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FOREST SUCCESSION IN RELATION TO RIVER TERRACE DEVELOPMENT IN OLYMPIC NATIONAL PARK, WASHINGTON[1]

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Abstract. The floodway zone of the Hoh River exhibits four terrace levels of different ages, formed by erosional activity of the river on valley fills. The vegetation in this valley is in a long-term seral sequence as shown by the zonal pattern in relation to aging and development of these land surfaces. Succession starts on gravel bars, which are dominated by *Alnus rubra* and *Salix scouleriana*. The following sequential forest communities, and associated ages of land surfaces, are found: *Alnus rubra* on alder flats (80–100 yr); *Picea sitchensis–Acer macrophyllum–Populus trichocarpa* on first terraces (400 yr); *Picea sitchensis–Tsuga heterophylla* on second terraces (750 yr); and *Tsuga heterophylla* on third terraces. The latter represents the climax community for the river terrace sere, and it occurs on surfaces exposed by retreating Pleistocene alpine glaciers. The first three terraces are derived from Neoglacial alluvial fills.

There is a strong correlation among zonation patterns, forest succession, age of terraces, soil moisture, and soil profile development. Available soil moisture is an important factor governing the zonal sequence. The younger land surfaces are significantly drier than the older terraces. Plants on alder flats and first terraces must withstand greater moisture stress than those of second and third terraces. As the land surface ages, the soil profile develops; deeper, more mature soils are found away from the river.

The term "Olympic rain forest" is inappropriately applied to this vegetation; "temperate moist coniferous forest" is more appropriate not only for forests in the Hoh Valley, but also for the rest of the Oympic Mountains and vegetation along the northern Pacific coast.

Key words: *Forest; Olympic forests; succession, forest; riverine; vegetation; zonation, forest.*

INTRODUCTION

For a number of years the forest vegetation of the glaciated river valleys of the western slope of the Olympic Mountains has been referred to in popular and scientific literature as the Olympic rain forest (Hult 1954, Sharpe 1956, Johnson 1965, Kirk and Namkung 1966, Billings 1970, and numerous National Park Service publications). Jones (1936) did not use the term, possibly because his work predated the concept. He designated the vegetation instead as part of the *Pseudotsuga menziesii* subclimax of the *Tsuga heterophylla–Thuja plicata* climax formation, and also as part of the *Picea sitchensis–Tsuga heterophylla* climax. Jones, however, classified the vegetation in the western valleys with that on the coastal plain. In this regard, he mistakenly included those forests dominated by *Picea sitchensis* and *Tsuga heterophylla* along the river with those dominated by *Thuja plicata, Tsuga heterophylla,* and *Pseudotsuga menziesii* elsewhere in the mountains. Franklin and Dyrness (1973) treated the vegetation in the valleys as part of the *Tsuga heterophylla* zone, without reference to rain forest. Regardless of terminology, implicit in these writings is the concept of a single forest unit. The one study that ostensibly attempted to dissect this unit was Sharpe's (1956) artificial classification into so-called pure stands, all of which were ultimately tied back into his concept of the rain forest.

Several ecologists have studied forest zonation and succession along eastern rivers, with perhaps the most significant work done in the Mississippi drainage. No western river has been investigated for zonal relationships, save for the Colville River in northern Alaska (Bliss and Cantlon 1957). This study examined herbaceous and shrubby willow communities that occupied various river terraces. Waring and Major (1964) studied vegetation in the coastal redwood region, but they did not focus on river zonation per se. One of the earliest works to develop the concept of community zonation and succession from the edge of the water was conducted on the South Canadian River, Oklahoma (Hefley 1937). Hefley described four topographic levels associated with the floodplain, concluding that the three youngest were probably the result of present-day river activity, but he gave merely reconnaissance level descriptions of the plant communities in the sere. Later Ware and Penfound (1949) focused more closely on vegetation of

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the first two levels of the South Canadian River. Shelford (1954) described biotic communities of the lower Mississippi floodplain, and Weaver (1960) worked on floodplains of the Missouri River in Nebraska. Perhaps the most extensive studies are those of Lindsey et al. (1961) on the Wabash and Tippecanoe Rivers in Indiana, Hosner and Minckley (1963) on tributaries of the Mississippi in southern Illinois, and Wistendahl (1958) on the Raritan in New Jersey. These authors focused on the shift from poorly vegetated river bars to mature forest with distance from the river.

All of the eastern studies clearly indicate a zonal pattern of hardwood tree species and environmental regimes. The vegetational sequence from various grasses, sedges, and annuals through progressively more mature forests is paralleled by shifts in temperature regimes, soil development, and moisture regimes. These studies show that the land surfaces develop through time to support a forest characteristic of the regional climax. Under usual seral conditions in the east, a coniferous stage, generally dominated by species of *Pinus*, precedes the hardwood climax. It is important to note that there is no coniferous stage for eastern river seres. In a situation analogous to the eastern rivers, *Pseudotsuga menziesii*, the tree species normally preceding the zonal climax in much of the Olympics (Fonda and Bliss 1969), has no role to play in river terrace succession.

The purpose of this study was to quantify the zonal sequence of forest communities as it indicates succession on river terraces in the western Olympics. The various plant communities, associated microclimates, and soil development will be discussed to support the hypothesis of river terrace succession. These forests are closely related to other vegetation formations in North America and throughout the world, and these will be reviewed to demonstrate that the term "rain forest" is inappropriately applied in the Olympics.

Nomenclature for this paper follows Hitchcock et al. (1955, 1959, 1961, 1964, 1969) for vascular plants, and Lawton (1971) for mosses.

Study Area

The Olympic Mountains occupy the central portion of a peninsula in northwest Washington. The geology of these mountains has been described by Weaver 1945, Danner 1955, Fonda and Bliss 1969, and Easterbrook and Rahm 1970. This study was centered in the valley of the Hoh River, located on the west side of the mountains. The Hoh Valley was carved to its present shape by alpine glaciers that extended down-valley during the advances of Pleistocene ice (Easterbrook and Rahm 1970). In cross section, the valley exhibits a characteristic U-shaped trough; in many places the valley floor is over 1 km wide from wall to wall. The Hoh River carries meltwater from at least five major alpine glaciers, a number of minor glaciers, and extensive subalpine snowfields in the upper reaches of the watershed. Still, compared to the width of the valley floor, it is a narrow river, and for much of its length has a shallow and poorly defined channel characteristic of braided streams.

This is a 4-fill, 4-cut, 4-terrace valley. It appears to have been filled at least four times since the last ice advance. The oldest fill is till from the glacier, while the three youngest fills are alluvial outwash from Neoglacial ice advances. Maximum elevation from the river to the top of the oldest fill is 20 m. Portions of each fill have been eroded by the meandering Hoh River, leaving behind the terraces upon which this study is based. During the most recent Neoglacial phase, alpine glaciers on Mt. Rainier have advanced and retreated in response to climatic fluctuations. Three principal periods of advance can be discerned, based on ages of trees growing on end moraines: 1217–1363; 1540–1635; 1800–1850 (Crandell and Miller 1964). Although quantitative data are lacking, the fills and terraces in the Hoh Valley seem to correspond to these advances on Mt. Rainier. Ages of trees give good indication that the present forest seres were initiated at approximately the same dates as the Mt. Rainier advances and retreats.

River terrace terminology varies from study to study. In this work the newest erosional surfaces formed by the present-day activity of the river are called gravel bars if lacking forest vegetation. The most recent true terrace supporting trees is an alder flat. Higher, older surfaces, formed much longer ago are called terraces, and will be numbered consecutively away from the river.

Bauer (1971) devised a classification system for rivers in northwest Washington that is based upon their geologic-hydraulic function and mechanism. Figure 1 shows the four major zones in the river classification, and their gradient and channel characteristics. Each zone is characterized on the basis of the size of the predominant channel particle, which is a function of the amount of energy represented by the current velocity of the river. A river moving through a zone with a steep gradient is capable of moving large boulders and cobbles; in a low gradient zone a river has considerably less energy, and can move only silt and mud. There are a number of factors contributing to the cutting action of a river, all of them greater in zones I and II. The river, therefore, is likely to be much more of an erosive force in these up-valley zones than in zones III and IV.

