may be called benches and they can be classified by their relative height above the zero water mark, a water level which coincides with a zero of the river gauge. The extent of a uniform bench usually coincides with a uniform even-aged stand of vegetation in primary successions under which deposits were laid down by intermittent overflow in a rate and extent influenced by the vegetation itself. Within these limits, soils, overflow conditions, and potential productivity are very similar. Different bench levels reflect variations in the time of establishment of the initial stand. The age of a primary stand is usually younger on a low bench than the age of a primary stand on a high bench.

TABLE IX. Primary Successions on Rock Outcrops

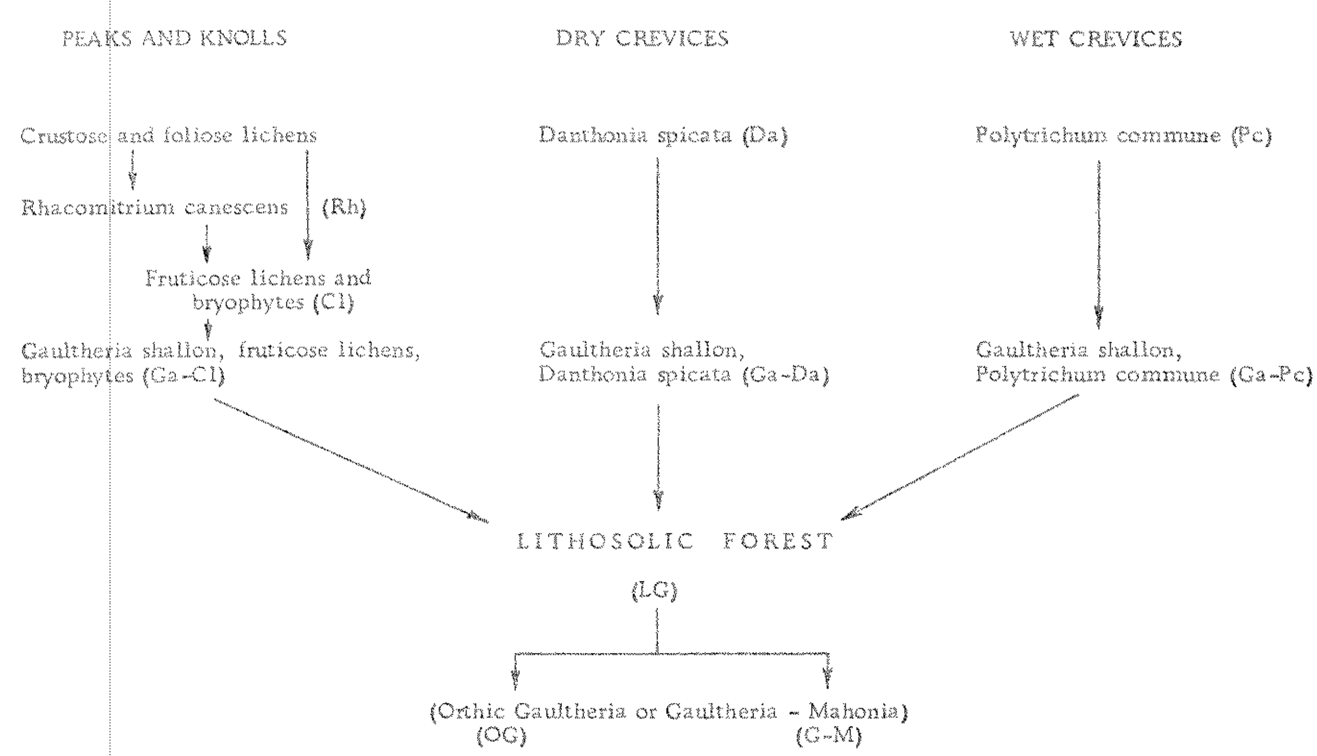


TABLE X. Successions in the Forest Ecosystems of the Coastal Western Hemlock Zone and the Adjacent Climax Areas

