

RIPARIAN FOREST STAND DEVELOPMENT ALONG THE QUEETS RIVER IN OLYMPIC NATIONAL PARK, WASHINGTON

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Abstract. A vegetation chronosequence spanning over 300 years was established in unconstrained reaches of the lower Queets River in Olympic National Park, Washington, USA, for an examination of riparian successional patterns. The Queets is an unconstrained, dynamic, mountain river located within a temperate rain forest environment. Ongoing channel movements create intricate patterns in the physical structure of the valley. Twenty-one plots containing a total of 4359 trees were mapped and measured for structural and crown characteristics. Snags, logs, and understory vegetation were also quantified. Recent alluvial deposits are colonized primarily by early-successional trees *Salix sitchensis* and *Alnus rubra*. Conifer seedlings, primarily *Picea sitchensis*, generally invade after the initial cohort of hardwood trees begins senescence: 20–30 years for *Salix* and 40–60 years for *Alnus*. Through accumulation of sediments from floods and channel downcutting, surfaces become perched above the reach of annual floods after 40–80 years and are then slowly colonized by late successional tree species *Acer circinatum*, *Acer macrophyllum*, and *Tsuga heterophylla*. Diverse, old-growth forests ultimately develop after 200–250 years, containing some of the largest known trees in the Pacific Northwest. However, canopy and stem densities remain lower than comparative *Pseudotsuga menziesii* forests from the nearby Cascade Mountains. Vast individual crowns can develop, with occasional *Picea* up to 25 m wide and 70 m deep. Individual stands may accumulate >200 000 m³/ha of canopy volume—among the highest recorded on earth. Mixed among the generalized successional sequence are variations created by uncommon channel movements. Avulsions followed by channel incision form cobblefields in abandoned channels or other surfaces which are isolated from subsequent inundation and sediment deposition. These cobblefields embark on a different successional trajectory, which often includes conifer seedlings present in the initial cohort. Ultimately, whatever the initial trajectory, soils become productive due to soil conditioning by *Alnus* and the decomposition of other plant material. These biophysical complexities, interconnected patterns, and system-scale resilience are summarized in a multiple-pathway successional model that may be applicable to floodplain riparian forests throughout much of the Pacific coastal ecoregion.

Key words: chronosequence; forest development; Olympic National Park; *Picea sitchensis*; riparian; stand structure; succession; Washington State (USA).

INTRODUCTION

Temperate rain forests along the Pacific coast of North America are the most extensive on the planet—an unbroken swath extending 2000 km from northern California into Alaska. The basic characteristics of the approximately 200 alluvial rivers originating within the Pacific rain forest are being continuously modified by variable and often stochastic physical environments. Forests in alluvial floodplains illustrate how and why riparian ecosystems throughout the Pacific coastal ecoregion are so dynamic and productive (Naiman and Bilby 1998). Interactions between geomorphology, hydrology, sediment, and riparian-derived large wood modify channel morphology and shape the attributes

of riparian forests throughout much of the region (Swanson and Lienkaemper 1982, Naiman et al. 2000, Abbe and Montgomery 2003). An understanding of ecological processes shaping these riparian forests is especially important because it determines the characteristics and fluxes of nutrients and organic matter to streams and estuaries, including large wood. Conversely, riparian-derived materials help shape biotic communities, and underpin processes related to channel morphology, flow conditions, sedimentation, and habitat complexity (Fetherston et al. 1995, Bilby and Bisson 1998, O'Connor et al. 2003). Forest structure and productivity dictate the fundamental characteristics, such as size, type, and amount, of materials that can enter the channel and fuel key biophysical processes.

Coastal temperate rain forests dominated by *Picea sitchensis* (hereafter *Picea*) represent not only the most abundant natural forest formation along the Pacific

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Northwest coast, but also among the most structurally complex. These forest formations hold some of the regions highest biological diversity (Franklin and Waring 1980, Kirk and Franklin 1992, Winchester and Ring 1999, Franklin et al. 2002), which is linked not only to the fluvial disturbance regimes, but also to the presence of enormous trees. Floodplain forests on the Olympic Peninsula contain some of the largest (to 337 m³) and tallest (to 93 m) members of the *Pinaceae* (Van Pelt 2001).

Three decades of research in the Pacific coastal ecoregion have led to significant advances in understanding the production dynamics and ecology of floodplain forests (e.g., Fonda 1974, Naiman et al. 2000, 2005, Balian and Naiman 2005), yet we are still missing how they develop their complex structure, and how this structure interacts with variable flows to modify channel morphology. This knowledge is prerequisite to understanding the interrelationships between structural complexity, biological diversity, and system productivity. Previous studies have focused heavily on mature forests dominated by *Picea*, *Tsuga heterophylla* (*Tsuga*), *Acer macrophyllum*, and *Acer circinatum* (Fonda 1974, McKee et al. 1982, Nadkarni 1984), but the successional pathways generating the structural complexity remain complex when viewed at the floodplain scale.

We know from earlier work that variation in stand structure and evolution is related to temporal and spatial patterns of species establishment. Despite the ultimate dominance by giant conifers, especially *Picea* and coast Douglas-fir (*Pseudotsuga menziesii menziesii*, hereafter *Pseudotsuga*), these species often establish several decades after initial colonization by *Salix* spp. (*Salix sitchensis* and *Salix scouleriana*, hereafter *Salix*), *Alnus rubra* (*Alnus*), and *Populus balsamifera trichocarpa* (*Populus*). The presence of *Alnus* is very important, as symbiotic N fixers (*Frankia*) in its roots quickly enrich mineral soils with nitrogen. Colonization of newly formed alluvial deposits is not uniform, but often starts with patches of seedlings developing behind a protective barrier such as large logs (Van Pelt 1991, Fetherston et al. 1995, Fetherston 2005). Depending on disturbance history, some of these young riparian stands contain abundant *Picea*, while in others this species is absent for several decades. Conifers that do establish during the initial pioneering stage often grow slowly. This is due in part to the scarce soil resources in newly formed gravel bars and exacerbated by shade and root competition with dense grasses and *Alnus* thickets. In dramatic contrast to newly formed bars, riparian soils after several decades of *Alnus* dominance are rich and fertile, and well known for supporting rapid growth rates (Franklin and Waring 1980, Hibbs et al. 1994).

Variation in stand structure and successional processes are also driven by dynamic channel movements in unconfined alluvial rivers (Latterell 2005). Substan-

tial reach-scale cut and fill alluviation on an annual or decadal basis is a hallmark of many rivers in the Pacific coastal ecoregion. Lateral erosion and deposition can be rapid; unconfined alluvial rivers can move many meters in a single year, reshaping the valley floor over a period of centuries to millennia (e.g., O'Connor et al. 2003). A large percentage of the unconstrained portions of the main stems of alluvial rivers may be also avulsive—rivers that are composed of a system of dominant and secondary channels that may repeatedly exchange roles over time through channel avulsion and incision (Richards et al. 1993). In the process, vegetation is undercut and trees topple into the river. The rapid lateral movements and avulsions create a spatially and temporally heterogeneous floodplain forest (Abbe and Montgomery 2003).

Finally, herbivory is important in shaping riparian young forest structure and stand evolution (Ripple and Beschta 2004). The rain forest valleys of the western Olympic Mountains support large and nonmigratory populations of Roosevelt elk (*Cervus canadensis roosevelti*). Large herds inhabit the Queets valley year-round (Ferry et al. 2001). As a result, young *Alnus* stands are often maintained as open, grassy glades by browsing, free of tall shrubs that dominate many Pacific coastal forests. The scope of impacts from these abundant, pervasive herbivores remains largely unknown (Woodward et al. 1994, Riege and del Moral 2004). However, their density and preferential grazing habits are certain to be an important determinant of forest structure and evolution.

We studied the structural development and multiple pathways of succession from a riparian chronosequence spanning more than three centuries. We examined the riparian forests for specific differences among stands on contrasting fluvial landforms and sought explanations for how and why conifers were initial or secondary colonizers in early stand development. Our specific, interrelated research questions were (1) How does vertical and horizontal diversification of the riparian forest develop given the short return interval of fluvial disturbances? (2) Are structurally complex, old-growth, riparian forests inevitable, or are there other potential endpoints? and (3) Are differing fluvial mechanisms responsible for the multisuccessional pathways observed? Finally, a conceptual model was created that incorporates varying successional patterns, time, alluvial landform evolution, and species characteristics.

STUDY SITES

The Queets River is situated on the western Olympic Peninsula in Washington State (47.61° N, 124.06° W). The climate, characterized by cool, wet winters and warm, dry summers, results in only 7% of the annual precipitation occurring during summer months. Starting in mid-October and often extending until mid-June, the rainy season is characterized by large, but mild, Pacific Ocean storms from the southwest (Franklin and

Waring 1980). With the Queets Valley draining the southwest portion of the highest peaks of the Olympic Mountains, the valley is ideally situated to intercept the maximum precipitation, which ranges from >600 cm/yr in the headwaters to an average of 360 cm/yr in its lower reaches.

The Queets River mainstem (drainage area 1153 km²) stretches westward over 80 km from the core of the Olympic Mountains. The glacial headwaters are underlain by marine and volcanic sediments, while the mainstem river courses through a wide alluvial floodplain valley flanked by Pleistocene glacial sediments (e.g., advance deposits, till, marginal, and recessional deposits) and across a coastal piedmont to the Pacific Ocean. Woody debris adds important roughness within these vast deposits of highly transportable glacial sediments (Abbe and Montgomery 2003). The mainstem Queets River may be considered a low-gradient (i.e., O'Connor et al. 2003) avulsive channel system (Richards et al. 1993) comprised of cobble–gravel beds with pool and riffle morphologies. Individual channels may exhibit meandering or braided patterns. This results in very complex floodplain forest–channel mosaics, reflecting the legacy of glaciation and modern channel movement continually redistributing those glacial deposits (Thackray 2001). Lateral channel migration rates averaging 13 m/yr limit floodplain half-life to ~385 years (O'Connor et al. 2003, Latterell 2005). Although the Queets River has a modest drainage area, the seasonality of precipitation creates a disproportionately large mean annual discharge (124 m³/s), with a hundredfold (or more) range between summer low flows (minimum 8.5 m³/s) and winter peak flows (maximum 3764 m³/s).

FIELD METHODS

The valley floor environment is a mosaic of different stand ages, which reflect past lateral migrations by the river. The most well-developed riparian forests are in the unconstrained reaches of the mid-to-lower Queets Valley. Although the mainstem riparian corridor remains largely intact, the lowest reaches of the Queets River pass through heavily logged subwatersheds so were thus avoided.

Plot establishment.—Plots were established in recent alluvium along the lower Queets River to capture a wide variety of ages and vegetative assemblages (e.g., see Balian 2001, Balian and Naiman 2005). Two study reaches were chosen in large, unconstrained reaches at river km 40 (elevation 44 m) and river km 58 (elevation 70 m). Mean annual channel migration rates at these locations were 12 and 22 m/yr, respectively. An initial reconnaissance survey was conducted to determine dominant tree heights and approximate ages before field plots were established (Fig. 1). Stands were chosen to represent each of 21 distinct, but internally homogeneous, forest patches represented by the establishment of an initial cohort of trees. Belt transects

(rectangular plots) were used instead of square or circular plots because they provide sampling convenience while retaining the ability to examine many spatial aspects of stand structure (Van Pelt 1995, Van Pelt and Nadkarni 2004).

Plot dimensions were scaled by tree height to capture variability in spatial patterns without over-sampling (Van Pelt et al. 2004). The length of each plot was made at least twice the height of the average dominant tree and was wide enough to capture spatial variability within the stand. Plots were oriented to avoid overlap with stand edges or adjacent stands. Due to the elongate shapes of many riparian forest patches, plot placement was constrained in small patches to fit within the stand. Larger patches allowed random plot placement. Plot area was at least $1.5(h^2)$, where h is the dominant tree height for the stand. In all, 21 plots were established ranging in age from 3 to 330 years. Plot size ranged from 45 m² to 9600 m² (Table 1). Throughout the text and tables, plot age appears in square brackets next to the plot name.