This study was conducted on the floodway zone

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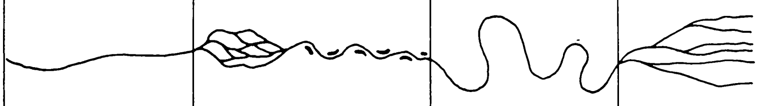
CHARACTERISTIC	BOULDER ZONE	FLOODWAY ZONE	PASTORAL ZONE	ESTUARINE ZONE
Stream course				
Channel type	Single channel, fixed	Braided channel with islands, or tight meanders with point bars; active erosion and accretion	Single channel, incised in wide meanders	Branched channel, drowned by tides
Gradient	>25%	5 to 25%	<5%	±0%
Bed material	Boulders, cobbles	Cobbles, gravels, sands	Sand to silt	Silt to mud

FIG. 1. Streamway classification based on the geologic-hydraulic function and mechanism of a typical mountain river in western Washington (after Bauer 1971). This study of forest succession was centered on the floodway zone.

of the Hoh River. The floodway zone is characterized by Bauer (1971) as having a gradient of between 5% and 25%, with a predominant channel material that ranges in size from cobbles to small gravel, and where the combination of current energy and increasing width of valley floor encourages meandering within a frequently flooded, multichannel streamway (Fig. 1). In the Hoh Valley this zone is typified by both braided streams and tight meanders with point bars. The cobbles and gravels carried by the river in this zone form an important diagnostic layer in determining terrace origin and soil development. The zone begins ca. 3 km upstream from Olympus Guard Station. It continues downstream, ending outside the park ca. 2 km from U.S. 101, with a total linear length of ca. 40 km. An occasional stretch of the boulder zone (Fig. 1) is encountered in this distance, but for the most part it is floodway; this is consistent with Bauer's theory. Because the floodway is liable to high velocity water movement during spring runoff, with resultant abrasion because of particle load, the river continually and throughout its history changes course. New channels are created and old ones abandoned; banks and terraces are flooded and undercut, and the load is deposited farther downstream in point bars.

The history of the Hoh Valley since retreat of Pleistocene ice has been an alternation of valley filling and river erosion, forming various terrace levels with accompanying vegetation changes. Instead of the forest unit accepted for so many years, there is a long-term successional sequence taking place in relation to establishment of land surfaces.

METHODS

Vegetation sampling

Quantitative data on community composition were gathered during the summer of 1970, with additional data gathered in spring 1971 and 1972. Because of the configuration and variable extent of terraces on a meandering river that has been actively eroding land surfaces, a single compass line of five points spaced about 60 m apart was used in sampling a given terrace stand. For most stands this produced comfortable spacing on the narrow terraces; in a few stands the distance between points was shortened somewhat, but in no case was the same plant sampled on more than one measured plot. Data on trees, shrubs, herbs, and tree reproduction were gathered at each point. Trees larger than 2.5 cm dbh were sampled for density and basal area using the combination 0.1 acre circular plot and prism method of Lindsey et al. (1958). Shrub and herb cover were estimated by cover class on plots nested over the central point, shrubs on 0.01 acre circular plots, herbs on 0.001 acre circular plots. The cover class estimates of Daubenmire (1959) were used, as were the midranges in analyzing the data, which are expressed as percent cover and frequency. Data on tree reproduction were gathered on the two smaller plots, those individuals less than 30 cm tall on the herb plots, those between 30 cm tall and 2.5 cm dbh on the

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shrub plots. Five stands were sampled on each of the four terrace levels.

Because newly formed gravel bars are colonized by scattered plants, with no development into a community structure, I made only a reconnaissance level survey of the bars.

Microclimate

Three principal microclimatic stations (one each in the *Picea–Acer–Populus*, *Picea–Tsuga*, and *Tsuga* communities) were established in mid-June 1970 and kept in operation until mid-September 1970. Data were gathered on air temperature (60 cm, shielded) and soil temperature (–10 cm) by single-pen distance thermographs, precipitation by plastic rain gauges centered under canopy openings at 60 cm, and soil moisture/temperature at –15 and –35 cm with thermistor blocks. In addition, a station with the same components except for a soil thermograph was established at 300 m elevation on the valley wall. Another station that lacked thermographs was in an *Alnus rubra* community. Instrument stations were attended weekly, when thermograph calibration was also checked. Periodic gravimetric soil moisture samples were taken for use in calibrating soil-moisture readings from the thermistor blocks.

The soil moisture blocks were calibrated using soil in which they had been placed. Soil was rolled to pass a 2-mm sieve, so that the values would be based on the same fraction as that on which soil moisture holding capacity was analyzed. The blocks were put in brass rings of a slightly larger dimension; soil was poured in around the blocks and prevented from falling out by cheesecloth screening on the bottom. The soils were saturated for 24 h, then allowed to drain; during this time readings and weights were taken. This produced a desorption curve, which was then readjusted according to gravimetric values taken in the field.

Soils

Soil development is an important process in the Hoh Valley. During vegetation sampling I examined the soils of each stand with a soil probe to a depth of one meter or to river cobbles, to be certain that there were no anomalies exhibited by the profile. Soil development shows less variability than vegetation composition from site to site; therefore in determining terrace relations stands originally were classified not by the existing vegetation, but rather on the basis of soil development.

Two soil pits from each terrace level were examined for profile development, rooting habits, and depth to river cobbles; composite samples from each horizon in each pit were taken for later analysis in the laboratory. Profile descriptions conform to nomenclature recommended by the Soil Survey Staff (1962). Soil colors were taken in natural light on moist soil, and follow the Munsell (1954) classification. In the laboratory, the soils were air-dried, then rolled to pass a 2-mm mesh sieve. Subsequent analyses were made on the 2-mm fraction, except for organic matter. Soil texture was determined following the hydrometer method of Bouyoucos (1951), except that sands were sieved out of the sample by a 53-μm sieve. Textural classifications follow Soil Survey Staff (1962). Soil organic matter was determined on the 0.175-mm fraction, obtained by grinding, following the chromic acid combustion method of Perrier and Kellogg (1960), except for two samples with over 10%. These were ignited in a muffle furnace at 700°C for 1 h as in Cox (1972). The Soil and Feed Testing Laboratory, University of Alberta, analyzed the soils for total %N, %P, and %Ca by atomic absorption; and pH using a glass electrode. Soil-moisture holding capacity was analyzed by the Botany Department, University of Alberta, using 0.3-bar and 15-bar porous plates after the method of Richards (1949).

Results

Vegetation

Gravel bars.—Gravel bars exhibit highly variable surface features, depending on the type of aggradation, how often the bars are flooded, and the proximity of backwater channels. The principal species on bars with a cobble surface are *Salix scouleriana, Panicum occidentale,* and *Rumex acetosella.* Individuals of *S. scouleriana* up to 1 m tall are the most prominent plants. Other abundant species are *Holcus lanatus, Trifolium repens, Hypochaeris radicata, Equisetum* sp., *Sedum* sp., and *Rumex crispus.* Widely scattered plants included *Ranunculus uncinatus, Agrostis* sp., *Plantago* sp., *Mimulus dentatus, M. guttatus, M. lewisii,* and *Carex deweyana.* Plant cover on these sites varies from less than 5% to about 20%.

