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Abundance and Production of Riparian Trees in the Lowland Floodplain of the Queets River, Washington

Estelle V. Balian,[1,2] and Robert J. Naiman[1]*

[1]School of Aquatic & Fishery Sciences, University of Washington, Campus Box 355020, Seattle, Washington 98195, USA
[2]Freshwater Biology, Royal Belgian Institute of Natural Sciences, 29 rue Vautier, 1000 Brussels, Belgium**

Abstract

Riparian zones associated with alluvial rivers are spatially dynamic, forming distinct vegetative mosaics that exhibit sharp contrasts in structure and processes related to the underlying biophysical template. The productivity of riparian plants, especially trees, influences streamside community characteristics as well as the forms and fluxes of organic matter to adjacent streams – thereby strongly impacting patterns of channel morphology, water flow, sedimentation, and habitat in rivers. As part of a comprehensive investigation of riparian dynamics in coastal rain forest rivers of the Pacific Northwest (USA), we examined riparian tree abundance (density, basal area, and biomass) and rates of production (basal area growth [BAI] and bole wood biomass increase [P]) of seven common species – red alder (*Alnus rubra*), Sitka spruce (*Picea sitchensis*), bigleaf maple (*Acer macrophyllum*), western hemlock (*Tsuga heterophylla*), black cottonwood (*Populus trichocarpa*), vine maple (*Acer circinatum*) and willow (*Salix* spp.) – in the lowland floodplain of the Queets River (Olympic National Park), Washington. Measurements were made annually for three years (1999 – 2001) in 16 permanent plots on three biophysical templates that formed a toposequence – active floodplain, young terrace and mature terrace. Stem density was highest in the active floodplain (~27,000 stems/ ha), decreasing in the young terrace (~2,700 stems /ha) and the mature terrace (~500 stems/ha). Basal area and total stem biomass were lowest in the active floodplain (~16 m^2/ha and ~18 Mg dry weight/ha, respectively) and higher on the young terrace (~32 m^2/ha and ~134 Mg dry weight/ha) and on the mature terrace (~69 m^2/ha and ~540 Mg dry weight /ha). Total plot-scale BAI was not significantly different among the physical templates with mean values ranging from approximately 1.4 (low terrace) to approximately 2.8 m^2/ha/y (active floodplain). In contrast, P was significantly higher on the mature terrace (10.3 Mg/ha) than the active floodplain (3.2 Mg/ha) but there was no significant difference between young terrace (6.5 Mg/ha) and mature terrace. For the entire Queets River floodplain (57 km^2 over 77 km of river length), the mature terrace contributed 81% of the total annual production (28,764 Mg) whereas the active floodplain and young terrace accounted only for 5 and 14%, respectively. Overall, we show that riparian trees grow quickly in this coastal Pacific Northwest system and that the older riparian forests on mature terraces are the main contributors to stem production at the plot and floodplain scales for at least 350 years after stand initiation. This suggests that, in combination with the rapid lateral migrations of many alluvial rivers, the older riparian forests on those terraces are important and sustained sources of organic

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*Corresponding author; e-mail: naiman@u.washington.edu
**Current address for Estelle V. Balian.

matter (especially large woody debris, LWD) that, over decades to centuries, shape the character of coastal rivers in the Pacific Northwest.

Key words: Pacific Northwest; basal area growth; tree growth; stem production; Riparian forest; production dynamics; alluvial river.

Introduction

Riparian forests associated with alluvial rivers may be key to understanding how and why the riverine systems are so dynamic and productive. Interactions between geomorphology, hydrology and riparian-derived large woody debris (LWD) in alluvial floodplains modify channel morphology and shape the nature of riparian forests throughout much of America's coastal Northwest region (Gregory and others 1991; Montgomery 1999; Naiman and others 2000, 2005a, b) – as well as in many other forested mountain regions (for example, Gregory and others 2003; Tockner and others 2003). Riparian forests are especially important because they determine the characteristics and the rates of nutrients and organic matter fluxes to streams, including LWD. Riparian-derived materials shape biotic communities and underpin processes related to channel morphology, flow conditions, sedimentation, and habitat complexity (Bilby and Bisson 1998). Forest productivity is especially important in shaping and modifying many of these physical processes.

Comparative data on tree production dynamics are important for understanding the interplay between channel movement and the ability of riparian forests to supply LWD of sufficient sizes and quantities to maintain riverine characteristics for the long term. Coastal alluvial rivers may annually move 10's of meters laterally, reshaping wide floodplains every 300–900 years (O'Connor and others 2003). In the process, forests are undercut and trees topple into the river. The rapid lateral river migrations present a conundrum. Riparian trees on floodplains 'appear' to quickly grow to large sizes but, before being undercut by lateral channel movement, are growth rates sufficient for the trees to attain sizes that can significantly contribute to the initiation of ecologically important LWD accumulations? Further, are riparian areas with large trees sufficiently abundant to provide a sustained source of LWD? These and other related questions fueled our initial explorations into the production ecology of riparian trees in a semi-pristine lowland floodplain of the Pacific Coastal Rainforest within the Olympic National Park, Washington.

Riparian forests in the Pacific Northwest are highly valued but little information on tree production exists. Previous observations primarily focus on hardwoods and shrubs (Campbell and Franklin 1979) or commercially valuable species like Douglas-fir (*Pseudotsuga menziesii*; Means and others 1996). Most riparian production studies in the Pacific Northwest are from constrained high-gradient headwater channels having narrow riparian corridors dominated by conifers (Edmonds and others 1993; Pabst and Spies 1999; Acker and others 2003). Increasingly, attention is being focused on large floodplains with heterogeneous physical conditions and species composition, and a greater abundance of hardwoods (Pabst and Spies 1999; Nierenberg and Hibbs 2000; Harner and Stanford 2003; Naiman and others 2005a). Nevertheless, information on riparian tree abundance and production remains limited.

In contrast, species composition (Lee 1983; Hanley and Hoel 1996) and successional dynamics (Fonda 1974; Agee 1988; Van Pelt 1991; Fetherston and others 1995; Poage and Spies 1996) of alluvial floodplains in the Pacific Northwest are better known. Younger stands tend to be dominated by red alder (*Alnus rubra*) and Scouler's willow (*Salix scouleriana*), and older stands tend to be dominated by Sitka spruce (*Picea sitchensis*) and occasionally western hemlock (*Tsuga heterophylla*) or western redcedar (*Thuja plicata*). Cottonwood (*Populus trichocarpa*) and bigleaf maple (*Acer macrophyllum*) are of intermediate dominance in older stands. The combination of frequent disturbance, patchy soils, uneven subsurface water flows, and variable nutrient fluxes drive heterogeneous patterns of vegetation colonization and growth by creating distinct biophysical templates on floodplains. Our use of the term 'biophysical template' refers to the physical environment that governs biotic responses (Webster and Meyer 1997; Urban and others 2000) and, to some extent, may be equated with the terms 'zone' and 'patch'.