A stem map was prepared to quantify stem structure and spatial patterns of distribution, and as a reference for repeat surveys. In stands >60 years old, all trees greater than 5 cm diameter at breast height (dbh) were mapped and measured for species, dbh, height, crown height, and four cardinal crown radii. In stands younger than 60 years, all stems >50 cm in height were mapped. In the three sites younger than 10 years, all plants of any tree species were mapped. Mapping was accomplished by setting a central transect line using 100-m tapes and rebar. The X coordinate of each tree was the distance along the tape at which the tree was found. An Impulse laser rangefinder (Laser Technologies, Centennial, Colorado, USA) was used to determine the Y coordinate, which was the distance from the tape.

All dead wood (>5 cm diameter) intercepted by the central tape was measured to quantify changes in coarse woody debris resources over the chronosequence. Measurements included species, diameter, decay class (Maser and Trappe 1984), piece length, and beginning and end points where the log intersected the tape. Diameter was measured perpendicular to the central axis of the log at the interception point. These data were used to calculate abundance and volume of dead wood in each plot (Van Pelt and Nadkarni 2004).

Also along the tape, within a belt transect scaled in width to 0.03 times the height of the average dominant tree, small individuals of trees not yet mapped but >50 cm in height, were measured for basal diameter, height, crown height, and average crown diameter. Tree seedlings (<50 cm tall) were tallied by species in a continuous string of 1 m diameter circles extending the length of each transect. For completeness, multiple transects were often used in order to accumulate more plots. Microplot number ranged from 24 in the youngest stands to 66–192 in mature stands for a total of 1232 seedling microplots.

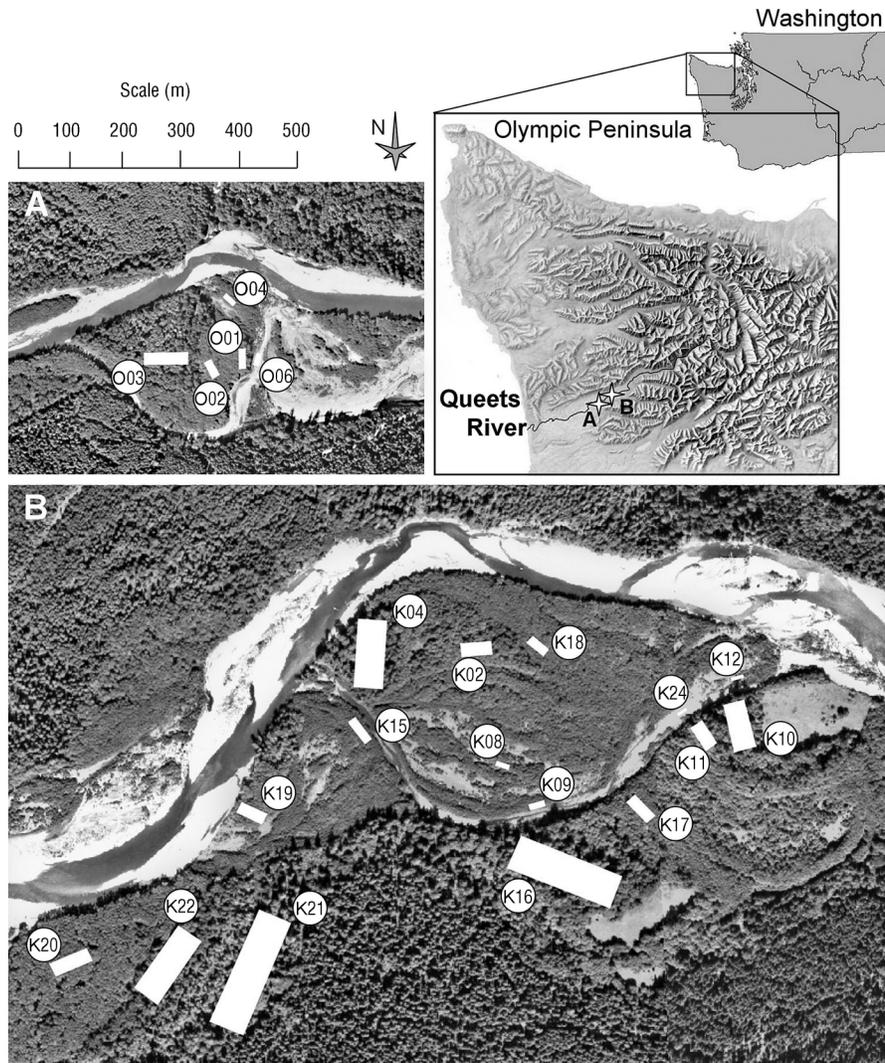


FIG. 1. Study site locations. The Queets River is the largest of the many rivers draining the Olympic Peninsula in the northwest corner of Washington State, USA. The two study reaches are located just above and below where Matheny Creek empties into the Queets River. The 21 plots are also indicated; plots were scaled by canopy height.

Soil particle size distribution, soil depth, and depth to summer low-flow channel were measured to evaluate potential substrate influences on forest development and succession. Particle size distribution for 0–20 cm depths was measured in samples from three soil pits in each plot. In rocky soils, coarse particles (>2 mm) were separated by sieving the material excavated from a 50 × 50 × 20 cm pit. In nonrocky soils, three samples were collected at 10 cm depth intervals using a 5 cm diameter steel tube. Particle size distribution for the fine earth (<2 mm) fraction was determined by the hydrometer method (J. S. Bechtold, *unpublished data*). Soil depth (to cobble subsoil) was determined as the average of six to 10 depth measurements of a steel rod driven into the soil until the cobble layer was reached. Height above channel was determined by surveying with an autolevel and stadia rod from plot centers to

the edge of the low flow channel during the summer (Table 1).

Stand age.—Most estimates of stand age were based on increment cores taken from between 10 and 20 stand-dominant trees per plot. For plots representing stands <50 years old, aerial photos were also used to estimate time of vegetation colonization. Newly formed alluvial surfaces may take up to a decade or more to become colonized in the Queets Valley, especially in cases where a site is subject to annual high flows that redistribute the substrate. In these cases, the photo record illustrates that stand ages can be a decade or more younger than the age of the surface they are growing on (Balian 2001), and our plot ages therefore refer to the date of colonization of the current vegetative cohort. The youngest stands were aged by counting bud-break scars on a subset of 10–20 individuals.

TABLE 1. A summary of plot characteristics, Queets River, Olympic National Park, Washington, USA.

Plot	Plot size (m ²)	Dominant vegetation	Soil texture (silt + clay, %)	Depth to cobbles (m)	Height above low-flow channel (m)
O06 [3]	144	HYRA/PLLA	8	0.0	0.3
K24 [4]	80	...	12	0.0	0.4
K12 [8]	45	HYRA/RACA	37	0.1	1.3
K09 [11]	96	RARE/TOME/STCO	31	0.1	0.5
K15 [12]	240	RARE/TOME/STCO	36	1.1	0.9
K08 [14]	150	POPR/RARE/RUUR	13	0.5	1.1
K18 [22]	1000	POPR/POPA/RARE	52	0.7	1.9
K19 [33]	875	POPR/POPA/RARE	26	0.5	1.6
K17 [39]	1200	POPR/POPA/RARE	47	0.6	1.7
O04 [39]	750	POPR/RARE/RUUR	40	0.6	0.7
K20 [51]	1875	POPR/POPA/RARE	36	1.1	2.0
O01 [51]	750	RARE/OXOR	27	0.3	1.4
O02 [51]	900	POPR/POPA/RARE	39	1.4	1.4
K11 [60]	1250	POMU/OXOR	44	0.5	2.0
K02 [84]	1500	POMU/OXOR	48	0.2	2.3
O03 [94]	2500	POMU/OXOR	48	0.9	1.9
K10 [130]	4400	POMU/OXOR	41	0.8	2.4
K04 [165]	5200	POMU/OXOR	38	1.3	2.2
K22 [185]	6500	POMU/OXOR	45	0.6	2.3
K16 [265]	9000	POMU/OXOR	49	1.0	2.6
K21 [330]	9600	POMU/OXOR	57	0.5	2.3

Notes: Values shown in the last three columns were garnered from this and related studies examining soil development, nutrient cycling, and hyporheic influences (Balin 2001; J. Bechtold, unpublished data). Ellipses indicate that not enough plant material was available to make an assessment. Values in square brackets next to the plot names indicate the stand age (in years). Plant species abbreviations are as follows: HYRA, *Hypochaeris radicata*; PLLA, *Plantago lanceolata*; RACA, *Racomitrium canescens*; RARE, *Ranunculus repens*; TOME, *Tolmiea menziesii*; STCO, *Stachys cooleyae*; RUUR, *Rubus ursinus*; POPR, *Poa pratensis*; POPA, *Poa palustris*; OXOR, *Oxalis oregana*; POMU, *Polystichum munitum*.

With the species present in the younger stands in the study, this method works well for trees up to 10–15 years in age (Table 1).

Stand profiles.—Four stands were selected for detailed stand profiles of vertical and horizontal vegetative structure (Fig. 2). This was accomplished by incorporating aspects of a stand cross-section and a stem map (Van Pelt et al. 2004, Van Pelt and Nadkarni 2004). Illustrations were created by using spatial positions and tree dimensions with additional notes and photographs on tree form and eccentricities. The four sites chosen were selected to represent two of the early successional trends (one with and one without conifers), a mature site partly dominated by *Populus* and an old-growth stand, representing the furthest successional trajectory before the river reclaims the site (Fig. 2).

Stem volume measurements.—A subset of trees was selected for volume measurements to develop a regression model that could be used to predict wood volume from tree height and dbh. Trees were selectively chosen to capture the full size range of each species. A Criterion 400® forest survey laser (Laser Technologies, Centennial, Colorado, USA) was used to collect a series of diameters up the stem of selected trees. The volumes of conic frustums were calculated for each section between diameters and then summed to estimate whole tree totals. An additional 54 trees were climbed and measured directly (R. Van Pelt, unpub-

lished data). In some cases the volume data from these sites were combined with data previously collected from riparian trees or nearby high-productivity forests (R. Van Pelt, unpublished data) and used to develop new regression equations for these species (Appendix A).