Older sites have sand over the cobbles, and are characterized by thickets of *Alnus rubra* and *Salix scouleriana.* These trees vary from 4 to 9 m in height. Inside the thickets the understory is characterized by *Agrostis* sp. and *Sedum* sp., while the borders show *Fragaria virginiana, Hypochaeris radicata, Holcus lanatus, Juncus effusus, Stachys mexicana, Rumex acetosella, Polystichum munitum, Athyrium felix-femina,* and *Carex deweyana.*

The Alnus rubra *community (alder flats).*—In the course of colonization of the river terraces the first stable community dominated by trees is the *Alnus rubra* community, which started on gravel bars. Maximum age of the pure form of the *Alnus* community is 65 to 75 yr. This correlates well with the

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TABLE 1. Mean composition of the tree layers for the five forest communities in the Hoh Valley. Density, frequency, and basal-area data are for all trees larger than 4 cm dbh. The *Acer macrophyllum* community represents data from one stand

Species	Trees/ha	% frequency	m^2/ha
Alnus rubra community (alder flat)			
Alnus rubra	763.0	100	36.4
Picea sitchensis	21.7	32	0.8
Populus trichocarpa	7.9	8	1.6
	792.6		38.8
Picea sitchensis–Acer macrophyllum–Populus trichocarpa community (first terrace)			
Picea sitchensis	100.8	80	19.8
Acer macrophyllum	81.0	72	11.6
Populus trichocarpa	65.2	64	14.8
Alnus rubra	10.9	16	1.2
Pseudotsuga menziesii	5.9	16	1.4
Tsuga heterophylla	4.0	8	1.6
	267.8		50.4
Acer macrophyllum community (second terrace)			
Acer macrophyllum	34.6	100	27.0
Picea sitchensis	7.4	20	2.0
	42.0		29.0
Picea sitchensis–Tsuga heterophylla community (second terrace)			
Picea sitchensis	116.6	100	15.6
Tsuga heterophylla	102.8	84	21.2
Acer macrophyllum	10.9	16	2.0
	230.3		38.8
Tsuga heterophylla community (third terrace)			
Tsuga heterophylla	216.2	100	33.5
Picea sitchensis	50.7	80	24.8
Pseudotsuga menziesii	1.2	8	0.5
	268.1		58.8

most recent (1800–1850) ice advance on Mt. Rainier. Stands older than this show invasion by other trees.

Alnus rubra is the single important tree species in this community (Table 1). Density ranges from 1140 trees/ha in young stands to 400 trees/ha in old stands, with a mean of about 800 trees/ha. *Alnus* will not maintain itself in this situation. Instead the community will gradually be dominated by *Picea sitchensis* and *Acer macrophyllum*, which are plentiful in the small size classes (Table 2).

The understory of the *Alnus* community is typically grassy with trailing vines. *Rubus ursinus* and *R. spectabilis* are the most common shrubs, while *Agrostis alba, Elymus glaucus,* and *Poa trivalis* account for most of the total herbaceous cover (Table 3). Mosses are almost completely absent, save for *Mnium punctatum* and *Eurynchium oreganum* on downed logs.

The Picea sitchensis–Acer macrophyllum–Populus trichocarpa *community (first terraces)*.—This terrace corresponds to the 1540–1635 ice advance on Mt. Rainier. It supports the most heterogeneous canopy layer of the five forest communities investigated in this study. *Picea sitchensis* dominates the forest, with *Acer macrophyllum* and *Populus trichocarpa* abundant (Table 1). Mean tree density is about 268 trees/ha. *Alnus rubra* and *Pseudotsuga menziesii* are present as relics of earlier stands or from blowdown invasion. *Tsuga heterophylla,* by contrast, begins to enter the seral pattern at this point. The climax species in this part of the Olympics, it is represented by scattered smaller individuals and some reproduction on downed logs. Because there are numerous seedlings of *Picea sitchensis, Acer macrophyllum,* and *T. heterophylla* (Table 2), these species will maintain a prominent position on these sites with time.

The understory of first-terrace communities demonstrates a grass–forb structure. *Agrostis alba* and *Poa trivalis* together maintain the grass component of the herb layer, with *Oxalis oregana, Polystichum munitum,* and *Circaea alpina* the most important forbs (Table 3). *Rhytidiadelphus loreus, R. triquetrus,* and *Eurynchium oreganum* are common mosses. *Acer circinatum* is abundant in the shrub layer (Table 3), but in this community it is a small understory shrub, different from the large, heavy-limbed plant found on the next higher terrace.

The Picea sitchensis–Tsuga heterophylla *community (second terraces)*.—This is a relatively stable community, presenting a noticeable contrast to the lower order communities. Dominant *Picea* are at least 500 to 600 yr old, which corresponds to the 1217–1363 ice advance on Mt. Rainier. *Picea sitchensis* and *Tsuga heterophylla* dominate the canopy layer. *Picea* has a higher density and frequency, *Tsuga* a greater basal area (Table 1). The greater number of *Tsuga* in the 11–60-cm dbh range accounts for the higher basal area, and also indicates the eventual dominance of *Tsuga* on these sites (Table 2). *Acer macrophyllum* is found in this community, but the species is present in low numbers.

The tall shrub layer is dominated by *Acer circinatum*, but there is significant cover of *Vaccinium* spp. and *Rubus spectabilis* (Table 3). *Acer circinatum* can be exceedingly dense, especially near channels of periodic creeks. Grasses are largely absent from the herb layer, which is now dominated by *Oxalis oregana* and the mosses *Eurynchium oreganum, Rhytidiadelphus loreus,* and *Hylocomium splendens. Polystichum munitum, Tiarella unifoliata,* and *Athyrium felix-femina*; numerous other herbs of lower frequency and cover round out the herb layer (Table 3).

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TABLE 2. Size class distribution for mean number of trees/ha in the five forest communities in the Hoh Valley

Species	0–30 cm tall	30 cm tall –4 cm dbh	4–10 cm dbh	11–30 cm dbh	31–60 cm dbh	61–90 cm dbh	91–120 cm dbh	120 cm + dbh
Alnus rubra community (alder flat)								
Alnus rubra	–	–	57.3	558.4	147.3	–	–	–
Picea sitchensis	98.8	–	10.9	7.9	3.0	–	–	–
Populus trichocarpa	–	–	–	–	3.0	4.9	–	–
Acer macrophyllum	494.2	–	–	–	–	–	–	–
Picea sitchensis–Acer macrophyllum–Populus trichocarpa community (first terrace)								
Picea sitchensis	1581.4	217.4	36.6	11.9	22.7	20.8	8.9	–
Acer macrophyllum	1680.3	–	3.0	49.4	28.7	–	–	–
Populus trichocarpa	–	–	–	12.8	34.6	16.8	1.0	–
Alnus rubra	–	–	1.0	4.9	4.9	–	–	–
Pseudotsuga menziesii	–	–	–	2.0	3.0	–	1.0	–
Tsuga heterophylla	296.5	–	–	2.0	2.0	–	–	–
Acer macrophyllum community (second terrace)								
Acer macrophyllum	–	–	–	–	–	14.8	17.3	2.5
Picea sitchensis	–	148.3	–	7.4	–	–	–	–
Picea sitchensis–Tsuga heterophylla community (second terrace)								
Picea sitchensis	8994.4	721.5	74.1	6.9	3.0	10.9	11.9	9.9
Tsuga heterophylla	11267.8	89.0	3.0	48.4	32.6	16.8	1.0	1.0
Acer macrophyllum	–	–	1.0	4.0	5.9	–	–	–
Tsuga heterophylla community (third terrace)								
Tsuga heterophylla	19273.8	654.8	21.0	96.4	56.8	27.2	13.6	1.2
Picea sitchensis	7165.9	568.3	16.1	–	3.7	9.9	12.4	8.6
Pseudotsuga menziesii	–	–	–	–	–	–	–	1.2

The Acer macrophyllum *community.*—This community commonly occupies rockslides where second terraces contact the valley wall. Other sites are convex domes on second terraces. These probably represent old landslides, dating from when the river was against the valley wall, and constitute a younger land surface than the second terrace with which they are associated. Most stands of *A. macrophyllum* are not sizeable, but one located about 1.5 km from the Hoh Ranger Station is extensive enough to sample according to the methods used on other terraces. The composition of this stand is given in Tables 1–3; other stands are similar.

Acer macrophyllum dominates this community, and is over three times as abundant here as on the rest of the second terraces, but not quite half as dense as on first terraces (Table 1). The only other tree in these glades is *Picea sitchensis*, which is encroaching from the surrounding forest on normal terrace soils. With no individuals less than 60 cm dbh, *A. macrophyllum* will not replace itself in this situation; rather the land surface eventually will be dominated by *P. sitchensis* and then by *T. heterophylla* (Table 2).

The herb layer shows affinities with the various younger communities, with a high coverage of ferns, forbs, and grasses, but a low coverage of mosses. *Polystichum munitum, Oxalis oregana, Agrostis alba,* and *Melica subulata* are the dominant herbaceous species (Table 3).

The Tsuga heterophylla *community (third terraces).*—Present-day third terraces, and ridges off the valley wall in similar position, are dominated heavily by *Tsuga heterophylla* (Table 1). This is the climax forest; it occurs on the surface formed by the original valley fill. The forest is dense for valley bottoms (268 trees/ha; Table 1), yet is more open than other forests in the mountains (Fonda and Bliss 1969). With 216 trees/ha, *Tsuga heterophylla* is present in density counts higher than any other species in any other community, save for *Alnus rubra* on the alder flats (763 trees/ha). *Picea sitchensis*, by contrast, is present at the lowest density (50 trees/ha) of any high frequency tree species in any community (Table 1). *Picea* in this community is represented by a few very large individuals (> 60 cm dbh) and abundant reproduction (Table 2).