	Coastal Douglas-fir zone*	Coastal western hemlock zone			Mountain hemlock zone**
	Wet subzone	Dry subzone		Wet subzone	Lower subzone
	Humid mesothermal ←			→	Perhumid microthermal
Xeric ↓	Rhacomitrium - Lichen	Lithosolic Gaultheria		Lithosolic Vaccinium - Gaultheria	Lithosolic Cladothamnus
	Gaultheria - Lichen	Gaultheria - Mahonia	Orthic Gaultheria	Orthic Vaccinium - Gaultheria	Orthic Cladothamnus
Mesic	Gaultheria	Plagiothecium - Mahonia	Orthic Plagiothecium	Orthic Vaccinium - Plagiothecium	Vaccinium - Rhytidiopsis
↑	Eurhynchium	Degraded Polystichum		Hygric Vaccinium - Plagiothecium	Degraded Streptopus
	Polystichum - Tiarella laciniata	Orthic Polystichum		Orthic Blechnum	Blechnum - Streptopus
Hygric	Lysichitum	Vaccinium - Lysichitum or Oplopanax - Adiantum			Chamaecyparis - Lysichitum

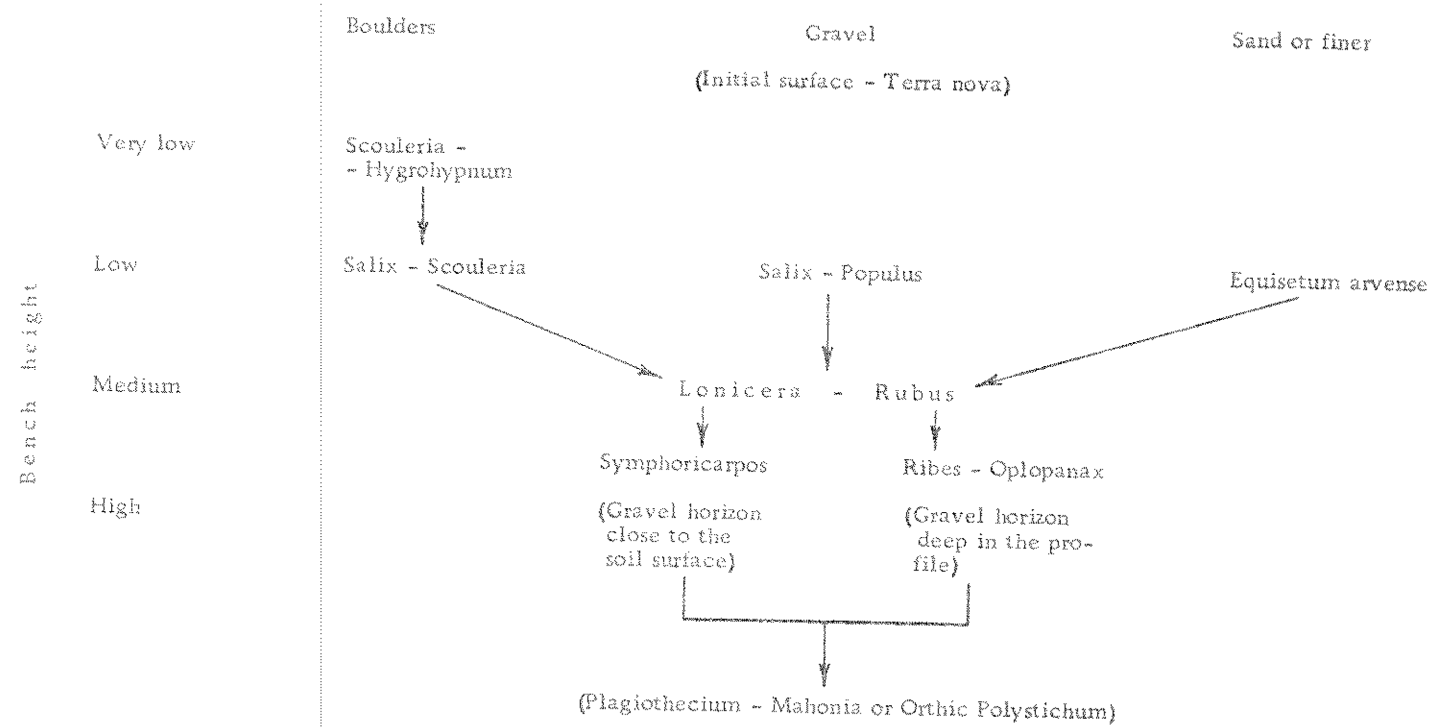
Theoretical convergence (Xeric → Mesic ← Hygric)

* After Krajina and Spilsbury (1953).