ANALYSIS

Crown models.—Crown models allow for an estimation of crown size and shape in three-dimensional space. The models were used to estimate crown locations based on mapped and measured parameters when shaped as simple conics (Van Pelt and North 1996, Van Pelt and Franklin 2000, Van Pelt and Nadkarni 2004). While this approach can be fairly crude when applied to individual trees, the models combine to accurately represent the forest at the stand scale (Van Pelt and North 1999). Simple shapes were chosen to represent the different species and sizes of trees based on observational and photographic analysis. The upper half of hardwood crowns was a half ellipsoid, while the bottom half was the difference between a cylinder and an ellipsoid. Paraboloids were used to represent *Tsuga*. Three shapes were used to represent *Picea*, depending on height. Cones were used to represent trees <35 m tall; paraboloids for trees taller than this but <65 m; and three-quarter ellipsoids were used for the tallest trees. The crown dimensions of all trees were summed

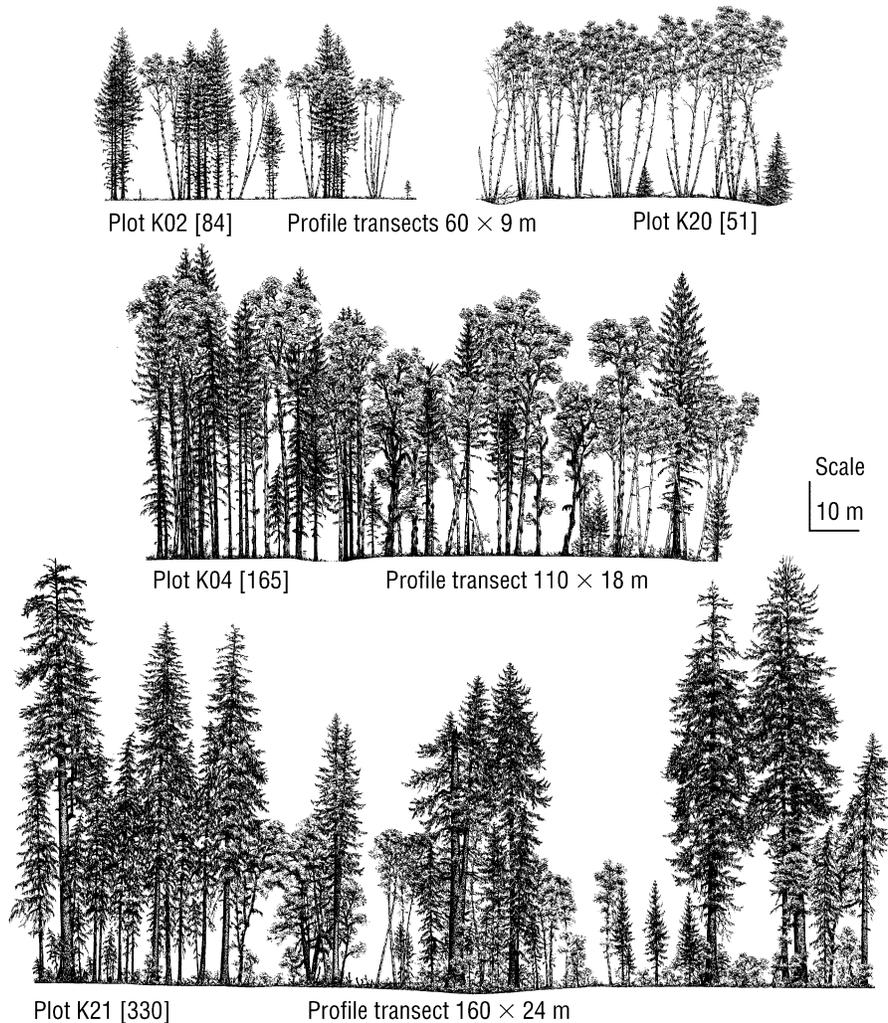


FIG. 2. Canopy profile drawings for four of the stands; stand age, in years, is given in square brackets. Plot K02 [84] and plot K20 [51] represent two possible early trajectories, with and without *Picea*. Plot K04 [165] is typical of the *Populus*-dominated stands during the second century. Plot K21 [330] represents the end point of structural complexity with an old-growth *Picea-Tsuga* forest.

to generate three-dimensional solid volumes of the amount of occupied space. Crowns were then vertically subdivided into 5-m sections. All sections were summed within each height class to establish vertical profiles.

Aerial photo interpretation and GIS analyses.—Historic aerial photographs (i.e., 1939–2002) were used to reconstruct the developmental history of each study site and to delineate the extent of distinctive fluvial landforms within the valley floor. Original photos were taken in mid to late summer (e.g., July–October) at varying scales (i.e., 1:12 000 to 1:60 000) and scanned so that ground resolution ranged from 0.4 to 1.5 m (Appendix B). Digital images were georeferenced, corrected for radiometric distortion, and converted to a common scale, coordinate system, and map projection with ERDAS Imagine (Leica Geosystems, Atlanta,

Georgia, USA). A geographic information system (ArcMap; ESRI, Redlands, California, USA) was used to create digital planiform maps of the valley floor based on vegetation characteristics (Latterell 2005). The boundaries of individual landforms were manually delineated with nonoverlapping polygons at a fixed (i.e., 1:2000) scale of magnification. The area of each polygon was calculated and summed for each landform type. Pathways of development were determined by reconstructing the physical development and disturbance history for landforms of similar age but with different forest structure and soil characteristics.

Semivariance analysis.—Semivariance analysis is an aspect of geostatistics that has been applied in ecological research for detecting patterns of scale, autocorrelation distances, and variance. It has been used to examine structural differences in forests using per-

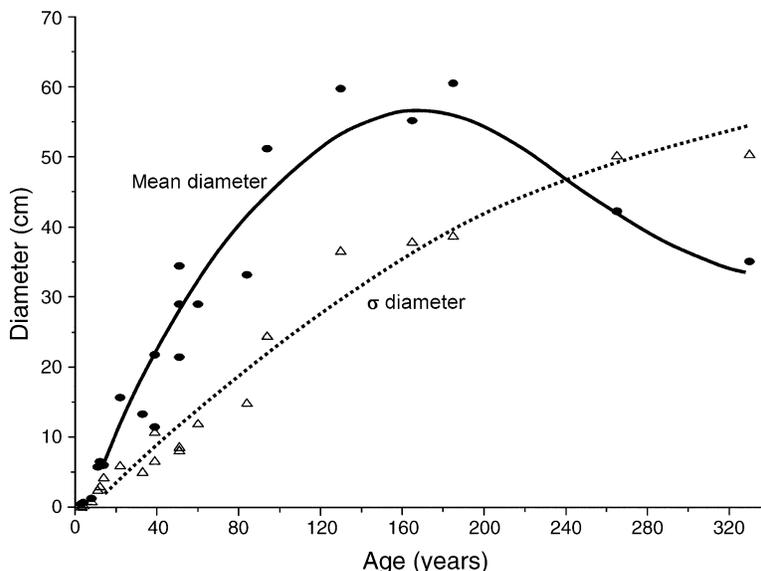


FIG. 3. Diameter change over time for the 21 stands. Circles represent the mean diameter of all stems >5 cm in diameter. Triangles represent the values for the standard deviation of diameter for the same stems. The latter curve rises more rapidly than an equivalent series in *Pseudotsuga*-dominated forests due in part to higher productivity, fast early *Picea* diameter growth, and the early growth and dominance of *Populus*.

manent plot data such as basal area, biomass, or canopy density (Van Pelt and Franklin 2000, Chen et al. 2004, Van Pelt and Nadkarni 2004). The dominant scale of pattern present in the data as determined by the analysis is termed the lag, which is often a reflection of gap size, crown size, or both. The analysis also determines the sill, which is a representation of the variance among the data, roughly equal to the square of the standard deviation.

To transform the canopy volume into a consistent, continuous form for semivariance analysis, a virtual cylinder was created at each sample point along the transects. This provided a "moving window" that measured canopy volume along the length of the transect (Van Pelt and Nadkarni 2004). The ideal cylinder size would roughly correspond to canopy diameters: very large cylinders would be highly autocorrelated and small cylinders would be at a scale too fine for the simple conic shapes of the crown models to detect. Because of this, and due to the wide variety of sizes and shapes of the plots used in this study, a 9 m diameter cylinder was selected and used on all but the smallest plots. The value for a given spot on a transect was the sum of all of the tree crown portions that fell within the cylinder. This was repeated every 2 m on all transects.

Principal component analysis.—Principal component analysis (PCA) was performed on a cross-products matrix of Pearson correlation coefficients (i.e., centered and standardized by the standard deviation [McCune and Mefford 1999]) among 13 stand-level structure variables (mean crown volume, standard deviation of crown volume, crown volume ratio, peak in crown vol-

ume, crown depth, *Picea* stem density, *Alnus* stem density, total stem density, *Picea* basal area, *Alnus* basal area, total basal area, standard deviation of dbh, and maximum height). The goal was to elucidate dominant patterns in stand structure among the 21 sites. The site scores were then scaled to rank from 1 to 0 to allow a comparison among sites along the significant axes. Last, correlation between these relativized stand scores and four environmental variables (age, soil texture, depth to cobbles, and height above low-flow channel) were used to suggest/evaluate environmental predictors of vegetative structure.

RESULTS

Stand characteristics.—A total of 4359 trees were mapped and measured among the 21 stands. Tree heights and diameters ranged up to 81.5 m and 377 cm, respectively. *Picea* and *Alnus* were the two species most consistently present. *Picea* was not present in five of the youngest plots, whereas *Alnus* was absent or scarce in the four oldest plots. In the context of a chronosequence, mean dbh steadily increased for the first 200 years and then began declining (Fig. 3, Table 2). Early dominance of *Populus* helps create the peak of stand average dbh. Loss of this cohort, and the development of understory *Acer circinatum*, *Tsuga*, and *Picea* caused a decline in mean diameter in the oldest stands (Fig. 3). Average diameters for *Picea* increased throughout the chronosequence and the two oldest sites had trees very large for the species (6 trees/ha >2.5 m dbh). The standard deviation of dbh steadily increased throughout the chronosequence, indicating rapid growth of original trees followed by regeneration filling

TABLE 2. Summary of tree size among the 21 plots.

Plot	Mean diameter (cm)			σ
	<i>Picea</i>	<i>Alnus</i>	Stand	
O06 [3]	0.2	0.5	0.5	0.2
K24 [4]		0.9	0.7	0.4
K12 [8]	0.3	1.4	1.3	1.0
K09 [11]		7.2	5.8	2.6
K15 [12]		6.7	6.6	3.1
K08 [14]	2.7	7.5	6.1	4.4
K18 [22]		16.1	15.7	6.1
K19 [33]		13.8	13.3	5.2
K17 [39]	5.3	27.6	21.8	10.8
O04 [39]	0.8	12.7	11.5	6.8
K20 [51]	12.8	29.9	29.0	8.2
O01 [51]	18.1	27.4	21.5	8.7
O02 [51]		34.5	34.5	8.3
K11 [60]	29.9	29.4	29.0	12.1
K02 [84]	35.1	33.4	33.2	15.0
O03 [94]	43.2	39.3	51.2	24.6
K10 [130]	73.5	79.8	59.8	36.7
K04 [165]	64.5	36.5	55.2	38.0
K22 [185]	73.8		60.5	38.9
K16 [265]	106.7	46.1	42.2	50.3
K21 [330]	92.6	33.5	35.1	50.5

Notes: The average diameter for *Picea* continues to increase throughout the age sequence while the total reaches a peak during the second century and then declines. Empty cells indicate that the taxon was not present in that plot; stand ages (in years) are in square brackets. The standard deviation (σ) of diameter continues to increase throughout the age sequence. Diameters are measured at a height of 1.37 m.

in from below (Table 2). *Alnus* reached 30–40 cm dbh within the first 50 years and tended to stay within that range throughout all of the older plots. Pioneer *Alnus* trees typically died after 50–100 years. A handful of anomalous *Alnus* were able to establish in gaps in pre-existing stands older than 100 years. The large average diameter value reported for *Alnus* in plot K10 is due to the only two remaining trees in the plot being unusually large (Table 2).

Once alluvial soils formed, trees colonized quickly. Stem densities exceeded 10 000 stems/ha for the first decade, then the hardwood component declined below 500 stems/ha by age 40 (Table 3). At this point, much of the competition-based mortality had concluded, the *Salix* component was largely gone, and the *Alnus* began to die from decay-based mortality. The conifer component then began to flourish, with *Picea* reaching stem densities in excess of 250 stems/ha between 60 and 90 years after stand initiation. With the exception of plot O02 [51], abundant *Picea* stems are present in all plots >30 years old. The two *Acer* species and *Tsuga* do not appear in significant numbers until the second century, and are only abundant in the oldest stands (Table 3).

Basal area and stem volume increased throughout the chronosequence and stabilized at ~ 100 m²/ha and ~ 2000 m³/ha, respectively (Table 3). *Picea* made relatively large contributions to the totals in plots K08 [14], O01 [51], K11 [60], K02 [84], and O03 [94]. At least some of the *Picea* in these plots represent trees that established concurrently with pioneering *Alnus*.