The understory of the *Tsuga heterophylla* community is not much different from the *Picea–Tsuga* community, except for the low cover of *Acer circinatum* (3%; Table 3). Shrub composition is about the same as in the second-terrace community, although percent cover may be a bit lower in response to the heavy reproduction of the canopy trees. Herb

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TABLE 3. Mean composition of the understory for the five forest communities in the Hoh Valley. Only those species that had at least 1% cover in at least one community are listed. C = % cover; F = % frequency

Species	*Alnus rubra*		*Picea sitchensis–Tsuga heterophylla–Populus trichocarpa*		*Acer macrophyllum*		*Picea sitchensis–Tsuga heterophylla*		*Tsuga heterophylla*	
	C	F	C	F	C	F	C	F	C	F
Shrub layer										
Rubus ursinus	14.4	76	2.5	40	0.5	20	3.5	8	–	–
Rubus spectabilis	9.5	56	1.6	24	1.0	40	4.3	36	1.2	24
Acer circinatum	–	–	15.1	52	59.5	100	32.3	80	3.0	25
Rubus leucodermis	–	–	1.7	12	–	–	–	–	–	–
Rosa nutkana	–	–	1.5	4	–	–	0.1	4	–	–
Vaccinium ovalifolium	–	–	0.1	4	–	–	5.4	40	2.9	80
Vaccinium parvifolium	–	–	0.3	12	–	–	2.7	48	1.3	80
Herbaceous layer										
Mosses	7.0	80	18.2	96	5.0	100	53.1	96	72.3	100
Agrostis alba	52.9	100	22.6	52	11.5	80	1.0	20	1.9	25
Elymus glaucus	32.5	80	3.1	44	0.5	20	0.1	4	–	–
Poa trivalis	29.6	96	24.5	68	–	–	–	–	–	–
Oxalis oregana	11.2	68	30.6	96	14.0	80	41.6	100	35.4	85
Polystichum munitum	1.5	40	22.3	88	19.0	100	22.4	76	2.6	30
Tiarella unifoliata	0.1	4	8.6	56	0.5	20	20.2	96	15.3	80
Rubus pedatus	–	–	–	–	–	–	8.6	40	13.6	45
Pteridium acquilinum	–	–	–	–	0.5	20	–	–	15.8	40
Circaea alpina	5.5	64	14.4	92	7.5	100	1.5	20	–	–
Stachys mexicana	12.5	88	9.2	80	–	–	0.1	4	–	–
Stellaria crispa	10.8	84	3.0	60	–	–	1.7	28	0.4	15
Athyrium felix-femina	0.3	12	0.6	24	0.5	20	10.5	56	2.6	30
Galium triflorum	0.8	32	8.2	72	4.5	80	1.0	20	–	–
Bromus sitchensis	2.2	28	7.0	64	–	–	1.5	20	–	–
Montia sibirica	6.3	92	4.3	72	3.5	40	1.5	40	1.8	20
Rumex crispus	6.1	48	0.5	20	1.0	40	–	–	–	–
Carex deweyana	0.2	8	6.6	84	7.0	80	4.8	56	1.0	20
Lactuca serriola	2.8	52	6.4	80	7.0	80	2.2	12	–	–
Adenocaulon bicolor	–	–	6.4	80	4.5	80	0.8	12	–	–
Trisetum cernuum	1.4	16	0.7	28	–	–	4.6	64	5.0	50
Maianthemum dilatatum	–	–	0.5	20	–	–	3.7	48	5.5	70
Blechnum spicant	–	–	0.1	4	–	–	2.9	20	5.8	60
Cornus canadensis	–	–	–	–	–	–	0.5	4	5.8	15
Ranunculus repens	4.6	32	3.7	12	–	–	–	–	–	–
Prunella vulgaris	2.7	48	4.6	64	–	–	–	–	–	–
Galium aparine	2.1	44	4.5	44	7.0	80	–	–	–	–
Gymnocarpium dryopteris	–	–	–	–	–	–	4.0	24	3.6	25
Dryopteris austriaca	–	–	–	–	–	–	1.0	8	4.5	35
Luzula parviflora	–	–	3.3	72	–	–	3.0	60	3.8	50
Oenanthe sarmentosa	2.8	48	1.3	12	–	–	–	–	–	–
Mimulus dentatus	1.9	36	2.0	40	–	–	–	–	0.1	5
Achlys triphylla	–	–	–	–	–	–	0.2	8	2.8	15
Stellaria simcoei	0.8	12	1.4	16	–	–	–	–	–	–
Melica subulata	0.6	4	1.2	28	14.0	80	0.6	4	–	–
Trifolium repens	0.1	4	1.0	20	–	–	–	–	–	–
Clintonia uniflora	–	–	–	–	–	–	0.2	8	1.0	15
Hydrophyllum tenuipes	–	–	–	–	2.0	80	–	–	–	–
Tolmiea menziesii	–	–	–	–	6.0	40	–	–	–	–
Fragaria virginiana	–	–	–	–	7.5	20	–	–	–	–
Rumex acetosella	–	–	–	–	3.0	20	–	–	–	–

layer composition shows dominance by mosses, with *Eurynchium oreganum* the most important, followed by *Rhytidiadelphus loreus*. There are only four important vascular species: *Oxalis oregana, Tiarella unifoliata, Rubus pedatus,* and *Pteridium acquilinum* (Table 3).

Valley wall forests.—There is a considerable difference between forests on the valley wall and those of the river terrace sere. In addition to visiting many others I sampled five valley wall stands upon which the following is based. Forests on the valley wall are dominated by *Thuja plicata* and *Tsuga heterophylla*, with varying percentages of *Pseudotsuga menziesii*. These three species are especially important in the canopy of forests on south-facing slopes. On north-facing slopes *P. menziesii* is not as common; instead *Abies amabilis* may be abundant. In seepage areas and in gullies, a few *Picea sitchensis* may occur.

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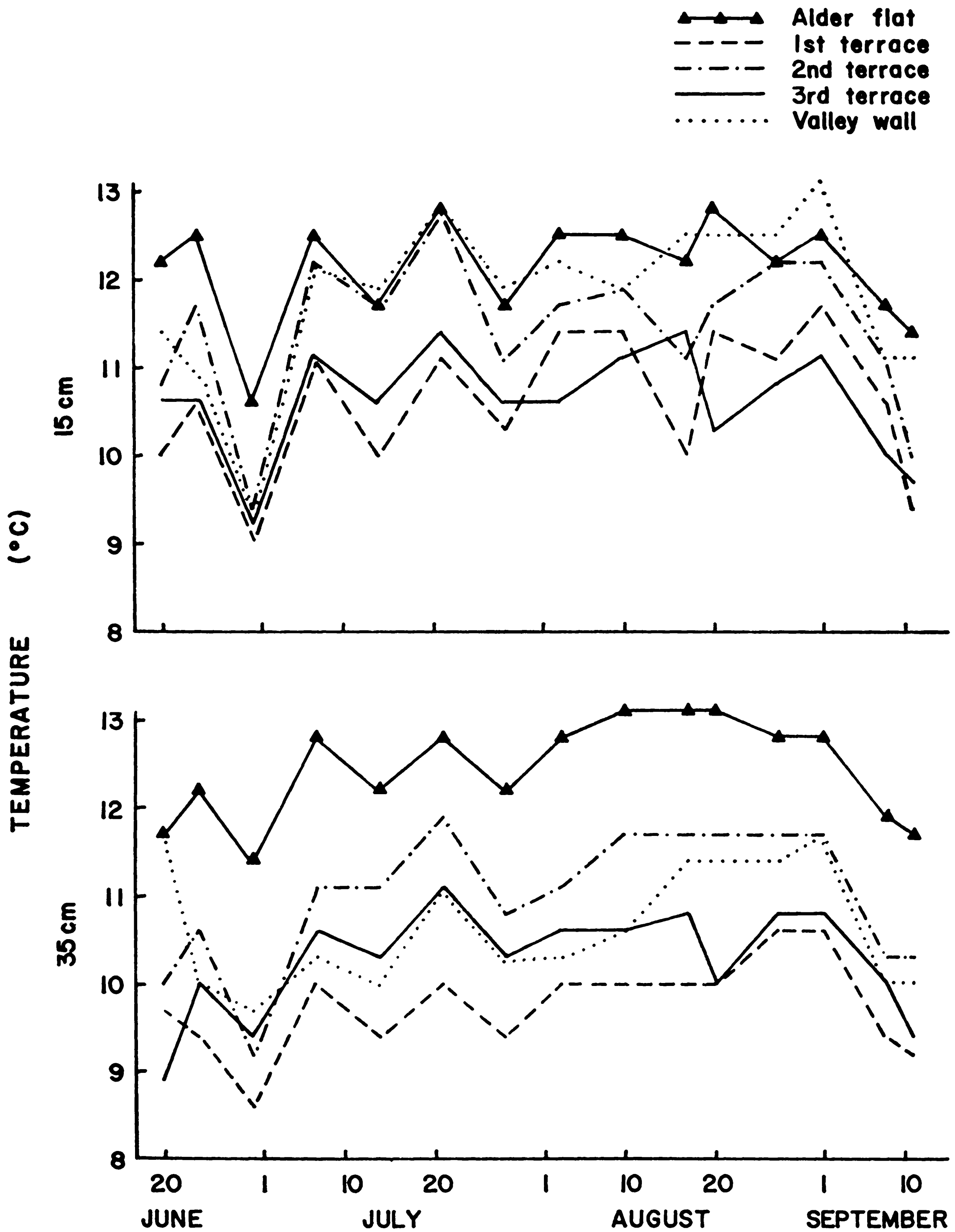