We identified three major physical templates differentiated by their geomorphology: active floodplain (for example, gravel bars colonized by shrubby willow and red alder), young terrace (for example, red alder dominated stands in old main or side channels), and mature terrace (for example, stands dominated by coniferous species). We examined the stand characteristics of these templates, of a variety of ages, to quantify production

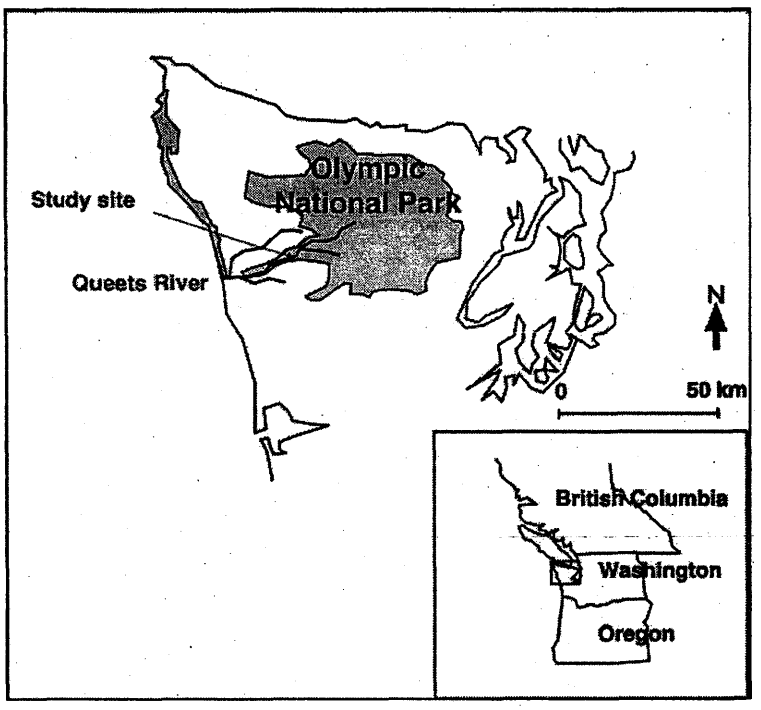

Figure 1. Location of the Queets River in the Olympic National Park, Washington.

dynamics. The biophysical templates and the associated vegetation represent, in general, a century-scale toposequence in this system (Van Pelt and others 2005). Our specific objectives in this article are to:

1. Quantify the density, basal area, and standing biomass of dominant riparian trees and evaluate variation in these attributes among and within physical templates.
2. Empirically describe tree production dynamics (that is, growth capacity and total production) among and within the biophysical templates in relation to the toposequence.
3. Estimate template-scale patterns of total stem production over the entire floodplain.
4. Develop a temporal model of productivity for each species.

Study Site

The Queets River catchment (1,157 km^2), on the west coast of Washington's Olympic Peninsula, lies mostly within Olympic National Park, and is one of the most pristine lowland floodplains in the western continental United States (Figure 1). Although there was some harvest of riparian trees by early settlers (ca.1890 and on a very restricted basis through the 1950's), the watershed is mostly natural and fire is rare (return interval ~450 y). The river originates from glaciers on Mount Olympus. The area is characterized by a uniformly wet and mild climate with dry summers, and high precipitation (~300–600 cm/y) during autumn and winter (Franklin and Dyrness 1973).

The study site, a 1-km long island and adjacent riverbank approximately 26 km from the Pacific Ocean, experiences repeated winter floods that modify channel morphology (Figure 2). Discharge varies from ~8 m^3/s in July–September to more than 3,000 m^3/s in winter, with a year-round mean discharge of ~120 m^3/s (US Geological Survey gauging station #12040500). Substrate is mainly coarse sediment (>50 mm diameter) supporting an extensive hyporheic zone (Clinton 2001). Soils on mature terraces are Entisols (Huel series) composed of moderately well-drained loamy fine sand with a weakly developed A and one or more C horizons (Bechtold and others 2003).

During the three years of data collection (1999–2001) there were only small deviations from long-term averages in precipitation and temperature. Precipitation in 1999 was 18% greater than the annual average (2773 mm; US Geological Survey weather station #451496). Growing degree-days (that is, sum of mean daily temperature for days between 10 and 30°C) in 1999 (572°C) was 12% lower than the 10-year-mean (652°C). Precipitation in 2000 was 26% lower than the annual

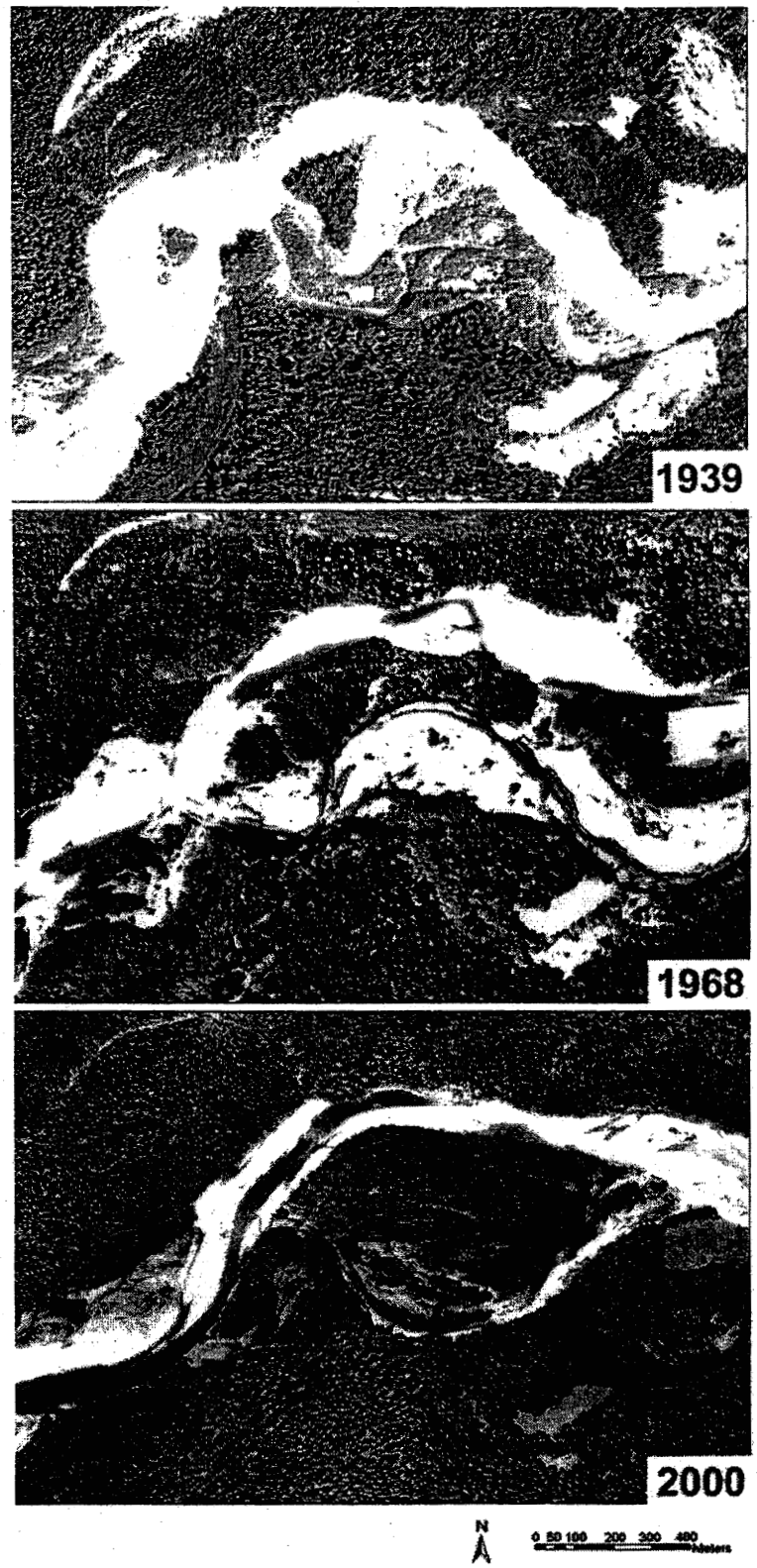

Figure 2. Dramatic physical shifts in the Queets River over 61 years illustrate the river's ability to drive spatial and temporal heterogeneity in the riparian system. The aerial photos (1939, 1968, and 2000) are of the main study site. Geographic coordinates are NAD 27, UTM 10T, 42800 E, 5273500 N.

average but the growing degree-days (629°C) were close to the 10-year-mean (−4%). Winter discharge followed the same trend as precipitation; 1999 had higher flows than the annual average and 2000 had lower flows with no unusual high flows.