The *Picea* presence in plots K12 [8], K19 [33], O04 [39], K17 [39], and K20 [51] represent individuals that established long after *Salix* and *Alnus*, or were presently establishing. Both *Salix* and *Alnus* reached their peak in stem volume within the first few decades (Fig. 4). *Populus* makes a significant contribution to basal area and stem volume values in the second-century (plots O03 [94], K10 [130], K04 [165], and K22 [185]). For example, we measured the tallest known individual of the species (54.3 m). We were unable to locate individual *Populus* trees over 200 years old. This suggests that the trees perish, likely from fungi and wind, before the third century. In the second and third centuries, *Picea* grew at phenomenal rates (Fig. 4), with individuals growing nearly 1 m³/yr of wood for two centuries. Though we did not work in stands on fluvial landforms older than 330 years, both of the oldest stands had *Picea* in smaller size classes, suggesting *Picea* will persist in subsequent centuries.

Vertical complexity.—Crown profiles illustrate how the height of forest stands increases over time, the lifting of crown bases in the young and mature stands, and the subsequent lowering and deepening created by the presence of shade-tolerant species in the older stands (Fig. 5). The youngest stands are dominated by *Salix* and *Alnus*, which give way to coniferous species in the older stands. Plots K08 [14], O01 [51], K11 [60], K02 [84] and O03 [94] represent stands with an early codominance by *Picea* by individuals that established concurrently with *Alnus* during cohort initiation.

Canopy volume increases slowly in the plots <100 years old, as the lower portion of the *Alnus* crowns recede at a similar rate to their height growth (Fig. 5). Crown volume rises dramatically to exceed 100 000 m³/ha as the *Picea* gain height and develop deep crowns (Table 3). The *Populus* also have crowns large in diameter but shallow in depth, which weakens their contribution to canopy volume, similar to basal area and stem volume. The addition of tree species and growth during the second and third centuries fills in many of the openings at all levels of the canopy with values sometimes exceeding 200 000 m³/ha (Table 3).

The values for the peak in these curves as well as the total canopy depth change consistently with stand age (Fig. 6). The total canopy depth rises more slowly than total tree height as the mature stands have tall, but shallow, crowns. In older stands, the crown depth resembles canopy height. Crown density peaks at 40 m (e.g., between 130–150 years) due in part to the presence of tall, high-crowned *Populus*. Once these trees die and are replaced by shade-tolerant *Tsuga* in the lower canopy strata, the peak drops to below 30 m (Fig. 6).

Horizontal complexity.—Canopy volume series along transects indicate the presence of canopy gaps, depicted as dips in the series. High points in the series represent either the crowns of dominant trees or dense clusters of trees. Only the 15 stands older than 15 years

had plots sufficiently large to analyze. Semivariance analysis determined the dominant scale (lag) among the 12 series that had plots large enough to portray the canopy volume series with enough length to analyze (Table 4). The sill is roughly equal to the square of the variance within the series. The dominant scale consistently increased with stand age. In most cases, the peaks had a horizontal spacing similar to the canopy gaps. Because of this it is difficult to tell which pattern had influenced the dominant scale as represented in the fitted curves. But, for comparison, the scale from the fitted curves was then compared to the average dominant crown diameters for trees within the same stand (Table 4). In nearly all cases, these two strongly agreed.

The ratio of the variance to the average crown volumes has been used as a measure of structural complexity (Van Pelt and Nadkarni 2004), so was examined with the 15 stands (Table 4). The higher values (>0.5) occurred only in the old-growth stands, with one exception. The two nearly homogenous *Alnus* stands (O02 [51] and K20 [51]) had relatively low canopy volumes. However, these stands contained abundant gaps that created high variability in canopy volume. As a result, the ratios for these two stands were relatively high. Both stands are in dynamic flux, with abundant tree mortality occurring annually (R. J. Naiman and T. C. O'Keefe, unpublished data). Relatively low ratios were observed in two plots dominated by *Populus* (K10 [130] and K04 [165]) (Table 4). Both of these stands had abundant hardwood species with very large crowns. These crowns contributed greatly to the overall canopy volume (99 143 m³ for K10 [130] and 72 743 m³ for K04 [165]; Table 3). More importantly their crown width is much higher for a given volume, when compared to conifers. This results in more of the canopy space being filled, thus reducing the horizontal variability and leading to a smoother canopy volume series and thus lower ratio values.

Coarse woody debris.—The volume of coarse woody debris on the forest floor generally increased through time; at least those endogenous in origin (Appendix C; see J. Latterell, unpublished manuscript, for estimates of fluvial deposits). The number of logs, however, varied widely among plots. Plots between 10 and 60 years old exhibited rapid thinning mortality. This produced large numbers of small-diameter, low-volume logs (Appendix C). Logs in the older stands (>150 years) were larger in diameter and hence contained substantially more volume. They also tend to persist longer in the stands, so are thus the result of several decades of treefall, rather than the immediate nature of the logs present in the younger stands.

During the first 50 years, snag numbers represent thinning mortality from competition and stand density (Appendix D). These snags had very small diameters and do not account for much wood volume. By 100 years, the number of snags per hectare was similar among stands. The fluctuations are probably idiosyn-

crasies associated with mortality events rather than site-specific trends, since snags are a more transient feature than logs. Snags greater than 10 m high and 25 cm dbh only appear in the oldest stands (Appendix D).

Principal components analysis.—PCA performed on a primary data matrix containing the 21 stands and 13 structural variables revealed that stand structure accounted for 61% of the total variability (Table 5). All of the significant correlations were related to stand crown or wood volume. Of the remaining 39% of the variability, the second component accounted for an additional 18% of the variation and was correlated with *Alnus* density and basal area. Since the *Alnus* stem and crown volume increased with time up to 50 years and then declined, this was a pattern different from overall structure, which increased continuously throughout the sere. The remaining 21% of the variation had a third component with but one significant correlation which was with *Picea* density.

The relativized stand scores along PC1 provided a clear ranking of overall structural complexity (Table 5), which is strongly correlated with stand age and, to a lesser extent, height above the summer low-flow channel (Table 5). PC2 and PC3 suggest differing pathways of succession, with PC2 indicating the dominance of *Alnus*: low values in young and old stands with high values at intermediate ages. All values in PC3 above 0.25 had a very strong *Picea* component; the zero value was a homogeneous *Alnus* stand. Depth to cobbles, which appeared to be an important determinant of *Picea* incidence during data collection, was not significant. However, the many changes in composition and soil development that occurred during the 330-yr chronosequence may have masked some of these patterns. When stands over 100 years old are excluded, a significant pattern emerges (Fig. 7). Since *Picea* only becomes ubiquitous after the *Alnus* decline, leaving the older stands out of the analysis allows the differing pathways to emerge.

Stand evolution and river dynamics.—Retrospective analyses of historic aerial photography allowed quantification of river channel movements between 1939 and 2002 (Latterell 2005). The location of the active channel was determined at 16 different times since 1900 (Fig. 8). Within the two study reaches, which were chosen in unconstrained river sections, 81% of the floodplain was reworked at one point during the past 100 years. For the Queets Valley as a whole, only 52% of the floodplain has been reworked, but with significant variability dependant on features controlling local channel migration potential (Latterell 2005). While many of the channel movements were slight drifts typical of meandering rivers, some were significant avulsions where the channel moved to a new location. The river movement at our sites averages between 16 and 26 m/yr. This pattern of channel avulsion can leave behind forested "islands" in a matrix of gravel bars and pioneering stands (Fig. 8).

TABLE 3. Stand-level characteristics by site and species.

Plot and species	Stem density (no./ha)	Canopy volume (m ³ /ha)	Basal area (m ² /ha)	Stem volume (m ³ /ha)	Maximum height (m)
O06 [3]					
<i>Salix</i> sp.	69	4	0.03	0.0	1.0
<i>Alnus rubra</i>	29 500	202	0.75	0.2	1.2
<i>Populus balsamifera trichocarpa</i>	2780	1	0.02	0.0	0.5
Totals	32 900	208	0.80	0.2	
K24 [4]					
<i>Salix</i> sp.	37 000	204	1.13	0.3	1.3
<i>Alnus rubra</i>	18 400	977	1.57	0.9	2.0
Totals	55 500	1182	2.70	1.2	
K12 [8]					
<i>Salix</i> sp.	54 000	5525	11.31	10.6	4.2
<i>Alnus rubra</i>	7560	3488	1.91	2.5	3.9
<i>Populus balsamifera trichocarpa</i>	3110	17	0.06	0.0	0.8
<i>Picea sitchensis</i>	889	2	0.01	0.0	0.3
Totals	65 600	9032	13.29	13.1	
K09 [11]					
<i>Salix</i> sp.	6460	8093	17.1	88.8	13.4
<i>Alnus rubra</i>	1150	15 398	6.7	46.0	16.0
Totals	7600	23 491	23.8	134.8	
K15 [12]					
<i>Salix</i> sp.	1210	2715	3.8	115.8	14.2
<i>Alnus rubra</i>	5580	27 218	23.9	143.0	15.1
Totals	6790	29 933	27.7	258.8	
K08 [14]					
<i>Salix</i> sp.	2400	38 748	14.7	271.0	13.4
<i>Alnus rubra</i>	1130	32 011	13.4	85.2	15.1
<i>Picea sitchensis</i>	4870	4404	1.9	2.0	4.0
Totals	8400	75 163	28.1	358.1	
K18 [22]					
<i>Salix</i> sp.	110	659	1.2	37.4	20.1
<i>Alnus rubra</i>	870	28 671	20.3	216.8	24.2
<i>Populus balsamifera trichocarpa</i>	4	1602	0.7	11.7	33.6
Totals	984	30 932	22.2	265.9	
K19 [33]					
<i>Salix</i> sp.	137	1126	1.1	17.9	13.5
<i>Alnus rubra</i>	1090	20 207	18.4	153.5	19.6
<i>Picea sitchensis</i>	78	348	0.1	0.1	4.7
Totals	1300	21 681	19.6	171.5	
K17 [39]					
<i>Alnus rubra</i>	592	31 106	36.6	510.9	31.2
<i>Picea sitchensis</i>	225	1670	0.4	4.2	7.6
Totals	817	32 776	37.0	515.1	
O04 [39]					
<i>Salix</i> sp.	240	796	1.2	35.9	16.0
<i>Alnus rubra</i>	1450	33 077	23.4	190.3	20.9
<i>Picea sitchensis</i>	67	3	0.01	0.0	0.9
Totals	1760	33 876	24.6	226.4	
K20 [51]					
<i>Alnus rubra</i>	379	36 451	28.2	435.3	35.4
<i>Picea sitchensis</i>	64	1037	0.3	3.8	12.4
Totals	443	37 488	28.5	439.0	
O01 [51]					
<i>Alnus rubra</i>	307	43 382	19.3	268.3	31.6
<i>Picea sitchensis</i>	560	19 906	16.7	281.2	23.4
Totals	867	63 288	35.9	549.5	
O02 [51]					
<i>Alnus rubra</i>	456	49 367	44.9	722.2	36.0
Totals	456	49 367	44.9	722.2	

TABLE 3. Continued.