FIG. 2. Soil temperature regime during summer 1970 at 15 and 35 cm. Data are shown for river terraces and the valley wall.

The understory of the valley wall resembles that of montane stands (Fonda and Bliss 1969). The well-developed shrub layer is a mixture of *Gaultheria shallon, Vaccinium parvifolium, V. ovalifolium, Berberis nervosa,* and *Rubus spectabilis. Gaultheria shallon* and *V. parvifolium* dominate the drier south-facing slopes, whereas *V. ovalifolium* and *R. spectabilis* dominate the moister north-facing slopes. The

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TABLE 4. Mean monthly air (+60 cm) temperature (°C) recorded on thermographs in the Hoh Valley during summer 1970. Values for June are based on 12 days of observation; for September on 10 days

Month	Alder flat	First terrace	Second terrace	Third terrace	Valley wall
June	14.1	14.1	15.0	16.3	13.0
July	–	15.0	15.3	15.4	13.7
August	–	14.8	15.3	14.7	13.8
September	–	11.3	11.5	11.8	10.4

herb layer is sparse, as in montane stands. The mosses *Hylocomium splendens* and *Rhytidiadelphus loreus* supply most of the plant cover, with *Oxalis oregana, Polystichum munitum, Tiarella unifoliata,* and *Blechnum spicant* the most abundant vascular plants.

Physical environment

Temperature.—Monthly mean air temperatures are given in Table 4. Figure 2 shows seasonal trends in soil temperature at 15 and 35 cm. Air temperatures were analyzed statistically by a paired *t*-test (Woolf 1968:76) of all possible combinations of data from thermograph daily means. The same test was used on soil temperature data from weekly thermistor readings. The critical region on which decisions of significance were made was set at the 1% level.

Air temperatures on the first terrace are significantly lower than those on the second and third terraces in June and September. At no other times were there significant air temperature differences among stations on the valley floor (Table 4). Air temperature at the valley-wall station was significantly lower than at any stations on the valley floor throughout the summer .

The highest soil temperatures occurred on alder flats, followed by second and third terraces, with lowest temperatures on first terraces (Fig. 2). Input of cooler water from precipitation on 30 June, 26 July, and 8 September lowered soil temperatures for a period of time. September rainfall brought soil temperatures on first, second, and third terraces to about the same point (9.5°C). Although the valley wall air temperatures are significantly lower than any of the valley floor stations, soil temperatures appear to be intermediate. Soil temperatures on the valley wall are not significantly different from those on the alder flats at 15 cm, nor from those on second and third terraces at 35 cm. Otherwise, all data in Fig. 2 are significantly different.

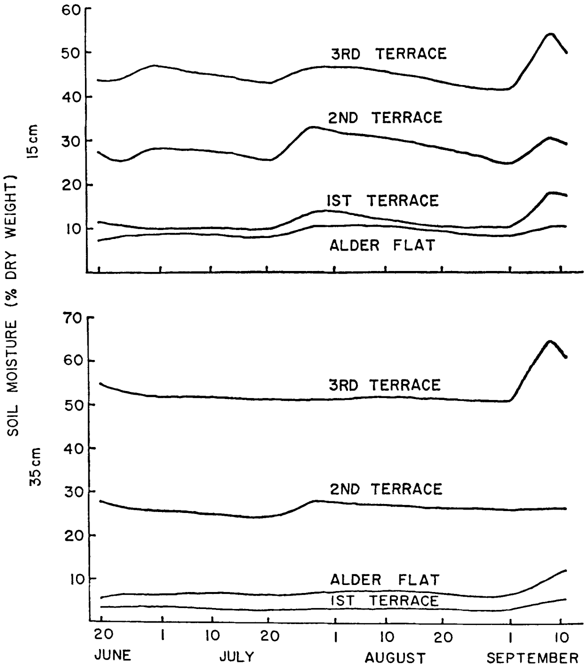

FIG. 3. Soil moisture regime at 15 and 35 cm on the river terraces in the Hoh Valley, summer 1970. Each site is significantly different (1% level) from all others.

Precipitation.—Precipitation data for summer 1970 are shown in Table 5. A comparison with the U.S. Weather Bureau station at Hoh Ranger Station is provided for 1970 and 1971. Precipitation is usually evenly distributed to the summer months, as in 1971, but this was not the case in 1970. The western Olympics experienced a severe drought during summer 1970, with only 86.8 mm of precipitation between 18 June and 31 August (Table 5). Only three times during this period (26–29 June; 24–28 July;

TABLE 5. Precipitation (mm) recorded in the Hoh Valley during summer 1970. USWB = U.S. Weather Bureau Station located at Hoh Ranger Station

Period	Alder flat	First terrace	Second terrace	Third terrace	Valley wall	USWB 1970	USWB 1971
18–30 June	16.8	17.3	16.0	15.0	9.2	16.2	70.6
1–31 July	44.2	41.1	35.2	35.8	35.2	49.8	70.0
1–31 August	17.5	12.4	11.9	11.9	11.2	20.8	68.4
1–10 September	97.2	93.2	85.1	85.1	67.1	106.9	65.4
Total (18 June–31 August)	78.5	70.8	63.1	62.7	55.6	86.8	209.0
% of USWB 1970 (based on total for summer)	90	85	77	77	63	100	140

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TABLE 6. Descriptions of soils found under the four major communities in the Hoh Valley