Physical Templates and Successional Patterns

Physical templates in the Queets River floodplain reflect interactions between channel movements, sediment and flow regimes, logjams, and vegetation development. Logjams initiate bar formation, which creates suitable conditions for vegetation establishment (Abbe and Montgomery 1996, 2003; Fetherston and others 1995) that follow complex successional pathways. In general, red alder and willow (Scouler's willow and Sitka willow; *Salix sitchensis*) quickly colonize these bars and increase substrate stability and fertility (Bechtold and others 2003; Naiman and others 2005a). Normally, red alder remains dominant for 60–80 y and is replaced by Sitka spruce and bigleaf maple. Western hemlock may appear in older stands (>100 years) and, along with Sitka spruce and bigleaf maple, can maintain a prominent presence for centuries (Fonda 1974; Van Pelt and others 2005). Due to recurrent disturbance of the floodplain forests however, hemlock normally do not have sufficient time to become the stand dominant trees, as in the upland forests. These processes result in contrasting vegetated landforms that form a toposequence: active channel with non-vegetated bars, newly formed but active floodplain colonized by willow and red alder, young riparian terraces with mature red alder and young Sitka spruce, and mature riparian terraces dominated by Sitka spruce and occasionally western hemlock (Table 1). On the mature terraces, black cottonwood and big leaf maple are intermediate species and vine maple dominates the lower canopy layer on older surfaces. Although western redcedar and Douglas-fir are rare in the floodplain forests they are more often associated with Sitka spruce in the surrounding uplands (Franklin and Dyrness 1973).

Methods

Plot Characteristics

Collectively the plots spanned geomorphic/vegetative landforms from active floodplain to mature riparian terrace, constituting a toposequence. Aerial photographs (1/12,000) and field surveys were used to establish 16 long-term study plots, ranging in size from 625 to 2500 m^2 (Table 2), and grouped according to three physical templates: active floodplain, young riparian terrace, and mature riparian terrace. No plots were established in the active non-vegetated channel or on glacial outwash terraces.

Stand age in year 2000 was determined for each plot from increment cores collected from ten stand-dominant trees and counting growth rings of the oldest tree. Subsequent investigations have shown this to be a valid approach (R.J. Naiman, unpublished data). Where trees were too small to be cored (diameter < 7 cm), such as in the willow-alder plots, ten stems from the same stand but outside the plot, were cut.

Aerial photos taken from 1939 to 2002 clearly illustrate the successional process of stand development, allowing reconstruction of the recent floodplain history and the colonization process in the study area (O'Connor and others 2003; J.J. Latterell and R.J. Naiman, unpublished data). In mature riparian terrace plots, the dominant trees are coniferous and normally, but not always, establish after the red alder stage (that is, several decades after stand initiation). Other studies and our own observations suggest that, on average, Sitka spruce over-top red alder approximately 50 years after stand initiation and that western hemlock may establish after about 120 years. Consequently stand age was estimated by adding 50 years to maximum tree age when the oldest tree was Sitka spruce and 120 years when it was western hemlock (Table 2). Resulting stand ages were confirmed by further investigations of landform ages and colonization processes in the Queets floodplain (Van Pelt and others 2005).

The size distribution of sediments (fines, gravel, cobble) and depth to cobbles was measured (Bechtold and others 2003), except in several terrace plots where the depth was more than 1 m (Table 2). Additional information on soil properties (percent moisture, pH, organic matter, total nitrogen, total phosphorus) is from companion studies by Balian (2001) and Bechtold and others (2003). Distance to the river margin (from plot centers) and the height above surface water at low flow provided an index of flooding.

Stem Density, Basal Area, and Biomass

In low-density plots (<1500 stems/ha), the diameter of all living stems larger than 1 cm was measured. In medium (1500–4000 stems/ha) and high-density plots (>4000 stems/ha) the diameter of all living stems larger than 1 cm was measured in ten randomly selected 25 m^2 sub-plots within each plot. Willow was surveyed without differentiating species. Measurements were taken in April–June 1999, April 2000, and May 2001. Outside bark diameter was measured at breast height (DBH) for trees with DBH greater than 7 cm and at the stem

Table 1. Basic Typology of Biophysical Templates in the Queets River Floodplain

Geomorphic Class	Age (years)	Morphology	Inundation Frequency	Vegetation Cover	Stand development	Sediments
Active channel	0–5	Low-relief depositional bars and shoals, pools, and riffles	Throughout much of the year	Absent or <2m *Salix, Alnus, Populus* pioneers patchily distributed	Fluvial disturbance and legacy creation (deposition of LWD & sediment), pioneers	Exposed cobbles with fines in interstices
Incipient floodplain	5–15	Emergent or abandoned bars and islands (usually tear, crescent, or wedge-shaped) with high surface relief	Annually or semi-annually during winter storms	*Salix, Alnus, Populus* saplings in dense thickets 2–10 m, *Picea* seedlings, mosses, forbs, grasses	Canopy closure by pioneer cohort, conifer establishment	Pulsed formation of sand cap through heavy sand & silt deposition in lee of vegetation during floods
Young riparian terrace	15–70	Elevated, uneven shelves of variable shapes sculpted by lateral channel movement	Interdecadally	Open stands dominated by *Alnus* and *Populus*, remnant *Salix*, echelons of *Picea* in understory, grass and forbs	Maturation of pioneer cohort	Modest aggradation of silt & clay in overbank deposition
Mature riparian terrace	70–100's	High, rolling benches usually flanked on opposite sides by valley walls and incipient floodplain or young terrace	Almost never flooded	Mature *Picea* forest with *Acer* and *Populus*, replaced by *Tsuga*	Vertical and horizontal diversification, pioneer cohort loss	Fixed 1–2 m sand & silt cap underlain by cobble

**Data (condensed from Latterell and others University of Washington, unpublished data). Stand development stages are adapted from Franklin and others 2002.*

Table 2. Characteristics of the Study Plots and Biophysical Templates: Soil and Subsurface flow

Parameter	Active Floodplain					Young Riparian Terrace			
Plot #	15	9	3	12	5	14	8	13	1
Dominant tree species	Red alder	Willow	Willow	Willow	Red alder	Red alder	Red alder	Red alder	Red alder
Plot size (m^2)	625	625	625	625	240	625	625	625	625
Max tree age (years)	8	9	9	13	13	18	23	38	41
Stand age (years)	8	9	9	13	13	18	23	38	41
Distance from channel (low flow; m)	12*	13*	105*	120	16*	100	112*	7	265
Height above channel (low flow; m)	1*	0.7*	1.7*	2	1.3*	1.2	1.7*	2	2.7*
Dominant soil fraction	Sand	Cobble	Cobble	Cobble	Sand	Sand	Sand	Sand	Gravel
Depth to cobble (m)	0.3	0.1	0.1	0.1	0.3	0.5	0.5	0.5	0.5
Soil moisture (%)	29.5 ± 7.3	25.8 ± 4.9	9 ± 2.2	20.1 ± 7.4	24.5 ± 1.5	20.4 ± 2.8	24.9 ± 6.5	17.3 ± 5.0	31.7 ± 3.2
Soil pH	5.32 ± 0.02	5.08 ± 0.26	5.33 ± 0.23	5.37 ± 0.03	5.06 ± 0.10	5.32 ± 0.02	5.42 ± 0.16	4.75 ± 0.11	4.75 ± 0.15
C/N	9.1 ± 2.2	8.6 ± 0.9	9.7 ± 1.0	11.0 ± 0.5	9.8 ± 0.7	9.5 ± 1.4	8.9 ± 1.5	8.2 ± 1.1	11.2 ± 1.0
Total carbon (mg/g)	7.4 ± 1.2	7.1 ± 1.4	6.6 ± 0.6	7.5 ± 0.5	8.4 ± 0.7	8.4 ± 2.4	10.5 ± 3.0	8.4 ± 2.2	17.7 ± 3.5
Total nitrogen (mg/g)	0.8 ± 0.1	0.8 ± 0.1	0.7 ± 0.0	0.7 ± 0.0	0.9 ± 0.0	0.9 ± 0.1	1.1 ± 0.2	1.0± 0.2	1.6 ± 0.2
Total phosphorus (µg/g)	6.3 ± 0.2	6.0 ± 0.1	7.1 ± 0.2	7.6 ± 0.1	8.0 ± 0.2	6.9 ± 0.2	6.8 ± 0.2	7.0 ± 0.2	8.5 ± 0.3
Hydraulic conductivity (10^{-4} m/s)	17.5	12.8	10.4	10.7	2.2	17.7	14.1	7.8	14.5
Water depth low flow (m)	0.9	0.8	1.7	1.7	1.2	2.2	1.1	2.4	1.2