Plot and species	Stem density (no./ha)	Canopy volume (m ³ /ha)	Basal area (m ² /ha)	Stem volume (m ³ /ha)	Maximum height (m)
K11 [51]					
<i>Acer circinatum</i>	8	277	0.02	0.2	6.9
<i>Acer macrophyllum</i>	8	16	0.03	0.1	3.3
<i>Alnus rubra</i>	256	18 737	18.9	235.8	27.7
<i>Picea sitchensis</i>	384	43 383	32.3	566.3	33.7
Totals	656	62 363	51.2	802.3	
K02 [84]					
<i>Acer circinatum</i>	20	1505	0.3	2.9	7.5
<i>Acer macrophyllum</i>	7	1130	0.2	1.8	21.6
<i>Alnus rubra</i>	153	19 326	14.6	187.0	29.0
<i>Picea sitchensis</i>	287	28 091	33.6	657.2	32.4
Totals	467	50 051	48.7	848.9	
O03 [94]					
<i>Alnus rubra</i>	72	20 976	9.1	129.0	35.5
<i>Populus balsamifera trichocarpa</i>	60	56 801	35.3	642.3	52.0
<i>Picea sitchensis</i>	350	26 675	23.8	504.2	49.7
<i>Tsuga heterophylla</i>	4	1375	0.7	13.4	35.3
Totals	486	105 827	68.9	1288.8	
K10 [130]					
<i>Acer circinatum</i>	64	12 016	1.3	17.1	13.1
<i>Acer macrophyllum</i>	36	30 344	8.3	142.1	38.7
<i>Alnus rubra</i>	5	6233	2.3	24.4	26.6
<i>Populus balsamifera trichocarpa</i>	50	50 549	34.7	615.0	51.8
<i>Picea sitchensis</i>	136	103 970	49.9	1064.8	56.8
<i>Thuja plicata</i>	5	2681	1.8	12.4	28.4
<i>Tsuga heterophylla</i>	20	5576	2.4	31.4	36.4
Totals	316	211 369	100.1	1907.3	
K04 [165]					
<i>Acer circinatum</i>	58	1339	0.2	2.1	10.9
<i>Acer macrophyllum</i>	17	28 333	7.4	140.3	40.3
<i>Alnus rubra</i>	67	13 273	7.7	112.1	37.9
<i>Populus balsamifera trichocarpa</i>	29	29 799	24.4	421.9	54.3
<i>Picea sitchensis</i>	166	56 096	40.3	896.1	61.9
<i>Tsuga heterophylla</i>	29	10 191	5.0	62.4	49.2
Totals	367	139 031	84.1	1634.9	
K22 [185]					
<i>Acer circinatum</i>	18	2554	0.3	3.7	12.8
<i>Acer macrophyllum</i>	40	17 206	7.4	124.7	39.8
<i>Populus balsamifera trichocarpa</i>	23	24 325	21.1	357.2	53.8
<i>Pseudotsuga menziesii</i>	2	363	0.2	45.5	25.5
<i>Picea sitchensis</i>	104	69 506	46.1	1070.6	64.7
<i>Tsuga heterophylla</i>	31	10 457	5.0	80.2	45.7
Totals	218	124 410	80.0	1681.8	
K16 [265]					
<i>Acer circinatum</i>	257	9413	1.8	19.3	16.2
<i>Acer macrophyllum</i>	69	36 585	17.1	318.4	39.7
<i>Alnus rubra</i>	14	5474	2.5	38.7	41.1
<i>Populus balsamifera trichocarpa</i>	10	4802	2.9	59.5	47.8
<i>Picea sitchensis</i>	267	77 427	70.1	1540.8	76.7
<i>Tsuga heterophylla</i>	33	14 381	5.6	92.5	51.7
Totals	650	148 081	99.8	2069.3	
K21 [330]					
<i>Acer circinatum</i>	156	13 072	1.8	21.7	13.7
<i>Acer macrophyllum</i>	17	26 152	10.8	199.5	38.6
<i>Alnus rubra</i>	27	12 360	2.7	33.8	32.6
<i>Pseudotsuga menziesii</i>	1	5858	2.8	46.5	62.8
<i>Picea sitchensis</i>	177	116 637	59.5	1268.4	81.5
<i>Tsuga heterophylla</i>	174	48 729	20.5	329.4	59.2
Totals	556	222 809	98.1	1899.3	

Notes: Data include all trees >50 cm in height. Canopy volume is proportional to the amount of foliage in the stands, whereas basal area and stem volume are related to the amount of wood in live trees in the stands.

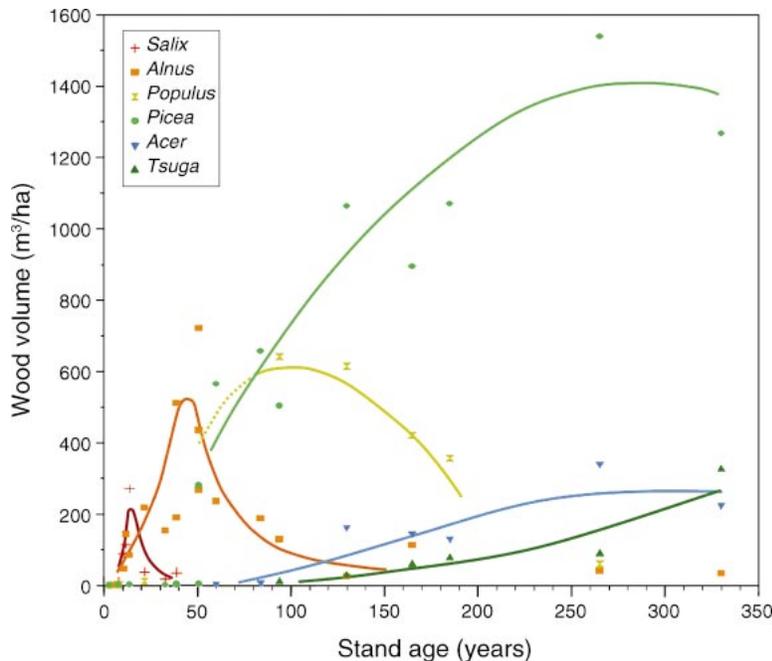


FIG. 4. Standing wood volume for the six main tree genera. *Picea* becomes the major component of the forest after the first century. The oldest stands had *Picea* in all size classes, indicating a potential *Picea* component into the future. Note the shifts in peak timing for the three “pioneer” hardwoods (*Salix*, 15 yr; *Alnus*, 45 yr; and *Populus*, 110 yr). In addition, both *Acer* and *Tsuga* are slow to establish (50–100 yr), and do not become a major feature of the stands until the third century. *Acer circinatum* and *A. macrophyllum* show similar patterns and appear as the combined *Acer*.

DISCUSSION

Fonda (1974), McKee et al. (1982), and Balian and Naiman (2005) collectively represent the extant body of knowledge on the structure and composition of rain forests of the Pacific coastal ecoregion in a successional framework. Our observations build upon this prior work and provide new insights and interpretations of the sources of heterogeneity in riparian stand structure, and the pathways through which riparian stands evolve. We determined that, while forest structure develops toward the *Picea*–*Tsuga* old-growth forest for which the area is famous, it is not a single, directional pattern of succession that leads to this. Forest evolution proceeds along multiple pathways determined by initial conditions and subsequent shifts in the fluvial disturbance regimes. These observations suggest the diverse and complex forests found along Pacific coastal rivers are inexorably linked to the rivers that created them. Just as these large rivers are influenced by the forest-derived wood that in part deflects their movement, understanding the succession of these riparian forests cannot be achieved without an examination of fluvial dynamics.

While giant trees in the Pacific Northwest are often given great ages in popular literature, we suspect most of the giant *Picea* trees in the Queets are <400 years old. Unlike their giant Cascadian counterpart, *Pseudotsuga*, the giant *Picea* in the western Olympic Mountains are much less likely to reach great ages. Their

wood lacks decay-resistant extractives, and the humid climate allows decay to proceed rapidly. Their incredible growth rates allow them to achieve enormous proportions in just a few centuries, but then they break up, either through root disease or structural failure in the wood (Peterson et al. 1997). Large living trees are notoriously difficult to age. McKee et al. (1982) estimated the age of the oldest *Picea* in their research along the South Fork Hoh River at 266 years. Similarly, ages of *Picea* in both the Carmanah and Walbran valleys on the west coast of Vancouver Island were found to be up to 300 years, with only suspicions of trees older than this (Peterson et al. 1997). The oldest verified age of a tree in this study was 225 years (*Tsuga*), so it is feasible that the *Picea* growing with this tree could be several decades to a century older, since they presumably established earlier. To the best of our knowledge, no *Picea* aged over 400 years have been found on alluvial sites. Our findings on river return rates suggest that standing individual *Picea* in excess of 500 years probably do exist on the alluvial soils of the Queets, but they would be in an advanced state of decay.

Fonda (1974) delineated at least four major surfaces with his first terrace (*Picea*–*Alnus*–*Populus*) 400 years old, with an upper *Picea*–*Tsuga* terrace 750 years old. Some of the surfaces included in that study were not considered in this study as not being strictly fluvial in origin. In addition, our analysis of river movements

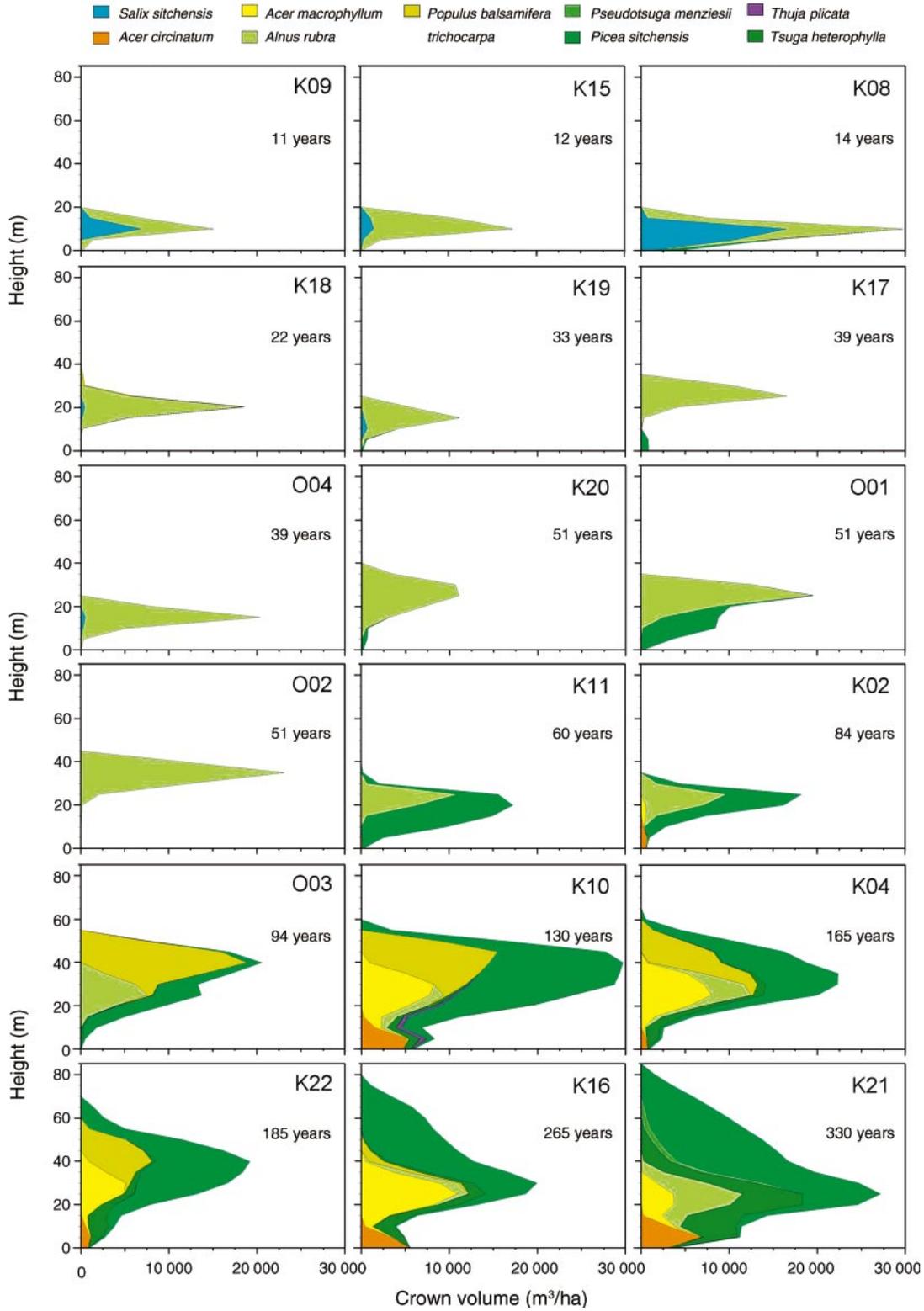


FIG. 5. Crown profile diagrams for 18 of the 21 plots. The three youngest plots were too small to show up well at this scale. Note not only the dominance by *Alnus* in all of the younger stands, but also how the crown depth does not appreciably increase as canopy height does. Early codominance by *Picea* is evident in plots O01 [51], K11 [60], and K02 [84]. Note also the brief, but powerful, presence of *Populus* in second-century stands. Crown depths become very deep in the oldest stands as more species are added.