Community	Horizon	Depth (cm)	Color	Texture	Structure
Alnus rubra community (alder flat)	A	0–7(8)	Very dark gray (10 yr 3/1) to black (5 yr 2/2)	Sand to sandy loam	Single grain to fine weak crumb
	C_1	7–60(90)	Black (5 yr 2/2)	Sandy loam	Single grain
	C_2	60+	—	River cobbles and gravels	—
Picea sitchensis–Acer macrophyllum–Populus trichocarpa community (first terrace)	O_1	1–0	—	Fresh litter	—
	A	0–8(10)	Very dark gray (10 yr 3/1)	Loamy sand	Compact single grain to weak crumb
	B	8–22(23)	Very dark gray (5 yr 3/1)	Loamy sand to sandy loam	Single grain to weak crumb to very weak subangular blocky
	C_1	23–41(42)	Black (5 yr 2/2)	Loamy sand	Single grain
	C_2	41+	—	River cobbles and gravels	—
Picea sitchensis–Tsuga heterophylla community (second terrace)	O_1	2–0	—	Fresh litter	—
	A_1	0–8(16)	Dark brown (10 yr 3/3)	Loamy sand to silt loam	Moderate crumb
	A_2	trace	Dark gray (10 yr 4/1)	—	—
	B_1	8–26(46)	Dark brown (10 yr 3/3) to very dark gray (5 yr 3/1)	Loamy sand to sandy loam	Crumb to weak subangular blocky
	B_2	26–40(57)	Very dark gray (5 yr 3/1)	Sandy loam to loam	Weak crumb
	C_1	40–120(150)	Black (5 yr 2/2)	Sand to loamy sand	Fine to moderate single grain
	C_2	120+	—	River cobbles	—
Tsuga heterophylla community (third terrace)	O_1	(10)8–0	—	Fresh litter	—
	A_1	0–5(6)	Very dark grayish brown (10 yr 3/2) to dark yellowish brown (10 yr 3/4)	Sandy loam	Weak crumb
	A_2	trace	Dark gray (10 yr 4/1)	—	—
	A_3	5–35(40)	Dark yellowish brown (10 yr 4/4)	Sandy loam	Crumb to weak subangular blocky
	B_2	35–104(108)	Dark brown (10 yr 3/3) to yellowish brown (10 yr 5/4)	Sandy loam	Weak subangular blocky
	B_3	104–134(150)	Dark brown (10 yr 3/3) to dark yellowish brown (10 yr 4/4)	Sandy loam to silty clay loam	Single grain
	C	134+	Dark brown (10 yr 3/3) to dark yellowish brown (10 yr 4/4)	Sandy loam to silty clay loam	Massive, but breaks irregularly subangular blocky

1 August) was any amount of rain dropped in the valley. The drought finally ended the first week of September, and it is noteworthy that more rain (106.9 mm) was received during that period than the previous 10 wk of this study (Table 5). Table 5 also provides an indication of the amount of throughfall to the forest floor. Gauges in the more open stands on alder flats and first terraces caught more rain in every measuring period than did those on second and third terraces.

Soil formation and development.—This is a most important environmental event taking place in relation to forest succession. Extremely faithful correspondence of profile development with plant-community composition occurs through the Hoh and in other valleys of the western Olympics. Composite profile descriptions of the soils under each terrace community are given in Table 6.

The *Alnus rubra* community occurs on soils with little profile development. The A horizon is quite

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TABLE 7. Chemical and physical properties of soils of the four terrace levels in Hoh Valley, at three different depths. Data given are means from two soil pits on each terrace level. MRV = moisture retention value

Property	Alder flat	First terrace	Second terrace	Third terrace
		Depth = 4 cm		
% nitrogen	0.77 ± .73	0.20 ± .05	0.14 ± .03	0.47 ± .13
% phosphorus	0.58 ± .03	0.70 ± .05	0.47 ± .06	1.08 ± .17
% organic matter	4.5 ± 1.4	7.2 ± 1.6	5.5 ± 1.0	18.6 ± 9.3
% clay	5.0 ± 2.0	4.8 ± .7	8.4 ± .8	15.1 ± 3.0
pH	5.0 ± .2	4.9 ± .3	4.5 ± .1	4.0 ± .1
% water @ 0.3 bar	11.5 ± 8.3	19.9 ± 3.2	26.9 ± 1.4	47.9 ± 6.1
% water @ 15 bars	3.1 ± 2.1	8.3 ± 2.5	7.2 ± .2	23.1 ± 6.5
MRV	7.4 ± 5.2	11.6 ± .8	19.7 ± 1.7	24.8 ± .4
		Depth = 20 cm		
% nitrogen	0.06 ± .02	0.03 ± .02	0.07 ± .02	0.16 ± .02
% phosphorus	0.64 ± .05	0.67 ± .02	0.48 ± .11	0.73 ± .11
% organic matter	3.5 ± .2	4.4 ± 0	4.5 ± .6	6.9 ± .3
% clay	6.0 ± 1.3	7.0 ± 2.3	5.6 ± 1.6	18.9 ± 0
pH	4.7 ± 0	5.0 ± .2	4.8 ± .1	4.4 ± .2
% water @ 0.3 bar	12.3 ± 3.4	12.4 ± 5.8	10.1 ± 2.8	39.1 ± 1.3
% water @ 15 bars	2.7 ± .7	3.3 ± 1.2	2.9 ± 1.5	20.2 ± 2.0
MRV	9.6 ± 2.7	9.1 ± 4.6	7.2 ± 1.3	18.9 ± 3.2
		Depth = 40 cm		
% nitrogen	0.06 ± .02	0.05 ± 0	0.04 ± .01	0.10 ± .01
% phosphorus	0.64 ± .05	0.63 ± .01	0.34 ± .03	0.55 ± .11
% organic matter	3.5 ± .2	3.5 ± .4	3.4 ± .5	3.6 ± .2
% clay	6.0 ± 1.3	4.7 ± .2	3.2 ± .8	20.5 ± 5.1
pH	4.7 ± 0	5.1 ± .1	4.9 ± .1	4.9 ± .2
% water @ 0.3 bar	12.3 ± 3.4	7.8 ± 1.0	5.2 ± 2.1	37.6 ± 1.7
% water @ 15 bars	2.7 ± .7	2.2 ± .1	1.2 ± .3	12.8 ± 1.2
MRV	9.6 ± 2.7	5.6 ± .9	4.1 ± 1.9	23.8 ± .3

shallow; the bulk of the profile is represented by the C horizon, with river cobbles within 60 to 90 cm of the surface under the older stands. Young stands have much thinner soils.

The soils are slightly better developed under the *Picea sitchensis–Acer macrophyllum–Populus trichocarpa* community. Although the A horizon is about the same thickness (8 cm) as in the *Alnus* community, a weakly developed B horizon is now present. In the two soil pits dug, mean depth to river cobbles (41 cm) is less than on the alder flats, indicating a shallower valley fill, or greater erosion or both.

The *Picea sitchensis–Tsuga heterophylla* communities on second terraces show greater accumulation of top soil over the river cobbles (Table 6). The A horizon varies from 1 to 16 cm in depth, and a trace of an A_2 layer can sometimes be found. The B horizon is considerably thicker (32 cm) than on first terraces, and more strongly developed with two recognizable subhorizons. Depth to river cobbles is well over 100 cm on the second terraces.

The soils of the *Tsuga heterophylla* community developed in glacial till. These soils have stronger profile development, thicker horizons, and heavier structure. Texture varies from sandy loams to silty clay loams, compared to sands and loamy sands of lower terraces. Occasionally layers of water-worked sands and pebbles alternate among the horizons composed of fine materials. The thick B_2 horizon may be divided into three subhorizons for convenience in handling analyses, but the differences are slight.

The trend in soil development is portrayed well in the descriptions in Table 6. Soils on young land surfaces are scarcely differentiated in horizons. Older land surfaces show emerging development of B horizons. Structure changes from single grain sands to subangular blocky with the accumulation of clays in the profile. The heaviest texture encountered was the silty clay loam in the C horizon on the third terrace, representing an increase of clay from 7% on the alder flats to 28% on the third terrace. Colors in the profiles become more reddish and brown with the addition of organic matter and clays to the black river sands.

Soil chemistry.—There are some variations in trends of soil properties across the terraces, but a general pattern relative to soil development can be seen in Table 7. Long term soil development is the strongest indicator of succession in this valley. Because this involves a change in total nutrients added to, and incorporated in, an originally sterile substrate, the data in Table 7 show percentages of nitrogen and phosphorus, rather than the more commonly expressed milliequivalents.

Soil properties that tend to increase with terrace age are phosphorus, organic matter, clay, water (held at 0.3 and 15 bars), moisture retention value (MRV), and acid content of the soil solution (decrease in

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pH). Nitrogen also shows an increase with terrace age when the 20 and 40 cm depths are considered; only at 4 cm is there an anomalous pattern. Note, however, that the actual values for nitrogen at 20 and 40 cm are lower than percentages at 4 cm (Table 7). This may reflect the trend for nutrients to become intrabiotic with time, and that only in the zone of active decomposition are nitrogen compounds free in the soil. Nitrogen is high on alder flats. Nitrogen enters roots of *Alnus rubra* via nitrogen-fixing bacteria, and subsequent leaf fall and decomposition adds nitrogen to the soil. Phosphorus percentages show subtle shifts from terrace to terrace, but the values are generally in the range of 0.5% to 0.7%. In all but one case, percentage of phosphorus is much higher than nitrogen (Table 7).