Parameter	Mature Riparian Terrace						
Plot #	11	2	7	10	6	4	16
Dominant tree species	Sitka spruce	Sitka spruce	Sitka spruce	Sitka spruce	Sitka spruce	Sitka spruce	Sitka spruce
Plot size (m^2)	1500	1250	900	2500	2500	2500	2500
Max tree age (years)	53	71	98	108	112	147	231
Stand age (years)	103	121	148	228	162	267	351
Distance from channel (low flow; m)	250	222	197	200	63	39*	90*
Height above channel (low flow; m)	3.5	3.5	3.5	3.5	2.5	2.5	2.5*
Dominant soil fraction	Sand/Gravel	Cobble	Cobble	Sand/Gravel	Sand/Gravel	Sand	Sand/Gravel
Depth to cobble (m)	0.2	0.1	0.1	>1	>1	>1	>1
Soil moisture (%)	33.7 ± 1.6	30.5 ± 7.7	31.8 ± 3.5	37.4 ± 1.0	31.9 ± 6.0	37.2 ± 3.6	44.1 ± 1.2
Soil pH	4.43 ± 0.10	4.49 ± 0.14	4.88 ± 0.09	5.24 ± 0.08	4.78 ± 0.09	5.17 ± 0.01	5.07 ± 0.09
C/N	14.9 ± 0.8	11.7 ± 1.4	12.8 ± 2.1	14.2 ± 0.6	9.9 ± 1.6	14.2 ± 0.5	15.1 ± 1.5
Total carbon (mg/g)	33.5 ± 6.3	17.6 ± 5.6	20.7 ± 6.8	32.3 ± 3.3	15.3 ± 4.1	28.7 ± 2.4	31.9 ± 9.1
Total nitrogen (mg/g)	2.2 ± 0.3	1.43 ± 0.3	1.5 ± 0.3	2.3 ± 0.1	1.5 ± 0.1	2.0 ± 0.1	2.05 ± 0.1
Total phosphorus (µg/g)	7.1 ± 0.1	8.2 ± 0.2	7.1 ± 0.1	8.5 ± 0.4	6.9 ± 0.3	8.6 ± 0.4	9.0 ± 0.4
Hydraulic conductivity (10^{-4} m/s)	12.8	13.7	12.0	2.5	3.8	1.3	2.5
Water depth low flow (m)	3.1	3.4	2.7	3.2	2.7	3.7	3.2

**Measured from Pebble Creek's channel.*
Measurements of soil properties (X ± SE) were taken at the beginning of the growing season (May 2001).

base for trees with DBH less than 7 cm. Stem density (stems/ha) was a direct count of all living stems in a plot (or sub-plot) and basal area (m^2/ha) was the sum of individual cross-sectional areas calculated from diameter and divided by plot area (or total area of sub-plots).

Species-specific methods were used to estimate stem biomass. Existing regression equations between DBH and stem biomass were used for western hemlock (BIOPAK; Means and others 1994). For Sitka spruce, red alder, and bigleaf maple we developed regression equations between DBH and stem biomass based on subsamples of trees measured for height (Balian 2001). Height and DBH measurements were converted to volume using a dimensional equation:

$$V = \pi r^2 \frac{H}{F}$$

Where, V = stem volume (m^3), r = tree radius (m) at breast height, H = height (m), F = tree form factor. F was approximated to 3 (cone shape) for conifers, and to 2 (paraboloid shape) for hardwoods (Hush and others 1982). Dry biomass was then calculated from volume and wood density (oven dry weight) according to Smith (1970) and Markwardt and Wilson (1935). Wood densities were assumed to be 0.43 mg/m^3 for red alder, 0.42 mg/m^3 for Sitka spruce, and 0.51 mg/m^3 for bigleaf maple. Finally, 20 willow with DBH less than 7 cm were harvested, their dry biomass (10 days at 60°C) determined, and a regression equation developed between diameter at stem base and dry stem biomass. We obtained total stem biomass within a plot (Mg/ha) by aggregating individual stem biomasses and dividing by plot area.

Growth and Production

Only stem growth (basal area increment: BAI) and stem wood production (P) were addressed; leaf, branch and root growth and production were not estimated. Vine maple, a dominant tree-like shrub in the understory of mature forest stands, was included because of its local abundance. A companion study determined the best growth and production estimation methods for each species (Balian 2001). Ring-width measurements (average 1990–1999) were used to estimate annual tree-specific BAI (m^2/y) and P (mg/y) for Sitka spruce, red alder, and bigleaf maple. Sequential measurements (average 1999–2001) were used to estimate annual tree-specific BAI and P for willow, western hemlock, and vine maple. For each species, regression models were developed between diameter outside the bark and individual BAI (cm^2/y) or P (mg/y), based on the two measurement methods of annual stem diameter expansion:

(1) *Ring-Width Measurements (RWM)*: Cores were collected in late summer 2000 from 64 Sitka spruce, 41 red alder, 28 bigleaf maple, and 10 black cottonwood. Two cores were collected for each tree at breast height (~1.5 m) and the DBH recorded at the same spot. In addition, small trees (DBH < 7 cm) haphazardly selected adjacent to the study plots were cut at the stem base and the ring widths measured directly from cross-sections for red alder (26 stems) and Sitka spruce (6 stems). Ring width was measured for ten growth years (1990–1999) using standard dendrochronology procedures (Phipps 1985; Stokes and Smiley 1968).

(2) *Sequential Measurements of Diameter (SM)*: Increment cores could not be taken for the other species so we used sequential measurements of diameter. Sixty-eight willow, 20 vine maple, and 17 western hemlock were numbered individually and measured annually for diameter growth. Each tree was tagged and the measurement point marked to ensure that diameter was measured at the same spot each year. All diameter classes were represented in each plot for the species present. Diameter was measured in spring 1999, 2000 and 2001 at breast height for stems with DBH greater than 7 cm and at the stem base when stems were less than 7 cm DBH. The resulting data cover two growth-years: 1999 and 2000.

Measurements of annual stem diameter increment (DI) for individual trees were converted to annual BAI (Hush and others 1982):

$$\mathrm{BAI} = \frac{\pi}{4}D_2^2 - \frac{\pi}{4}D_1^2 = \frac{\pi}{4}(D_2 - D_1)(D2 + D_1)$$

$$\mathrm{BAI} = \frac{\pi}{4}DI(D_2 + D_1)$$

Where, BAI units are cm^2/y, $DI = D_2 - D_1$ = outside-bark diameter increment (cm/y), D_1 = diameter measured at year X, D_2 = Diameter measured at year $X + 1$. Biomass equations based on outside-bark diameter were used to convert outside-bark DI into annual P. The RWM measurements gave inside bark diameter increments that were converted to outside-bark increments by adding the bark thickness measured on the cores. We assumed bark thickness to be constant over ten years.