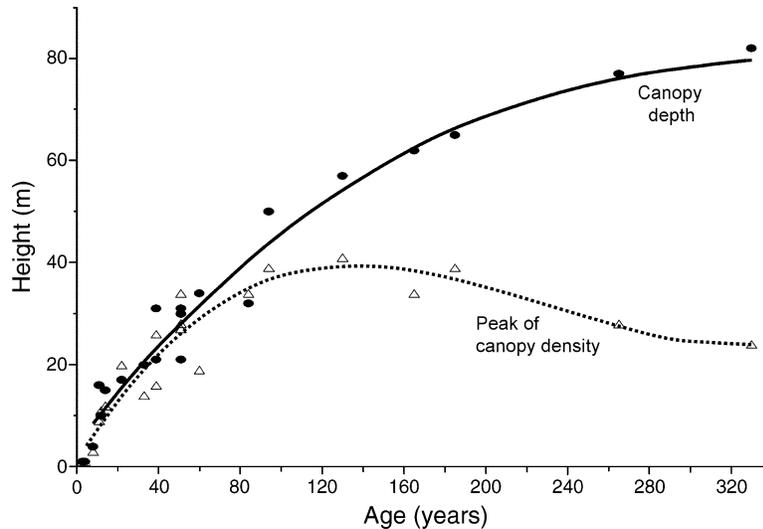


FIG. 6. Curves of canopy depth and the peak in canopy density for the 21 sites. Canopy depth becomes synonymous with the height of the tallest tree after about 150 years due to canopy infilling from below. The curve for the peak in canopy density drops after 150 years due both to the loss of the shade-intolerant hardwoods (*Alnus* and *Populus*) and the increase in abundance of regenerating shade-tolerant *Tsuga*.

indicates that there are many more than four major surfaces present in these valleys. Major avulsion events occur several times during one century, and at least some surfaces are altered each year. The valley floor environment represents a four-dimensional gradient of disturbance, with each small patch reflecting its own particular disturbance history.

As stands are captured by river movements, wood from living trees, logs, and snags are redistributed downstream by floodwaters. The largest “key” pieces are essential to the formation of logjams (Abbe and Montgomery 2003). They catch in the channel and capture additional floating logs. Accumulations of small, “jam-building” logs greatly increase the hydraulic and geomorphic impact of the key pieces. Previous studies

suggest the stability of logs in rivers is strongly related to the ratio of log length to channel width (Lienkaemper and Swanson 1987). In rivers like the Queets, the channel is wider than even the tallest trees. Thus, other factors, such as the presence of a rootwad and the log diameter are of primary importance (Abbe and Montgomery 2003). Other studies have considered key pieces to consist of logs with basal diameters >60 cm (Hyatt and Naiman 2001). On the Queets, Latterell (2005) found that the mean diameter of key pieces of 222 logjams in the active channel was 109 ± 3.4 cm (mean \pm SE). While some jams were initiated by relatively small pieces, over 50% of the logs exceeded 1 m in diameter. Thus, we considered trees exceeding 1 m in diameter to represent potential key pieces. For com-

TABLE 4. Results from semivariance analysis.

Plot	Sill	Lag	r^2	cv	$\sigma^{1/2}/cv$	DCD
K17 [39]	6057	6.9	0.57	205	0.380	6.4
K20 [51]	15 350	7.3	0.47	198	0.529	7.4
O01 [51]	3952	6.8	0.62	175	0.360	8.2
O02 [51]	11 030	7.7	0.53	249	0.497	8.2
K11 [60]	17 030	11.7	0.42	556	0.235	9.1
K02 [84]	44 270	12.3	0.60	871	0.241	9.7
O03 [94]	86 960	13.2	0.91	681	0.433	14.3
K10 [130]	329 700	17.3	0.77	1890	0.304	15.8
K04 [165]	88 000	12.6	0.36	1075	0.276	13.5
K22 [185]	174 500	14.8	0.62	743	0.562	14.8
K16 [265]	380 300	15.2	0.41	1205	0.512	16.5
K21 [330]	1 023 000	21.6	0.22	1646	0.615	20.9

Notes: Only plots large enough to generate an appropriate series were used for this analysis. For consistency, the spherical model was the only model used for fitting the curves. The sill is roughly equal to the variance (squared) in the data or the “roughness” of the outer canopy. Lag, the distance at which the data are no longer autocorrelated, is the dominant scale represented in the data. cv represents the average crown volume as calculated from the cylinders. DCD represents the dominant crown diameters, which were calculated separately. Note how similar the lag is to the DCD of trees in the plot.

TABLE 5. Results from PCA.

Parameter	PC1	PC2	PC3
Structural measures			
Mean crown volume	-0.94	-0.13	0.19
σ crown volume	-0.88	-0.29	0.04
Crown volume ratio	-0.36	-0.59	-0.35
Peak in crown density	-0.81	0.39	-0.14
Crown depth	-0.98	0.05	-0.03
<i>Picea</i> stem density	0.23	0.02	0.89
<i>Alnus</i> stem density	0.55	-0.71	-0.21
Total stem density	0.58	-0.66	-0.04
<i>Picea</i> basal area	-0.92	-0.23	0.08
<i>Alnus</i> basal area	0.26	0.83	-0.24
Total basal area	-0.98	-0.01	0.06
σ dbh	-0.97	-0.18	0.01
Maximum height	-0.98	0.05	-0.05
Rejuvenated stand scores for each plot			
O06 [3]	0.03	0	0.02
K24 [4]	0	0.24	0.20
K12 [8]	0.07	0.28	0.34
K09 [11]	0.23	0.62	0.20
K15 [12]	0.19	0.75	0.18
K08 [14]	0.21	0.68	1
K18 [22]	0.29	0.85	0.21
K19 [33]	0.24	0.80	0.22
K17 [39]	0.33	0.92	0.11
O04 [39]	0.26	0.80	0.17
K20 [51]	0.38	0.75	0
O01 [51]	0.37	0.83	0.31
O02 [51]	0.38	1	0.03
K11 [60]	0.43	0.77	0.29
K02 [84]	0.46	0.77	0.24
O03 [94]	0.62	0.70	0.22
K10 [130]	0.91	0.44	0.27
K04 [165]	0.74	0.66	0.28
K22 [185]	0.80	0.51	0.20
K16 [265]	0.92	0.45	0.25
K21 [330]	1	0.35	0.26
Secondary matrix			
Age	0.84	0.04	0.01
Soil texture	0.54	0.04	0.05
Depth to cobbles	0.20	0.24	0.02
Height above low flow	0.69	0.05	0.01

Notes: First, 13 structural measures from each of the 21 stands were compared; σ represents the standard deviation. The first axis captures 60.7% of the variability and is related to structural complexity. Next, rejuvenated stand scores from the first comparison are shown. Then, a secondary matrix containing the principal components from the 21 stands compared to age, soil texture (percentage of silt and clay), depth to cobbles, and height above summer low flow channel is shown. Boldface values represent significant correlations.

parison with other studies, we also calculated the density of logs/trees >50 cm. Pieces larger than 50 cm are common in stands older than 100 years (Table 6). Such stands even have some potential pieces above 100 cm diameter, but such pieces are only abundant in the oldest stands.

The role of conifers in early succession along the study reaches of the Queets River varies considerably from stand to stand. Young stands with abundant conifers may flank stands with none. This pattern has been witnessed on rivers elsewhere in western Washington (Van Pelt 1991). Fetherston (2005), who worked in the upper Queets drainage, showed that nearly all regen-

eration occurs on some form of woody debris. Our analysis in established stands is consistent with these prior findings, however, we determined that *Picea* is also able to colonize newly formed substrates in the absence of wood, provided there is some protection from annual flows and their associated abrading disturbances (these areas occur in ephemeral or abandoned channels). Our youngest plots (O06 [3], K24 [4], and K12 [8]) were largely cobblefields sprinkled with tree seedlings, yet conifer seedlings were abundant in two of these. For example, per hectare seedling densities in plot O06 [3] were 560 *Picea* and 420 *Tsuga*; plot K12 [8] had 2500 *Picea* and 980 *Tsuga* seedlings per hectare. A vast majority of these plants were <10 cm tall. Young conifer seedlings can be killed by burial or washed away during an inundation event, but established trees, especially *Picea*, readily survive and have the ability to develop adventitious roots from the newly buried stem.

Conifer seedlings are at a competitive disadvantage in the resource-poor conditions of newly formed alluvial deposits. If present, however, their shade-tolerance will allow them to persist in young, deciduous stands of *Salix* and *Alnus*. Throughout the first cycle of *Alnus*-dominated forest, the soil productivity grows considerably (Balian 2001; J. S. Bechtold, unpublished manuscript). By the time conifers establish (after the collapse of this initial forest), soils are sufficiently rich to allow conifers to grow at rapid rates (Balian and Naiman 2005). The result is that, by 100–150 years, it is difficult to differentiate between *Picea* that established at the same time as the initial alder cohort and those that were secondary colonizers that came in after the collapse of the initial hardwood stand (Fig. 9). Plotted with the *Picea* data in Fig. 9 are curves for site index 42-m *Picea* stands in Alaska and British Colum-

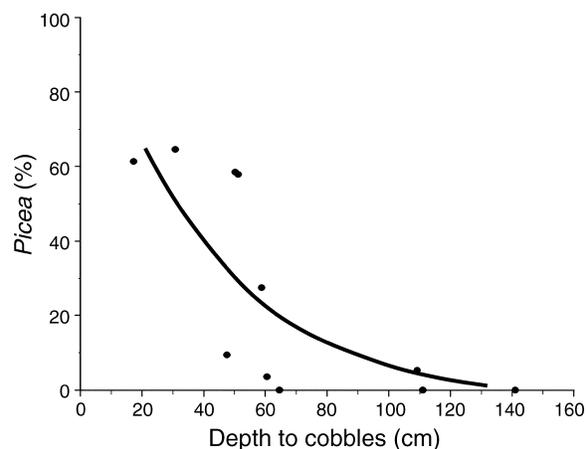


FIG. 7. Relationship between the percentage of *Picea* stems in the plot and the depth to cobbles. Only stands <100 yr old are shown (the four youngest stands, which are still on bare cobbles, were excluded). While the relationship is not strong ($r^2 = 0.63$), there is nonetheless a pattern of more abundant *Picea* on shallow soils.