Soil moisture.—Data on percent soil moisture were analyzed statistically by the paired *t*-test (Woolf 1968:76); all possible combinations at 15 and 35 cm were compared, with the critical region at the 1% level. Seasonal values for each terrace were significantly different from those on all other terraces, for both 15- and 35-cm depths (Fig. 3). At 35 cm there was little change during the summer from the values of mid-June following major draw-down, until recharge began in September. Soil moisture at 15 cm was more strongly affected by precipitation, and use by the dense ground flora in the forest, than at 35 cm. The prominent humps in the curves at 30 June, 28 July, and 8 September mark measurements made after periods of rain during the summer (Fig. 3). This added water had little effect on soil moisture at 35 cm.

Youthful soils retained 10% to 20% water at 0.3 bar, compared to heavier-textured mature soils that held over 37% water (Table 7). The same separation holds for 15 bars, at which soils on the alder flats, first, and second terraces held 2% to 3% water. Third-terrace soils retained about 20% water in the upper horizons, and 10% to 13% in the deeper soil (Table 7). Within a given soil there is a decrease in moisture retention with depth, as sands and gravels are approached.

Gravimetric samples taken in April 1971 showed the following soil-moisture values, progressing from alder flat to the third terrace: at 15 cm, 30.6%, 30.5%, 32.5%, 52.0%; at 35 cm, 23.1%, 11.6%, 59.1%, 67.2%. All soils, therefore, reach field capacity with the winter rains, and plants begin growth in spring with fully available water.

Discussion

Zonal pattern of vegetation

From fresh gravel bars to fully developed land surfaces in the Hoh Valley the sere comprises four discrete communities. The successional sequence can be interpreted from the zonal pattern on present-day land surfaces of varying ages. The *Alnus rubra* community on alder flats is the earliest forest in the sequence. These surfaces are about 80–100 yr old. First terraces, which arose about 400 yr ago, are occupied by the *Picea sitchensis–Acer macrophyllum–Populus trichocarpa* community. Second terraces were exposed by the river about 750 yr ago. Today these sites support the *Picea sitchensis–Tsuga heterophylla* community. These three communities occur on land surfaces derived through the erosional activity of the Hoh River on Neoglacial alluvial fills. Third terraces, formed in the till deposited by the retreating alpine glaciers in Pleistocene, represent the oldest land surface in the valley bottom. These sites support the climax *Tsuga heterophylla* community.

These differences in parent material are insufficient to cause different forest communities to be restricted to certain terraces in their distribution, although they are confined to the valley bottoms. Forests on the valley wall are totally different in origin, species composition, and physiognomy. In the valley bottom there is a clear progression leading from *Alnus rubra* to *Tsuga heterophylla* as the dominant tree in the climax community on the valley floor. The greater number of seedlings of *T. heterophylla* in the *Picea–Tsuga* community show that *P. sitchensis* will be replaced as the dominant canopy tree (Table 2). This is consistent with what is known silviculturally about the trees in the Pacific Northwest (U.S. Forest Service 1965, Franklin and Dyrness 1973). Shifts in understory composition parallel those in the tree layer.

To detail this zonal change in composition and growth form associated with terrace levels, a 600- × 12-m transect was taken from the river to the third terrace (Fig. 4). All trees and *Acer circinatum* larger than 2.5 cm dbh within 6 m of the centerline were tallied by species, and the data expressed as trees per hectare. Shrub, forb, grass, and moss growth forms were tallied at each 1-m interval, with the data shown as number of contacts per 25-m segment of line. Because there is no spot where a single line can be extended across all four terraces with good forest development on each, this transect was in two parts: the first 150 m across an alder flat, with the remaining 450 m across contiguous first, second, and third terraces. Bliss and Cantlon (1957) used a transect to show zonal patterns in willow communities along the Colville River in Alaska, and Wistendahl (1958) did the same for floodplain vegetation on the Raritan River, New Jersey.

There was a successive change from trees that tolerate open, drier sites to trees that require more moisture and tolerate shade with an increase in terrace height. Beginning with the dense stands of

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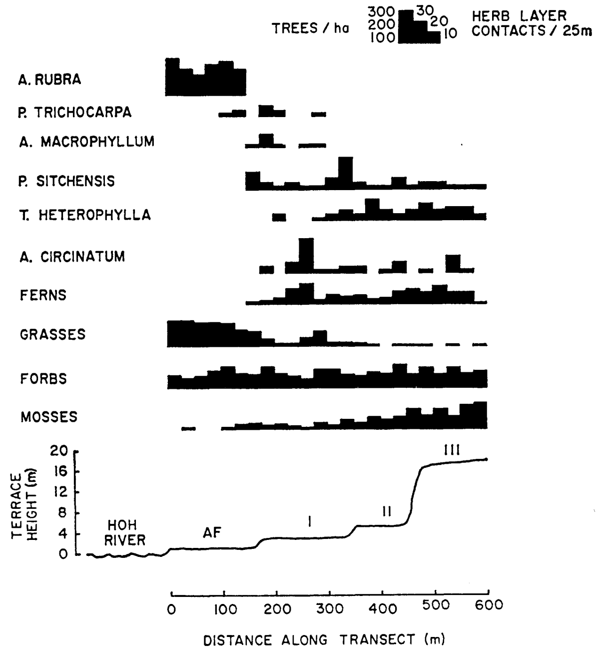

FIG. 4. A transect from the Hoh River to midway on the third terrace, showing distribution of trees and understory species, terrace height profile, and distance from the river. Data for trees and for *Acer circinatum* are expressed as trees/ha, while those for understory species are expressed on contacts at 1-m intervals for each 25-m segment of line as shown in legend.

Alnus rubra, the transect intercepted in turn *Populus trichocarpa, Acer macrophyllum, Picea sitchensis*, and finally the climax species *Tsuga heterophylla* (Fig. 4). *Acer circinatum* occurred irregularly, consistent with the sprawling tangles in which it grows. Along the entire 600 m only 17 contacts were made with shrub species, but these are not shown in Fig. 4. Shrubs are clearly a minor component in these communities. I have found a third terrace stand in the Queets Valley, however, in which *Vaccinium ovalifolium* and *V. parvifolium* are more abundant than in the Hoh Valley stands.

The herbaceous layer varied sharply across terraces. The trend towards ultimate dominance of mosses, especially *Eurynchium oreganum*, is easily seen in Fig. 4 and Table 3. Grasses dominated the lower terraces, but rapidly dropped out in the forests with a denser canopy. Mosses increased as the grasses diminished. Forbs tended to remain constant, although Table 3 indicates a floristic shift. Ferns increased in density on first, second, and third terraces, and this largely reflects the changing ground surface. Sterile, coarse, sandy soil on the alder flats progressively improves to decaying litter and loams with abundant litter on second and third terraces. It also reflects a shift in forest energetics from a producer-based grazing food chain on alder flats and first terraces to a detritus-based food chain on second and third terraces.

The data in Tables 1–3 and in Fig. 4 show that distinct groupings of plant species are associated with definite river-terrace levels in this valley. Here is a dynamic system that is continually changing in relation to the activities of the river and the development of soil surfaces with time. This long-term seral sequence is a result of the coincidence of two factors: the life span of the dominant species and the life span of a given land surface as the river does its work in the valley.

The *Acer macrophyllum* community is the only anomaly in the zonal patern. This represents a younger seral stage on disturbed substrates. The interesting feature of this community is not that there is an unusual abundance of *A. macrophyllum*, but rather a general lack of large *Picea sitchensis* or any other tree species to fill in the gaps in the canopy. These open areas are created by natural disturbance, and they are maintained because there is little pressure on them in the form of invading species. There are few downed and rotting logs on which seedlings can start, so that there is little reproduction of either *P. sitchensis* or *T. heterophylla* in these areas. Nor however, is there any *A. macrophyllum* reproduction. Where a tree from the surrounding forest has fallen into the plot to provide a seedbed, there are seedlings and saplings of *P. sitchensis*, but this must be an exceedingly slow process of invasion. Consistent with other long-term events in this valley, these *Acer macrophyllum* glades will eventually be replaced by coniferous communities.