Individual annual BAI and P were measured by SM (averaged over 2 years) for willow, vine maple and western hemlock and by RWM (averaged over 10 years) for red alder. Regression analysis was

Table 3. Regression Models Developed to Estimate Individual Basal Area Increment (BAI; cm^2/y) and Stem Production (P; kg/y) Based on Stem Diameter Outside Bark (D) Measured at Breast Height (DBH > 7 cm) or at Stem Base (DBH < 7 cm)

Species		Model Selected to Estimate BAI	Model Selected to Estimate P
Big leaf maple	Source	No model selected (r^2 too small).	**RWM**
	Model	Use mean BAI from RWM measurements (134.3 cm^2/y)	ln (P) = 0.043 *D +0.992
	N	28	28
	D range	16.4–78.9	16.4–78.9
Vine maple	Source	Use mean BAI from SM	Use mean P from SM
	Model	measurements (2.2 cm^2/y)	measurements (1.2 kg/y)
	N	20	20
	D range	2.2–22.0	2.2–22.0
Black cottonwood	Source	Use mean BAI from RWM	Use mean P from SM
	Model	measurements (34.3 cm^2/y)	measurements (32.3 kg/y)
	N	10	20
	D range	37.9–104.4	37.9–104.4
Western hemlock	Source	**SM**	**SM**
	Model	$BAI = 2.753 * e^{-0.034D}$	$P = 1.786 * e^{-0.053D}$
	N	17	17
	D-range	11.0–71.5	11.0–71.5
Red alder	Source	**RWM**	**RWM**
	Model	$\ln(BAI) = 0.963 * \ln(D) - 0.467$	$\ln(P) = 1.73 * \ln(D) + 3.525$
	N	67	67
	D range	2.0–51.9	2.0–51.9
Sitka spruce	Source	**RWM**	**RWM**
	Model	$\ln(BAI) = 5.41 * (1 - e^{-0.0287 * (D - 6.762)})$	$\ln(P) = 5.744 * (1 - e^{-0.0298 * (D - 19.07)})$
	N	70	70
	D range	2.1–243.8	2.1–243.8
Willow	Source	**SM**	**SM**
	Model	$\ln(BAI) = 3.16 * (1 - e^{-0.337 * (D - 2.778)})$	$\ln(P) = 1.886 * (1 - e^{-0.2667 * (D - 6.21)})$
	N	68	68
	D range	1.0–8.45	1.0–8.45

used to model the relationship between stem diameter and BAI or P, and subsequently predicts BAI and P for all stems in each plot (Table 3). Summing individual BAI or P values, and dividing the total by plot surface area, provided estimates of total annual BAI ($m^2/ha/y$) or P (Mg/ha/y) for each species on each plot.

No reliable models could be developed for estimating BAI and P for vine maple and cottonwood, or for estimating BAI for bigleaf maple. Cottonwood is not well represented near the study sites (it is more abundant further downstream) and, therefore, few measurements were available. We used the means of individual BAI or P, based on SM, to estimate plot-scale growth variables for vine maple. We calculated the mean BAI or P based on RWM for big leaf maple and black cottonwood and applied them, respectively, to all individuals in the riparian community.

Regression models and total BAI and P estimates resulting from RWM and SM were compared for each species using trees surveyed with both methods (a total of 467 trees was included in the comparison) to ensure that using different measurement methods did not introduce significant differences in BAI and P estimates (Balian 2001).

Stem Production Estimates at the Floodplain Scale

Stem production estimates at the floodplain scale were extrapolated from an exhaustive digital map (that is, polygon coverage) of major physical templates on the valley floor of the Queets River. The map was created from digital geo-referenced panchromatic aerial photograph mosaics in a geographic information system (ArcMap, ESRI, Inc., Redlands, California). Original photos were 1:15,840 scale and ground resolution in all digital photos was approximately 0.75 m. The valley floor was considered to be the area from the active

channel and low gradient expanses flanked by steep glacial outwash terraces and hillslopes. Physical templates and the extent of the valley floor were manually delineated (that is, digitized) from digital imagery and topographic maps. The outer margin of the valley floor was assumed to be coincident with the distinctive gradient breaks at the toe of steep outwash terraces and hill slopes (O'Connor and others 2003), as indicated by topographic contours derived from a 10-m Digital Elevation Model (DEM; Courtesy of PRISM, University of Washington). Distinctive physical templates were manually delineated with individual, non-overlapping polygons at a fixed (1:3,000) scale of magnification. Readily observed attributes such as patch texture, color, shape, and height were used to discriminate between templates, according to the characteristics of areas where template type was determined in the field. The extent of human-impacted areas (for example, previously-logged or cultivated areas) was determined from digital georeferenced aerial photograph mosaics spanning the period between 1939 and 2002. The area of each 'patch' was calculated in ArcMap and summed for each biophysical template. Annual plot-level total P (Mg/ha/y) for each biophysical template was multiplied by total template area (ha) to obtain the contribution of each template to the total P (Mg/y) for the entire floodplain within the boundaries of Olympic National Park.

Analyses

The results are analyzed and presented at four levels of resolution: species, community assemblages (that is, plots), biophysical templates (that is, toposequence), and total floodplain. Levels of statistical significance for all tests were adjusted with Bonferroni corrections when the variances were homogeneous; otherwise we used a Tamhane post hoc test.

Variability in vegetation (stem density, basal area, standing biomass, community composition) and environmental (soil, subsurface flow, flooding frequency, and intensity) characteristics were quantified within and among physical templates. Stem density, basal area, and stem biomass were compared among species, plots, and biophysical templates. We performed a repeated measures analysis with a between-subject-factor referring to the three biophysical templates. Data were transformed (natural logarithms) to obtain a constant variance if Levene's test for homogeneity-of-variance showed non-constant error variance (Neter and others 1996).

Stem density, basal area, and stem biomass are reported as the mean of 1999, 2000, 2001 values for each biophysical template. Mean values of soil, subsurface, and flood-related variables were calculated for each template and compared among templates using one-way ANOVA and a Tamhane post hoc test.

We quantified the variability of plot-level total stem growth and production among physical templates and within templates (for all species combined and for each species separately). Annual BAI (m^2/ha/y) and annual P (Mg/ha/y), for all species combined, were compared among physical templates using one-way ANOVA and a Tamhane post hoc test. Likewise, for each species, annual BAI estimates and annual P estimates were compared among templates using one-way ANOVA and a Tamhane post hoc test.

Regression analysis was used to model the relationship between plot-level BAI and P (that is, including all species in a plot) and stand age to discern changes over time. In addition, species-specific stem growth and production were plotted against stand age to characterize the contribution of each to total production over a possible chronosequence.

Results

Biophysical Template Characteristics

Stand Age. Active floodplain plots ranged in stand age from 8 to 13 years, young terrace plots 18 to 41 years, and mature terrace plots 103 to 351 years. The youthful stands (18 and 23 years) on the young terrace were colonized by mixed willow and alder whereas the older stands (38 and 41 years) were nearly pure stands of red alder. The younger stands (103 to 148 years) on the mature terrace were mainly Sitka spruce with a few senescent red alder whereas the older stands (228 to 351 years) were mature forests dominated by Sitka spruce but with more tree diversity than the young terrace stands.

Soil Characteristics

Several soil properties that may underpin growth and production are closely allied with the toposequence. Soil C/N ratios were significantly higher on the mature terrace (± SE = 13.2 ± 0.7) but were not significantly different between the active floodplain (9.6 ± 0.4) and the young terrace (9.5 ± 0.6). Total carbon and total nitrogen concentrations were not significantly different between the active floodplain and the young terrace

Table 4. Regression Equations used to Calculate Stem Biomass as a Function of Diameter

Species	Equation	Sample Size (n)	Coefficient of Determination (r^2)	DBH range (cm)
Willow	ln (B) = 2.960 + 2.846 ln (D)	24	0.88	1.0–7.0
Red alder	ln (B) = 3.668 + 2.723 ln (D)	34	0.99	1.3–45.2
Sitka spruce	ln (B) = 2.498 + 2.851 ln (D)	41	0.99	1.0–190.0
B. leaf Maple	ln (B) = 12.202 + 0.040 D	10	0.96	39.3–89.6
W. hemlock[1]	ln (B) = 3.969 + 2.599 ln (D)	207	0.94	8.9–134.7

[1]*Equation from Biopack (Means and others 1994).*
n = number of observations.
r^2 = coefficient of determination.
B = dry biomass (g).
D = DBH (cm) for stems with DBH > 7 cm
Diameter at stem base for stems with DBH < 7 cm.