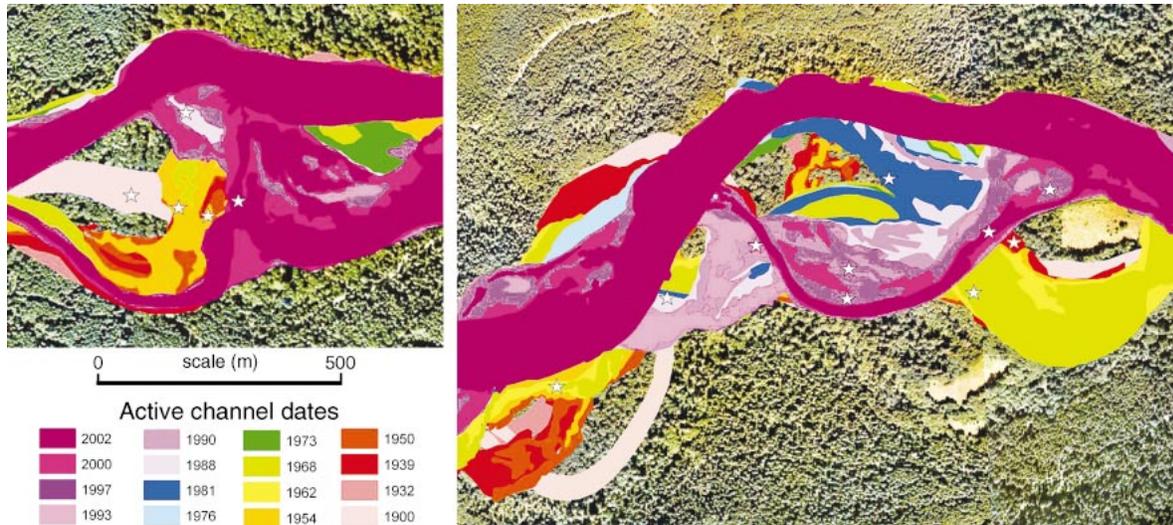


FIG. 8. Twentieth-century disturbance maps for the two study reaches. The 16 dates represented are not specific years of major river action, simply the years for which we have accurate spatial data. The maps therefore represent a minimum of river activity; a complete coverage would undoubtedly show as of yet unmapped river movements. The stars represent plot locations of stands that originated within the 20th century.

bia (Peterson et al. 1997). A 42-m site index (the height of an unencumbered tree after 50 years) represents very high productivity. The combined hindrances of slow early growth rates and delayed colonization work together to “shift” the ultimate productivity 50 years into the future (Fig. 9).

Riparian forests of the Queets River achieved old-growth characteristics early in the second century—much sooner than upland forests. The standard deviation of diameter has been used as a measure of old-growth characteristics in *Pseudotsuga* forests of the Cascades and Coast Range (Spies and Franklin 1991). Values above 26–30 represented old-growth stands in their study, as well in other studies (North et al. 2004).

TABLE 6. Abundance of potential LWD (large woody debris) contributions per stand.

Plot	Trees >50 cm (no./ha)			Trees >100 cm (no./ha)		
	Live	Snags	Logs	Live	Snags	Logs
Young plots	0	0	0	0	0	0
K20 [51]	0	0	0	0	0	0
O01 [51]	13.3	0	0	0	0	0
O02 [51]	0	0	0	0	0	0
K11 [60]	40.0	0	0	0	0	0
K02 [84]	60.0	0	0	0	0	0
O03 [94]	100.0	8.0	8.0	12.0	0	0
K10 [130]	136.4	11.4	11.4	45.5	0	0
K04 [165]	109.6	7.7	23.1	32.7	0	0
K22 [185]	104.6	9.2	4.6	29.2	3.1	0
K16 [265]	78.9	2.2	11.1	28.9	1.1	2.2
K21 [330]	59.4	6.3	14.6	29.2	4.2	5.2

Notes: Only endogenous wood is included. The 10 youngest plots all had zero values and were combined. Note that significant logs are not created for the first 50 years and large logs are not produced until well into the second century.

These values were reached within 200 years on the Queets River. This was due in part to the high productivity, with *Picea* diameters increasing faster than *Pseudotsuga* of similar ages from Cascadian forests. Another contributor to this high value during the second century was the rapid growth of large *Populus* trees. *Populus* can achieve heights of >45 m and diameters >100 cm dbh during the first century and maintain a dominant presence throughout the second century. Standard deviation values above 50 have previously only been recorded from the most structurally complex stands in the Pacific Northwest (Van Pelt and Nadkarni 2004).

Stand basal area and stem volume increase throughout the age sequence, as expected. As more species become important, these values rise rapidly to maximums of about 100 m²/ha and 2000 m³/ha. While these values are large, they are not uncommon in Pacific Northwest old-growth forests. The open nature of these forests prevents values attaining the 130 m²/ha and 3000 m³/ha that a superlative *Pseudotsuga* forest could obtain (Van Pelt and Franklin 2000, Van Pelt and Nadkarni 2004). Crown volumes, however, continue to increase to values in excess of 200 000 m³/ha, which with the exception of certain *Sequoia* forests (Van Pelt and Franklin 2000), are among the highest values known. Ironically, the more open canopy allows the dominant *Picea* to develop unusually large and deep crowns, leading to these record crown volumes.

The Queets Valley has many well developed stands of *Populus*, which can dominate stands during their second century. Many stands include individuals >50 m in height, including the tallest currently known. However, younger stands often have no *Populus*, beg-

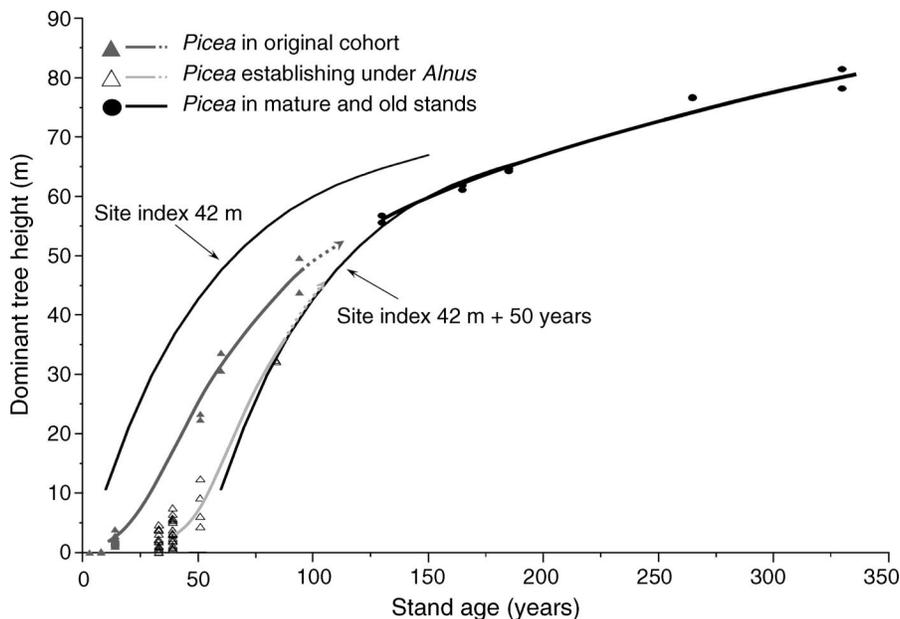


FIG. 9. Growth of *Picea*. Two dominant early growth patterns of *Picea* among our plots are illustrated by the triangles and gray lines. Site index curves for highly productive *Picea* sites appear as thin black lines (Farr 1984, Peterson et al. 1997); 42 m refers to the height of an unencumbered tree after 50 years. The two curves differ only in that one has been shifted 50 years. *Picea* trees in the younger plots were grouped into two categories based on their age vs. the stand age. Filled triangles represent trees in plots that established concurrently with *Alnus* and *Salix*. The open triangles represent those sites where *Picea* established in the understory of an *Alnus*–*Salix* forest. The filled circles represent the tallest two trees from all stands >100 yr old. Both early colonizers on poor soils and late colonizers on good sites, even if their ages are several decades apart, end up with similar conditions after the first century.

ging the question as to the origin of the *Populus*-dominated stands. *Populus* on newly formed bars often show evidence of heavy browsing by native elk. Population fluctuations of elk have been dramatic since the influx of western European humans in the mid-19th century, which have some bearing on the current riparian forest conditions regarding *Populus*. A general decline in elk numbers from coastal regions of the Pacific Northwest was witnessed throughout the latter half of the 19th century (Washington Department of Fish and Wildlife 2004) at the same time that wolves, a primary predator, were eliminated from the park. Within the 20th century, populations have fluctuated from an estimated 2000 animals on the Olympic Peninsula in 1900 to a peak of over 15 000 animals in 1980 (Ferry et al. 2001). The current estimate for the Peninsula is 11 000, 4000–5000 of which reside at some point within Olympic National Park and 3500–4000 of which never leave the Park.

Apart from heavily browsed *Populus* seedlings and two sites with an occasional tree, this species is nearly absent from all stands less than 90 years of age. Initial establishment of *Populus* can be heavily substrate as well as water level dependant (Braatne et al. 1996). Within the *Salicaceae*, *Salix* tends to do well in gravel and cobbles, whereas *Populus* performs better on moist sands and silts (Van Pelt 1991). Along many Pacific Northwest rivers of this size, newly formed bars are

composed of sands and silts; along our study reaches of the Queets River the newly formed surfaces are composed largely of cobbles. The extremely dynamic nature of annual fluctuations of the Queets maintains a cobble-dominated system far down into the valley. It may be only under extreme circumstances that moist sand and silt are present at the time of *Populus* seed dispersal in this section of the valley. The combination of lack of ideal colonization substrates, heavy elk populations, and a paucity of predators throughout most of the 20th century may have led to the situation of very few *Populus* in young stands. Ripple and Beschta (2003, 2004) have observed changes in vegetation patterns in Yellowstone National Park mediated through behavior changes in elk foraging in riparian zones associated with reintroduction of wolves.

The successional fate of these forests, given enough time by the river, is unclear. Fonda (1974) indicated that *Picea* was successional to *Tsuga* in the oldest terraces, while McKee et al. (1982) found that there was enough *Picea* regeneration on the oldest riparian surfaces to allow the maintenance of this species. While we recorded that *Tsuga* had its highest abundance in the oldest stands, *Picea* regeneration was also present in smaller numbers. The longer life of *Picea*, when combined with the relatively open canopy of the oldest stands, might combine to allow persistence in the stand. However, our chronosequence is too short, even at

300+ years, to make a definitive assessment. Many of the oldest stands in the Queets Valley have been eliminated by river movements, thus making it difficult to adequately determine the successional dynamics between these two species. It is our feeling that while the adjacent glaciofluvial and glaciolacustrine terraces share many characteristics with the oldest alluvial surfaces, their soils, site productivity, and successional history are sufficiently different to warrant leaving them out of an analysis of riparian structural development (Thackray 2001; J. S. Bechtold, *unpublished manuscript*). In addition, merely identifying the contact zone between ancient alluvial sites and glacial terraces is difficult, once the pioneering cohort of trees is gone. Any relief in the contact zone will have led to slight soil mixing over the millennia. It should be noted that many very old, pure *Tsuga* forests are present in the Queets Valley, but these seem to be restricted to the glacial terraces.

A successional model for riparian forests in an unconfined rain forest alluvial valley

On the Queets River, the formation and destruction of riparian forests is a relatively continuous process influenced by external factors (e.g., floods), internal factors (e.g., succession), and past events (e.g., channel movements). The Queets River valley floor reveals a four-dimensional gradient of disturbance, with each forested landform reflecting a specific history of disturbance and successional processes. The inherent complexities and heterogeneities encountered in this investigation follow a complex but understandable patterns that can be summarized in a successional model. The model consists of primary and secondary successional pathways with reasonably clear mechanisms underpinning the ultimate expression of the vegetative community. The successional model provides for various successional trajectories dependant on spatial location and elevation relative to the main channel (Fig. 10). The nomenclature was developed concurrently with a model describing the origin, development, and attributes of fluvial landforms, with respect to forests, soils, litterfall, and fluvial deposits of large wood (Latterell 2005).