** After Peterson (1964) and Brooke (1964)

Note: Transitional and high moors are not considered.

TABLE XI. Primary Successions on the Squamish Flood-plain, Benches*



* Oxbow lakes are not discussed in this paper.

It is possible to distinguish between the benches and the terraces in spite of their similarity in form. Hefley (1937) correctly pointed out that benches (or levels) are aggradation forms within a flood plain and they are attributable to the action of overflow water, wind, and vegetation. Terraces, on the other hand, mark a former valley floor level as stated by Thornbury (1958), and are largely the products of stream erosion rather than deposition (Gilbert 1877).

At the upper limit of the Scouleria - Hygrohypnum bench, the spaces among boulders are filled with sand and the establishment of willows, Alnus rubra, and Populus trichocarpa may take place. The boulders become fully or partially covered by sand while the bryophytes disappear gradually as they become buried. The establishment of Elymus glaucus, Lonicera involucrata, and Rubus spectabilis increases. At this stage the stand is 20 to 30 years old, Populus trichocarpa dominates in the crown canopy, and Picea sitchensis is abundant in the shrub layer. The soil is from two to three feet deep and consists of sand underlain by gravel or stones.

On the Equisetum arvense bench, development leads also to a Lonicera - Rubus community, in which the soil is similar to that just described except that boulders are not present in the subsoil and the sand is somewhat deeper. Development on the gravel benches converges also to a Lonicera - Rubus community.

The Lonicera - Rubus bench is frequently flooded but the deposited sediments are finer than before. Eventually a loamy sand surface horizon accumulates and the proportion of Lonicera involucrata decreases. The establishment of Symphoricarpos rivularis on this bench level indicates that a gravel horizon is close to the soil surface and follows a recent shift in the position of the river bed. Oplopanax horridus and Ribes bracteosum are specific to deep loam soils. In both the Symphoricarpos and the Ribes - Oplopanax community, Picea sitchensis and Populus trichocarpa dominate at the beginning, and subsequently Picea sitchensis alone. On this level, overflow is extremely rare and vegetation is conditioned by underground movement of water which varies with the water level of the stream.

Development on the Symphoricarpos and the Ribes - Oplopanax bench is very slow and if the habitat is no longer influenced by flood-water but seepage is present, the stand will remain rich in deciduous trees and herbs. These conditions promote an efficient decomposition of the organic matter and melanization. If no seepage is present in the soil, the stand will be dominated by conifers and raw humus accumulates. This leads to podzolization of the soil. Melanization and seepage are associated with the abundant occurrence of Polystichum munitum, and the podzols with raw humus inhabiting plants.

Ecosystem patterns of a flood plain are in a continuous flux. As the meanders migrate from one side of the valley to the other, benches and plant communities are destroyed along the outside bank. Development of an alternate channel can initiate substantial changes in the floristic structure of the plant communities through changes in the patterns of overflow and post-flood drainage. The distance of flow is always shortened by the alternate channel; this increases the river gradient. A new equilibrium is achieved by downcutting in the river bed.

If the break-through occurs across a medium bench, a unique situation can develop. Overflow duration is drastically reduced on the benches due to downcutting which results in a relative increase of bench height. Soil depth remains as before because bench level is increased by downcutting and not by sedimentation. The lesser vegetation will undergo rapid changes but the crown canopy will remain essentially unaltered for a certain period of time depending on the stand age.