(C: 6.6 to 17.7 mg/g; N: 0.7 to 1.6 mg/g) but were significantly higher on the mature terrace (C: 15.3 to 33.5 mg/g; N: 1.4 to 2.3 mg/g; Table 2). Red alder as a nitrogen fixer may contribute to this increase in soil nitrogen (Bormann and others 1994). Soil moisture (9–44%) was also significantly higher on the mature terrace but showed no significant differences between active floodplain and young terrace. Soil moisture had higher coefficients of variation (CV; in terms of spatial variability) on the active floodplain (36%) and on the young terrace (26%) than on the mature terrace (13%). In contrast total carbon and total nitrogen had higher coefficients of variation on the young terrace, 51 and 32% respectively, than on the active floodplain (CV for total C 25% and total N 17 %) or on the mature terrace (CV for total C 43% and for total N 27%). In contrast to other soil characteristics, there was no significant difference among templates in soil acidity (pH = 4.4 to 5.4) or total phosphorus (6.0–9.0 μg/g).

In general, the plots were characterized by high subsurface hydraulic conductivity (>1 × 10^{-3} m/s) due to the underlying gravel-cobble substrate, but no significant differences could be shown among templates. Depth to the water table during late summer low flow period varied among templates with water closer to the surface on the active floodplain (0.8–1.7 m), slightly deeper (but not significantly different) on the young terrace (1.1–2.4 m) and deepest on the mature terrace (2.7–3.7 m; Clinton 2001).

Vegetation Characteristics

Stem Biomass Estimation. Stem biomass was strongly correlated with diameter ($r^2 \geq 0.88$) for all tree species (Table 4). Sample sizes were unbalanced for willow and red alder, which had fewer observations at the larger diameters and may result in some bias for estimates of larger trees. The diameter range for bigleaf maple includes only larger trees (>39 cm DBH) and therefore may be biased against smaller individuals.

Vegetation Cover. Stem density, total basal area, and total stem biomass varied significantly across and within templates (Table 5). Stem density was highest on the active floodplain, decreasing through the young terrace to the mature terrace. In contrast, basal area and total stem biomass had lower values in the active floodplain and higher values on the young terrace and the mature terrace.

Stem density, basal area, and total stem biomass varied significantly within the toposequence. On the active floodplain, stem density (12,253–38,000 stems/ha), basal area (8.0–20.8 m^2/ha) and stem biomass (5.8–24.9 Mg (DW)/ha) all showed significant differences ($P < 0.05$) among plots. Likewise, the young terrace stands were significantly different from each other ($P < 0.05$) in stem density (1,269–5,269 stems/ha), basal area (24.7–46.5 m^2/ha) and stem biomass (69.0–235.5 Mg (DW)/ha), as were the mature terrace stands in stem density (261–800 stems/ha), basal area (31.5–97.3 m^2/ha) and stem biomass (147.5 to 1,090.9 Mg (DW)/ha).

The analyses above provide evidence of trends in density, basal area, and biomass related to stand age (Figure 3). Stem density decreased as stands aged with an exponential decline in the first 20 to 30 years, slowing after 50 years. Average total stem density declined approximately 90% between 10-year-old stands in the active floodplain and 20-year-old stands on the young terrace. Total basal area and stem biomass followed the opposite trend, increasing with stand age. Total basal area doubled in the 10 to 20 years between active floodplain (8- to 13-year old) and young terrace (19- to 44-year old) stands, while total stem biomass increased 7-fold during the same period. Similar trends were

Table 5. Mean Stem Density, Basal Area, and Stem Biomass of Riparian Tree Species in each Physical Template

Tree Species	Stem Density* (stems/ha)	Basal Area* (m^2/ha)	Stem Biomass* (Mg (dry weight)/ha)
Active floodplain			
Willow	22210.7 ± 3035.3	10.4 ± 1.5	8.1 ± 1.8
Red alder	4480.0 ± 2108.4	5.1 ± 2.1	10.0 ± 4.3
Sitka spruce	18.7 ± 18.7	<0.1	<0.1
Black cottonwood	8.0 ± 8.0	0.0 ± 0.005	<0.1
Total	26717.3 ± 4584.0	15.5 ± 2.4	18.1 ± 3.8
Young riparian terrace			
Willow	1070.7 ± 631.1	4.1 ± 2.3	7.1 ± 4.3
Red alder	1563.3 ± 333.8	28.1 ± 7.0	127.1 ± 41.5
Sitka spruce	60.4 ± 41.9	0.1 ± 0.0	0.5 ± 0.0
Vine maple	6.7 ± 6.7	0.0± 0.0	<0.1
Total	2701.0 ± 734.0	32.2 ± 5.0	134.2 ± 27.8
Mature riparian terrace			
Willow	0.6 ± 0.6	<0.1	<0.1
Red alder	114.3 ± 43.6	8.4 ± 3.1	53.7 ± 20.6
Sitka spruce	246.3 ± 63.0	44.5 ± 7.3	350.1 ± 113.7
Vine maple	82.2 ± 56.8	0.8 ± 0.5	5.4 ± 4.0
Big leaf maple	24.7 ± 8.1	5.1 ± 1.9	44.4 ± 16.2
Black cottonwood	11.8 ± 6.4	7.8 ± 3.9	70.9 ± 34.6
Western hemlock	12.2 ± 5.9	2.1 ± 1.0	15.2 ± 7.1
Western red cedar	1.1 ± 1.1	0.3 ± 0.3	2.0 ± 2.0
Total	493 ± 75.6	68.9 ± 7.9	541.7 ± 128.3

**Mean value of 1999, 2000, and 2001 estimates for all plots in each physical template.*
Data are shown as $\bar{X}$ ± SE

observed over the next 100 years as basal area and biomass increased 70% while stem density decreased 75%.

Species Composition. Willow dominated the active floodplain in stem density (86%), basal area (71%), and stem biomass (52%). Red alder represented only 14% of the stems but the contribution of red alder to basal area (8–62%) and biomass (17–84%) varied strongly among plots depending on the relative sizes of red alder and willow (Table 5). Young Sitka spruce and black cottonwood (>1 cm diameter) occurred sporadically in some active floodplain plots but represented <0.2% of stem density.

Red alder was generally dominant on the young terraces (70% of stem density, 84% of basal area, and 91% of biomass). Concomitantly, willow's contribution to density (27%), basal area (16%), and biomass (10%) decreased. The young terrace supported two types of communities: younger stands (18 and 20 years) colonized by both red alder (62% and 73% of stems, respectively) and willow (26 and 37%), and older stands (38 and 41 years) colonized by mostly red alder (98% of stems for each). Sitka spruce was just beginning to appear in the understory (2% of stems, 0.1% of basal area, and <0.1% of biomass).

All plots on the mature terrace were dominated by Sitka spruce in density (48%), basal area (64%), and biomass (60%). Red alder was second in density (20%) and basal area (16%), and third in biomass (19%), although present in only two plots. Although Sitka spruce was dominant on the mature terrace, occasionally other species had a higher density (72% for vine maple in Plot 16) or stem biomass (45% for black cottonwood in Plot 10).

Growth and Productivity

Species-level Patterns. Total BAI for all species did not show a significant trend as a function of stand age, whereas total P significantly increased over time (Figure 4a). Species-specific BAI (up to 3.2 m^2/ha/y) was highest for willow in the active floodplain plots while species-specific P rates were highest for Sitka spruce (up to 13.9 Mg/ha/y) on the mature terrace (Figure 4b).

Production dynamics closely followed age-related changes in the toposequence (Figure 5). Fast

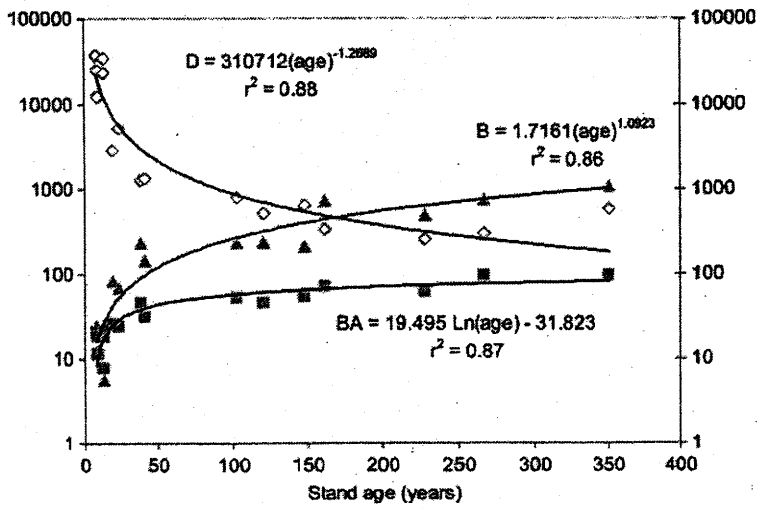

Figure 3. Temporal trends in stem density (D; stems/ha; ◇), basal area (BA; m^2/ha; ■) and stem biomass (B; Mg/ha; ▲) with increasing plot age. All trees within a plot are included.