Primary biophysical pathway.—The primary biophysical pathway illustrates the more common pathway in meandering sections of the Queets. The river gradually changes its course from year to year, causing adjacent forests to be removed on the outward curve while new surfaces are formed on the inward bend. The location of jam-forming wood diverts the flow of water allowing a surface to develop behind the jam. This results in bar formation that gradually undergoes aggradation through inundation and siltation. The pioneer bar represents a recently formed gravel bar that is being colonized by tree species. These surfaces, due to their proximity to the active channel, both in terms of height and horizontal displacement, will be under water for a

good portion of the winter high flows, at least during their formative years. *Alnus*, *Salix*, and to a lesser degree, *Populus* seem to be the only species able to survive well through this stage. These surfaces are also subject to disturbance by high flows and the occasionally large debris that are carried by these flows.

Incision (river downcutting), accompanied by less frequent inundation ‘lifts’ this surface, allowing more protection to the young trees. Concurrently, less frequent inundation and the presence of many young stems trap progressively finer sediment. Very dense stands of young trees result on what we term the developing floodplain, as illustrated by plots K09 [11], K15 [12], and K18 [22]. Conifers are sometimes excluded from these stands for several decades, but they eventually invade. The timing of this invasion depends in part on soils, proximity to inundating flows, competition from grasses and trees, and tree mortality. This can occur early (plot O04 [39], 15 years), as the *Salix* die (plot K19 [33], 24 years), or as the *Alnus* die (plot 17 [39], 30 years). The established floodplain is inundated less frequently, and the inundations are of low velocity, allowing the established trees to grow relatively undisturbed. This is accompanied by intense, within-stand competition among the young trees, of which 90% of the stems die during this period.

Once the relative height of the surface is high enough to escape flooding, the floodplain becomes a terrace. This terminology is consistent with other, earlier research and seems to best describe the environment within the Queets Valley (Fonda 1974, McKee et al. 1982, Peterson et al. 1997). However, the extreme variability of flow levels (normally, annual discharge varies by two orders of magnitude) are such that lower terraces may indeed be inundated, however briefly and infrequently. The transitional fluvial terrace is the youngest surface free from flooding. In many cases, the vegetation may be similar to some established floodplain forests. The difference is in their flooding regime (usually in the form of brief, low-velocity, flood events), which may not result in significant mortality. It is at or about this time that the dominant *Alnus* begins to succumb to root disease, stem rot, windthrow in wet soils, or a combination thereof. *Picea* is often present at this point in either small or large numbers, at which point they increase both their growth rates and numbers, usually establishing on wood present in the understory.

Once conifers become established on the now-rich soils, the forest develops rapidly into a multistructured, multispecies stand termed the mature fluvial terrace (plots O03 [94], K10 [130], K04 [165], and K22 [185]). These typically second-century forests grow very rapidly, many with a strong *Populus* component. During the second century, now that inundations from river floods are restricted, these forests begin to develop healthy populations of *Acer circinatum*, *Acer macrophyllum*, and *Tsuga*. *Alnus* does not make it through

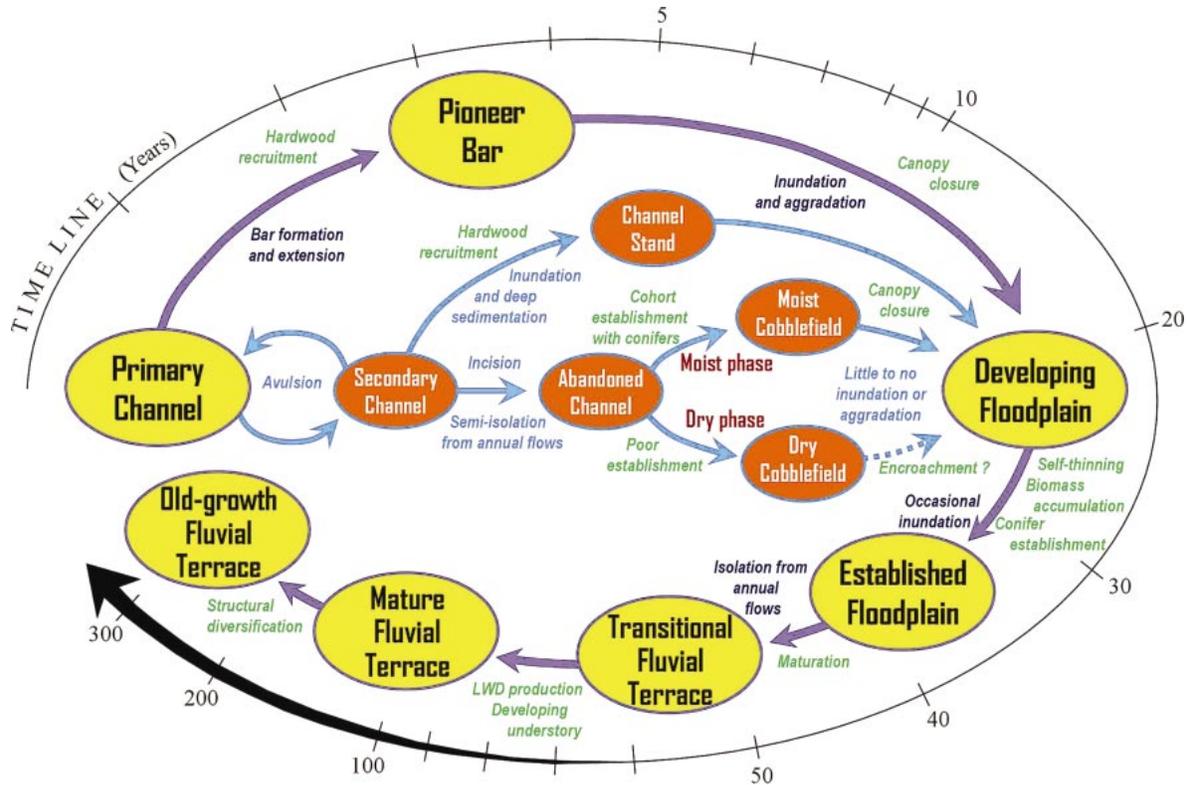


FIG. 10. Biophysical model for the middle Queets Valley. Purple arrows indicate the primary biophysical pathway, while the light blue arrows indicate possible secondary pathways. Yellow is used to indicate the primary landforms along the primary biophysical pathway, while orange indicates landforms along the secondary biophysical pathway. Dark blue text refers to geomorphic events occurring during that stage of the pathway, whereas green text relates to forest developmental events. The outer curve represents an approximate time line of these developments. Keep in mind that all landforms can return directly to the primary channel box during severe flood events.

this second century. The few individuals in our oldest plots are younger trees that managed to establish within an existing stands on mineral soil from tip-up mounds or the rare brief inundation. Similarly, the *Populus* component, while fast-growing and occasionally dominant during this second century, decay rapidly, and few trees survive into the third century. Ultimately, if allowed to fully develop before again being reclaimed by the river, an old-growth fluvial terrace will result, dominated by *Picea*, *Tsuga*, and the two species of *Acer* (plots K16 [265] and K21 [330]), all four of which seem to be able to maintain some form of regenerative component in perpetuity.

Secondary biophysical pathway.—Avulsion events may take the landforms on a different biophysical pathway, and thus a different vegetative successional trajectory. Avulsions can move the main river channel to a new location (Fig. 10). If the channel is still subject to occasional seasonal inundation and aggradation, very deep soils with high proportions of sand and silt can result. These channel stand landforms typically fill with *Salix*, *Alnus*, and then grasses. The relatively rich soils attract ungulates that, through herbivory, often maintain them as predominantly grassy *Alnus* glades

for many decades (plot O02 [51], K20 [51]; Jenkins and Starkey 1984, Riege and del Moral 2004). Plot O02 [51] had the deepest soils of any of our plots, and even after 51 years there are still no conifers present throughout most of the stand.

Contrarily, sections of the Queets that avulsed, and were accompanied by an incision of the active channel, can leave the newly abandoned channel above typical overflow levels. Succession here may proceed in a much more disturbance-free environment. These abandoned channels and the near-edge surfaces may escape chronic inundation and deposition, resulting in an environment where small conifer seedlings may survive. As succession proceeds, these moist cobblefields do not accumulate deep layers of silt. Silt, if it occurs, is often only a few centimeters or decimeters above the cobbles that formed the original channel bed. These stands are more likely to have conifers sharing dominance during the first wave of *Salix*–*Alnus* forest. Any partly buried wood present also greatly aids in conifer establishment. Isolation from annual disturbances in the form of flowing water and waterborne debris allows the small conifer seedlings to successfully colonize (plot K12 [8]). Based on the aerial photo, soil depth,

and soil texture analyses, four of the plots younger than 100 years codominated by *Picea* were the result of incision events—events where conifer seedlings were allowed to develop where major aggradation and inundation events were minimized. In these stands, the *Salix* and *Alnus* mature concurrently with *Picea*, resulting in mixed stands (K08 [14], plot O01 [51], plot K11 [60], plot O03 [94]).

The highest portions of newly created surfaces may be relatively free from inundations for a number of reasons. Spatially large surfaces may develop natural levees near the edges where brief inundations deposit the bulk of their sediment, both lifting the inundation level as well as preventing much of the fine sediment from reaching the center. Further, an avulsion/incision event could create an elevated surface away from an annual flood zone. The result is a dry cobblefield, many of which are often slowly colonized by *Racomitrium* (a drought-tolerant moss) and weedy annuals. Tree or shrub regeneration is poor or absent on these sites and even tree encroachment from the edges appears to be slow. Plot K02 [84] had the shallowest soils of all but the youngest stands, which may indicate existing as a dry cobblefield early in its development. In addition, most of the stems date from the late 1950s to the early 1960s, even though a few stems of *Picea* colonized earlier and a few stems of *Alnus* date to the 1920s. This could indicate slow colonization or slow encroachment from the edges.

CONCLUSION

Questions regarding the dynamics of forest succession, along with the delivery, distribution, and roles of large wood, fueled our initial explorations into the dynamics of riparian trees in alluvial lowland floodplains of the Pacific coastal rain forest. Within the Queets Valley, the biophysical cycle created by dynamic rivers interacting with highly productive soils and fast-growing trees, which in turn are removed by the river but to some extent influence the river movements themselves, make the alluvial forests of the valley some of the most dynamic and diverse in the Pacific coastal ecoregion.

The substrate origin and its relationship with the river during the first few years appear to be crucial. In anastomosing rivers such as the Queets, many situations of early substrate formation exist. The common scenario of bar establishment, inundation and deposition, and aggradation gradually results in the substrate “rising” relative to the water level certainly is common along the Queets. Other scenarios have the river avulsing to a new location, followed by incision, leaving the newly formed surface to proceed through succession with only minor further disturbances. And, of course, many scenarios exist that fall in between these two extremes. Months of submersion during the winter, frequent floods, and encounters with the large, waterborne debris can be hard on the survivability of a tiny

tree seedling. Substrates that go through a more typical meandering scenario are less likely to have a significant conifer presence during their first wave of growth. The successional paths young surfaces experience can be quite varied.

Ultimately silt deposition and soil development do occur, to a greater or lesser degree, which combined with several decades of *Alnus* occupation, leads to rich and productive soils. At this point, the differences of early formation blur, and succession proceeds toward a structurally complex *Picea-Tsuga* forest. This succession is often interrupted as sites are reclaimed by the river. In our study reaches, 81% of the alluvial valley floor was less than 100 years old. Small sections of landforms may escape the river for three or four centuries, possibly more, but will ultimately be reclaimed. Despite the apparent levels of chaotic destruction the riparian vegetative community is highly resilient as it quickly reorganizes into a diverse and productive ecological system via several possible successional pathways.

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APPENDIX A

A table showing regression equations used for calculating wood volume (*Ecological Archives* M076-011-A1).

APPENDIX B

A table showing the years, scale, type, and sources of the photo series used in the GIS analysis (*Ecological Archives* M076-011-A2).

APPENDIX C

A table showing log characteristics for each site (*Ecological Archives* M076-011-A3).

APPENDIX D

A table showing snag characteristics (*Ecological Archives* M076-011-A4).