The overflow pattern in the unique situation just described resembles that of the Ribes - Oplopanax type. The soil profile which contains a gravel horizon close to the soil surface is similar to that of the Lonicera - Rubus type. The rate of sedimentation is low, and therefore no significant increase in soil depth can be anticipated. The crown canopy consists of deciduous trees in the early developmental stages (as in the Lonicera - Rubus type) but these give way later to the conifers (as in the Ribes - Oplopanax type). In the lesser vegetation, Symphoricarpos rivularis is the most abundant species.

The Symphoricarpos type always indicates a gravel horizon in the soil profile close to the soil surface, but this horizon does not necessarily indicate an earlier downcutting in the river bed. The tributary streams can dump gravel even on the high benches of the main stream.

REFERENCES

Armstrong, J. E. 1956. Surficial geology of Vancouver area, B. C. Geol. Surv. Can. Paper 55-40.

__________. 1957. Surficial geology of New Westminster Map-area, B. C. Geol. Surv. Can. Paper 57-5.

Braun-Blanquet, J. 1932. Plant sociology, the study of plant communities. (Trans. by G. D. Fuller and H. S. Conard.) New York McGraw-Hill.

Brooke, R. C. 1964. Personal communications.

Cowles, H. C. 1901. The physiographic ecology of Chicago and vicinity; a study of the origin, development, and classification of plant societies. Bot. Gaz. 31:108, 145-182.

Eis, S. 1962. Statistical analysis of tree growth and some environmental factors of plant communities. Ph. D. Thesis, Dept. Biol. and Bot., Univ. of B. C.

Gilbert, G. K. 1877. Report on the geology of the Henry Mountains. U. S. Geol. Geogr. Surv. of the Rocky Mountain Region (Powell) Washington: 120-127.

Halliday, W. E. D. 1937. A forest classification of Canada. For. Serv. Bul. 89. Can. Dept. Mines and Res. Ottawa.

Hansen, H. P. 1947. Climate versus fire and soil as factors in post-glacial forest succession in the Puget lowland of Washington. Am. Jour. Sci. 245: 265-286.

Hefley, H. M. 1937. Ecological studies of the South Canadian river flood-plain in Cleveland County, Oklahoma. Ecol. Monogr. 7:345-402.

Krajina, V. J. 1959. Bioclimatic zones in British Columbia. Univ. of B. C., Bot. Ser. No. 1, Vancouver, B. C.

__________. 1964. Ecology of the forests of the Pacific Northwest. 1963 Prog. Report, Nat. Res. Coun. Grant T-92, 71-87.

__________, and L. Orloci. 1963. Biogeoclimatic forest zones on the lower mainland of British Columbia. 1962 Prog. Report, Nat. Res. Coun. Grant T-92, 18-24.

__________, and R. H. Spilsbury. 1953. Forest associations on the east coast of Vancouver Island. Forestry Handbook for British Columbia, 1st. ed. (1953). Forest Club, University of British Columbia.

Lesko, G. 1961. Ecological study of soils in the Coastal Western Hemlock Zone. M. Sc. Thesis, Dept. Biol. and Bot., Univ. of B. C.

Orloci, L. 1964. Vegetational and environmental variations in the ecosystems of the Coastal Western Hemlock Zone. Ph.D. Thesis, Dept. Biol. Bot., Univ. of B. C.

Peterson, E. B. 1964. Plant associations in the Subalpine Mountain Hemlock Zone in southern British Columbia. Ph.D. Thesis, Dept. Biol. and Bot., Univ. of B. C.

Rowe, J. S. 1959. Forest regions of Canada. For. Br., Bul. 123. Can. Dept. Nor. Aff. and Nat. Res. Ottawa.

Thornbury, W.D. 1954, 1958, 1962. Principles of geomorphology. John Wiley & Sons, Inc. New York and London.

Whitford, H. N. and R. D. Craig. 1918. Forests of British Columbia. Can. Com. Cons. Ottawa.

Whittaker, R. H. 1953. A consideration of climax theory: the climax as a population and pattern. Ecol. Monogr. 23:41-78.