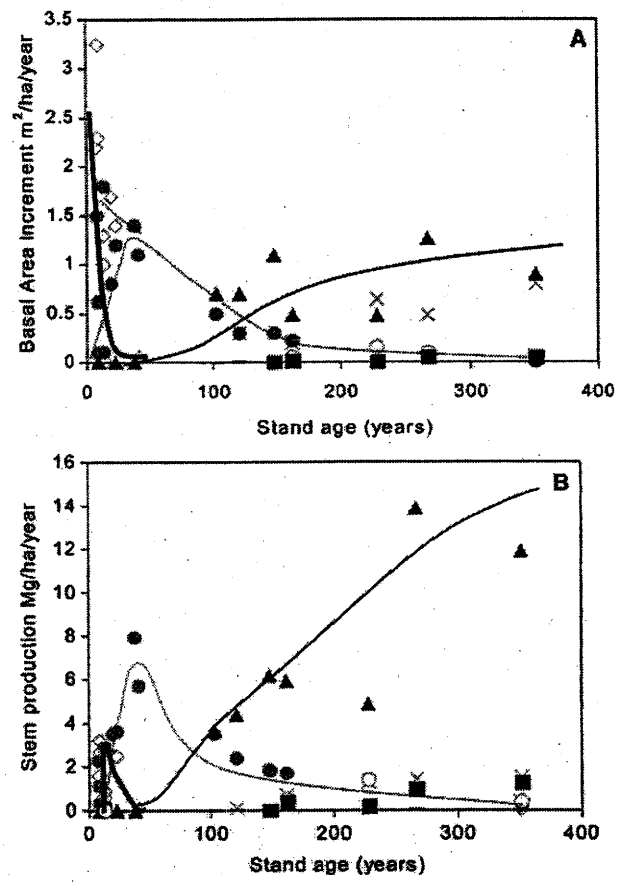

Figure 4. Basal area growth and stem production changes over time: (**A**) BAI and (**B**) P changes over time for each tree species. Trend lines added for willow (◇;—), red alder (●; ---) and Sitka spruce (▲; —). Key for other species: vine maple (-), bigleaf maple (x), black cottonwood (o), western hemlock (■).

growing communities of small willow reached maximum productivity at approximately 10 years,

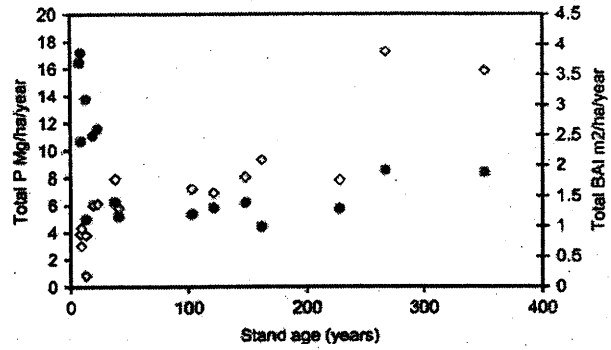

Figure 5. Total BAI (●) and total P (◇) trends over time (all tree species included).

but total P remained relatively low (up to 4.3 Mg/ha/y). Willow was replaced in the next 10 years by red alder that reached maximum productivity around 40 years with both high BAI (up to 1.4 m^2/ha/y) and high P (up to 7.9 Mg/ha/y). Finally, Sitka spruce replaced red alder with a fast and continuous increase in P between 40 and 140 years, reaching rates up to 13.9 Mg/ha/y after 150 years. The other species, present only on mature terrace plots, showed little change in productivity with increasing stand age (Figure 4b).

Biophysical Template Patterns. Total BAI was not significantly different among biophysical templates (Table 6). In contrast, P was significantly higher on the mature terrace (10.33 ± 1.63 Mg/ha) than the active floodplain (3.17 ± 0.63 Mg/ha; Table 6) but there was no significant difference between young terrace (6.46 ± 0.49 Mg/ha) and mature terrace. Within the active floodplain, BAI and P vary by 17% and 19% respectively among plots. Plot 12, colonized by very young willow, exhibited

Table 6. Stem Growth (BAI; m^2/ha/y) and Productivity (P; Mg/ha/y) Estimates for each Riparian Tree Species in the Three Biophysical Templates

Tree Species	BAI (m^2/ha/y)	P (Mg/ha/y)
Active floodplain		
Willow	2.01 ± 0.40^{a}	1.80 ± 0.50^{a}
Red alder	0.82 ± 0.35^{b}	1.36 ± 0.54^{a}
Sitka spruce	$< 0.01^{c}$	$< 0.01^{b}$
Black cottonwood	$< 0.01^{c}$	$< 0.01^{b}$
Total Average	2.84 ± 0.50^{x}	3.17 ± 0.63^{x}
Young riparian terrace		
Willow	0.80 ± 0.44^{a}	1.28 ± 0.71^{a}
Red alder	1.13 ± 0.13^{a}	5.18 ± 1.04^{b}
Sitka spruce	$< 0.01^{b}$	$< 0.01^{c}$
Vine maple	$< 0.01^{b}$	$< 0.01^{b}$
Total Average	1.92 ± 0.37^{x}	6.46 ± 0.49^{y}
Mature riparian terrace		
Willow	$< 0.01^{a}$	$< 0.01^{a}$
Red alder	$0.19 \pm 0.07b^{c}$	1.38 ± 0.51^{b}
Sitka spruce	0.80 ± 0.11^{d}	7.27 ± 1.5^{c}
Vine maple	0.02 ± 0.01^{c}	0.09 ± 0.07^{d}
Big leaf maple	0.35 ± 0.12^{b}	0.72 ± 0.26^{b}
Black cottonwood	0.04 ± 0.02^{c}	0.46 ± 0.20^{b}
Western hemlock	0.02 ± 0.01^{c}	0.42 ± 0.20^{b}
Total Average	1.42 ± 0.13^{x}	10.34 ± 1.63^{z}

a, b, c, d: For each variable, values followed by dierent letters within a physical template are significantly dierent ($p < 0.05/3$).
x, y, z: values followed by dierent letters are significantly different among physical templates ($p < 0.05/3$).

considerably lower BAI (1.1 m^2/ha/y) and P (0.8 Mg/ha/y) than other active floodplain plots. On the young terrace, older stands dominated by red alder tended to have a lower BAI (1.4 and 1.2 m^2/ha/y) than the younger mixed alder-willow stands (2.5 and 2.6 m^2/ha/y), but this trend was not found for P, which was similar in all stands (5.8 to 7.9 Mg/ha/y). In contrast, more variability was detected for P (from 6.9–17.2 Mg/ha/y; CV = 42%) than for BAI (1.0 to 1.9 m^2/ha/y; CV = 24%) on the mature terrace. Overall, the highest values of BAI were found in the active floodplain (3.9 and 3.1 m^2/ha/y), and the highest values of P were found on the mature terrace for the two oldest stands (15.8 and 17.2 Mg/ha/y).

In the active floodplain, willow contributed more (70%) than red alder to total (plot-level) BAI due to its dominance in stem density, but total P was more equally distributed between willow and red alder (56 and 49%, respectively). The largest proportion of plot-level total BAI and P was represented by red alder (58% of total BAI and 80% of total P) on the young terrace, and by Sitka spruce (56% of total BAI and 70% of total P) on the mature terrace.