Environmental gradient

A basic tenet of the present theory of succession is that the organisms themselves modify and gain control of the physical environment (Odum 1969). Fritts et al. (1965) demonstrated control of the moisture variable by forest stands in work with tree-ring response to environmental gradients. Dense stands of trees modify and control the moisture regime. Isolated trees, by contrast, are largely controlled by the physical environment. In the Hoh Valley the increasing modification and control of the physical environment by successively more mature forest stages is clearly seen in the correlation between zonal pattern of vegetation and changes in soil factors. Deeper, more mature soils are found on older land surfaces under the climax *Tsuga heterophylla* and near-climax *Picea sitchensis–Tsuga heterophylla* communities (Table 6). At the same time nutrient content, clay, and organic matter increase as the terrace ages and the vegetation composition shifts; pH decreases with the shift from deciduous to conif-

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TABLE 8. Internal water potential (bars) on a gravel bar and the higher terrace levels in the Hoh Valley. *Alnus rubra* and *Salix scouleriana* were analyzed on the gravel bar on 3 September 1972. *Picea sitchensis* was used for the higher levels, with analyses made on 24 August 1972. Mean values underlined are not significantly different (1% level)

	Gravel bar		Alder flat	First terrace	Second terrace	Third terrace
	Alnus rubra	*Salix scouleriana*		*Picea sitchensis*		
Mean	−12.29	−13.89	−12.17	−11.98	−10.96	−8.99
Range	−11.37 to −13.31	−13.37 to −14.81	−10.21 to −13.38	−11.24 to −13.53	−8.61 to −13.18	−7.04 to −11.73

erous trees (Table 7). The most important change, however, is in moisture balance across the terraces. Significantly more water is retained during the summer on higher terraces; this means that the plants growing there are not subjected to moisture stresses as great as those of the gravel bars, alder flats, and first terraces. The change in moisture balance with distance from the river has been investigated in other studies of riverine zonation, and has been found to be an important controlling factor. Although Lindsey et al. (1961) studied only sand bars, river banks, and the floodplain proper, they found a clear increase in moisture held at 0.3 and 15 atmospheres, and in the moisture retention value, with distance from the river and development of the land surface. Vegetational zonation along the Missouri River was found to be controlled primarily by aeration and constancy of water supply, with more favorable moisture relations under the more stable communities away from the river (Weaver 1960).

The increase in clay and organic matter under more mature forest stages accounts for the increased moisture-holding capacity of the older soils (Table 7). The process of soil development produces significant differences in the ability of the soil to retain water throughout the summer. The only deviation from a progressive increase in stored water with increasing terrace age was seen at 35 cm, where the first terrace soils were significantly drier than those on the alder flat (Fig. 3). As clay content and organic matter increase across the terraces there is a corresponding change in moisture held at 0.3 bar (Table 7). At 20 cm, for example, soils of the *Alnus rubra* community contained 3.5% organic matter, 6.0% clay, and retained only 12.3% water at 0.3 bar. At approximately this same depth soil moisture under this community varied between 8% and 10% during the summer of 1970 (Fig. 3). By contrast, the mature soils under the *Tsuga heterophylla* community had 6.9% organic matter, 18.9% clay, and retained 39.1% water at 0.3 bar (Table 7). Soil moisture at this depth was over 40% all summer (Fig. 3). A similar relationship between clay, organic matter, and moisture retention was found along the Wabash and Tippecanoe Rivers, with higher values found under the more mature stages of forest development (Lindsey et al. 1961).

To further investigate plant response to the moisture gradient, I determined plant internal water potential on a short term basis using a Scholander-type pressure bomb, after the method of Waring and Cleary (1967). On 24 August 1972 water potential was measured in *Picea sitchensis* from the third terrace to the alder flats (Table 8). This is the only species found on all four terrace levels, so that it represented a good control to assess the moisture variable. Young saplings were chosen for measurement, with 6 different trees used at each site. Plants that were growing on logs were not used. All samples were clipped from below 1 m in height from saplings in shade preceding time of clipping. On 3 September 1972 I measured water potential in five seedlings of *Alnus rubra* and *Salix scouleriana* on a gravel bar (Table 8). These plants were in the sun, were less than 2 m tall, the sample coming from less than 1 m off the ground.

The data in Table 8 show a pattern of moisture balance in the plant that corresponds to that in the soil. On these dates only third-terrace trees were significantly different from those on the alder flat and first terrace, based on the paired *t*-test (Woolf 1968:76). But despite the lack of significant differences for all terrace levels, the pattern of plant water potential correlates with the pattern of soil moisture in Fig. 3. Third terraces show the highest potentials, with lower potentials developing as the river is approached. Mean values decrease towards the river, while the range of values increases. The mature communities moderate the environment, thereby showing less variability in this factor compared to the youthful alder flats and first terrace communities.

The values of a number of other environmental factors were determined, but all appear to be secondary to soil moisture. Phosphorus and nitrogen contents increase with terrace age (Table 7), but the percentages of both span the distribution of all tree

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species involved in the zonal pattern. This would indicate that neither is limiting the range of species in the valley. The decrease in soil pH results from the change from deciduous to coniferous species, rather than causing the shift. Air and soil temperature regimes are similar at all stations (Table 4, Fig. 2). The minor differences in either of these factors almost certainly reflect differences in the modification caused by the communities.

The concept of ecocline describes the situation in which the vegetation coenocline varies in parallel with the environmental complex-gradient (Whittaker 1970). Although Whittaker's examples of ecoclines deal with variability through the spatial dimension, time is also a dimension through which vegetation and environment vary in parallel. The communities in the Hoh Valley are an example of vegetation and environment varying through space and time. The correlation among zonation patterns, forest succession, age of terraces, soil moisture, and soil-profile development (increase in clay and organic matter) is in concert not only with Whittaker's concept of ecocline but also with the concept that organisms modify and gain control of their environment (Odum 1969).

Phytogeography

Along the Pacific Coast, forests dominated by *Picea sitchensis* reach to Alaska and merge with the coastal redwoods in southern Oregon. The forests in the western Olmpic river valleys, especially those in which *P. sitchensis* is a prominent tree, are the optimum development of these coastal forests. Franklin and Dyrness (1973) recognized a *Picea sitchensis* Zone in Washington and Oregon, and included both coastal and river valley forests in it. Although *P. sitchensis* is seral to *T. heterophylla*, they suggested that the *P. sitchensis* Zone could be considered a variant of the *T. heterophylla* Zone. The Hoh forests, as represented by the climax *T. heterophylla* community, are different enough from others in the *T. heterophylla* Zone by virtue of floristic composition, history, development, and topographic positioning to warrant subdivision. I believe, therefore, that this is a useful separation; it serves to clarify relationships among the various forests in the Pacific Northwest in which *P. sitchensis* occurs.

The popular term Olympic rain forest has had widespread adoption, primarily because there has been no quantitative inquiry into the structure and dynamics of these forests. The *Picea sitchensis–Tsuga heterophylla* community is usually emphasized in writings about the Hoh vegetation, and is incorrectly put forward as the best example of the rain forest. The data in Tables 1–3 coupled with Fig. 4 demonstrate that the vegetation in the valley bottom of the Hoh River cannot be treated as a single homogeneous unit, and that one community no more characterizes the vegetation than another community.

The forests of the Hoh Valley are not rain forests in the most widespread use of the term. Both Richards (1952) and Polunin (1960) set forth the structural characteristics of the tropical rain forest, and it is clear that they bear little resemblance to the Hoh forests. Billings (1970) applied the term temperate rain forest to vegetation on the northwestern Pacific Coast. Polunin (1960) recognized a warm temperate rain forest formation, but referred to the Pacific coastal forest as a principal type in the larger coniferous forest formation. It is important to note that both authors were considering global vegetation patterns, and were treating formations of wider distribution than the Hoh Valley when they used those terms. Differences in their treatments are largely terminological, encumbered perhaps by the abstract use of "rain forest." More recently the term temperate moist coniferous forest was suggested (Billings, *pers. comm.*). This better fits the vegetation of not only the Hoh Valley, but also most of the western Olympics (Fonda and Bliss 1969), and still emphasizes worldwide relations. On a regional scale the significant tie of the Hoh forests with various associations in the Pacific coastal forest formation is more clearly seen when the former are freed of the burdensome term rain forest. And on a local scale it is possible to treat the Hoh climax forest as a more mesic variant of the forest formations in the Olympics, and to show its proper relationship in forest patterning in these mountains.

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