Stem Production at the Floodplain Scale. The total area of the Queets' floodplain is 57.3 km^2 over a distance of 77 km, including non-vegetated surfaces. The active floodplain and the young terrace represented 8.5 and 10.8% respectively of the total floodplain area. The mature terrace covered the major part of the floodplain with 39.2% of the total area; the rest of the floodplain was wetted river channel, meadows, and second growth forest. The total stem production for the floodplain (not including meadows and second growth) reached an estimated 28,764 Mg/y across all the biophysical templates. The active floodplain and the young terrace accounted for 5 and 14%, respectively, of the floodplain's total stem production whereas the mature terrace contributed 81%.

Discussion

Production dynamics of the riparian trees are closely related to spatial position in the toposequence and to environmental factors inherent in the biophysical templates. Stand-level BAI rates are highest on young physical templates, decreasing as the trees age and species composition shifts from hardwood to conifer-dominated communities. In contrast, stand-level stem production reaches maximum values in older stands on mature terraces. Although age-related processes strongly influence production changes over time, local environmental factors introduce considerable variability in BAI and P within stands of similar age, especially on active floodplains and on mature terraces.

Stem Growth and Production: Spatial and Temporal Variation

The toposequence on the Queets floodplain is typical of many coastal alluvial rivers in the Pacific Northwest (Fonda 1974; Hawk and Zobel 1974; Helm and others 1984; Van Pelt 1991; Walker 1993). However, the combination of disturbance regimes and local geomorphic characteristics may generate stochastic events leading to a variety of community assemblages (Bonan and Shugart 1989; Halpern 1989; Cook 1996; Hughes 1997). For example, seed sources are available from older black cottonwood in mature forest stands but no regeneration was observed on bare surfaces. Preferential browsing by Roosevelt elk (*Cervus elaphus roosevelti*) and black-tailed deer (*Odocoeileus hemionus columbianus*; Bell and others 1992; Case and Kauffman 1997), or

unfavorable conditions for seedling establishment and survival (for example, intermittent summer floods), limit black cottonwood regeneration in most years (Roe 1958; Braatne and others 1996, Harner and Stanford 2003). If subtle changes occur in these conditions, black cottonwood again could be a significant part of the vegetation, modifying community-level production dynamics.

Several researchers have argued that biomass accumulates rapidly early in succession when net production is highest, and then increases more slowly to an asymptote as respiration increases and nutrient availability decreases (Peet 1981; Ryan and others 1997; Seymour and Kenefic 2002; Acker and others 2002). Others have documented high production rates in mature forests and rejected the hypothesis that older forests are not productive due to an increase in respiration or a decline in nutrient availability (MacMahon 1980; Grier and others 1989; Franklin and others 1981; Kimmins 1997; Tappeiner and others 1997). In our study, the relative rate of biomass increase was rapid in the first 50 years but the absolute amounts increased substantially in later years with P peaking in older stands on mature terraces, around 250 years (Figure 5). Production tends to stabilize with increasing age (50 to 250 years) but does not decline. Stand-level BAI follows a contrasting pattern, with a peak early in succession when pioneering willow and red alder develop quickly on new surfaces. Stand-level BAI decreases sharply with increasing stem density and concomitant competition for light and nutrients, and slightly increases again when fast growing conifers overtop red alder. As trees age, stand-level BAI tends to level off. In terms of species-specific stem production, Sitka spruce is the main contributor to total P in older stands. Willow and red alder stem production begins with a steep increasing phase followed by a decline to values close to zero. In contrast, Sitka spruce stem production is characterized by a slow but continuous increase from 50 to 300 years (stand age). Sitka spruce is still young (250 years) in stands 300-years-old and its productivity would not be expected to plateau for some time as this species may live for 700–800 years in the Pacific Coastal Rainforest (Ruth 1965).

Environmental Factors Influencing Growth and Production

The toposequence reflects river history as well as local environmental conditions, thereby influencing stand development and stem production dynamics. In the Queets floodplain, soil characteristics were statistically similar within each biophysical template but subsurface hydraulic conductivity could be highly variable (CV from plot-to-plot = 51%). Additionally, distance from the channel and height above the channel at low flow showed great variability among plots (CV = 102 and 39%, respectively). It is well documented that sediment retention, summer water availability, flood intensity and frequency, and browsing generate variation in vegetative communities depending on interactions between local micro-environments and species-specific life history traits (Case and Kauffman 1997; Kozlowski and others 1991; MacBride and Strahan 1984; Walker and others 1986). This was particularly evident among the active floodplain plots and was expressed in differing species assemblages and P. For instance, densities and basal areas of red alder were particularly variable among the active floodplain plots (respectively CV = 105 and 90%). Two of these plots showed large alder densities, basal areas and P, whereas one plot showed a very low density, basal area and P (respectively 12%, 48%, and 75% lower than the average value for the active floodplain). All these plots being even-aged, variations in initial environmental factors are likely responsible for such differences in the red alder stands.

All measured environmental variables except acidity and total phosphorus were correlated with stand age. The principal temporal changes in substrate characteristics were increases in C and N concentrations, soil moisture, template height above channel, and depth to water table – which are concordant with previous studies of substrate characteristics across riparian toposequences (Luken and Fonda 1983; Viereck and others 1993). The presence of red alder in the stands may influence nitrogen concentration but estimates of nitrogen accumulation in red alder stands show high variability. For example, at age 0–30 years estimates range from 27 to 320 kg/ha/y (Binkley and others 1994). Red alder may tend to increase N availability but there is no evidence that red alder influences species replacements, or that base cation loss affects subsequent forest growth or species composition (Van Miegroet and Cole 1984). In terms of total N, a comparison of 150 studies of primary succession shows that total N in soils, with or without a dominant N-fixer, is not statistically different (Walker 1993).

Water availability is known to be important in the production dynamics of vegetation. We expected a negative correlation between P and water table depth (Minore and Smith 1971; Brinson

1990) but the results show the opposite trend. On the mature terrace where the water table was approximately 4 m deep, capillary movement of water, a dense network of fine roots, and soils characterized by higher organic matter content and fine texture potentially resulted in sustained water-holding capacities that contributed to good water availability during summer.

Comparisons to Other Riparian Systems and to Upland Forests

Density, Basal Area, and Biomass. Temporal patterns of density, basal area, and stem biomass reported here are similar to those previously documented for alluvial floodplains; however, the absolute amounts are among the highest measured in riparian and upland forested systems. The youngest stands in the Queets River floodplain, dominated by willow, exhibit mean densities 73% greater than values for 10-year-old stands in Alaska (Bormann and Sidle 1990) and densities of red alder measured in our 40-year-old plots were 3- to 7-fold greater than densities recorded from the Kadashan River, a coastal rainforest river in SE Alaska (Hanley and Hoel 1996). Tree density and basal area on the mature terrace of the Queets River floodplain were greater (84 and 37%, respectively) than those reported by Fonda (1974) for the lower terrace of the nearby South Fork Hoh River. Density on the mature terrace of the Queets was 8-fold greater than observed by McKee and others (1982) on the Hoh River but basal area, dominated by large Sitka spruce (DBH >100 cm) on the Hoh, was similar. Additional studies confirm that stand densities on mature terraces (125 to 150-years-old) in Alaska and Oregon are much lower (114–191 stems/ha) than those on same age surfaces in the Queets (340–800 stems/ha). However, basal area estimates remain in the same range: 50.9–82.8 m^2/ha in Alaska and Oregon and 46.4–71.0 m^2/ha in the Queets.

Stem density and basal area on mature terraces are within the range of density and basal area observed in same age stands of regional upland forests (Figure 6). However, species contributions to density and basal area differ between riparian and upland stands (Figure 7). Sitka spruce density and basal area are greater on mature terraces of the Queets River ($\bar{X} = 246$ stems/ha and 44.5 m^2/ha, respectively) than in similar-aged upland stands ($\bar{X} = 66$) stems/ha and 12.4 m^2/ha; Fonda 1974; Alaback and Juday 1989; Harcombe and others 1990; Edmonds and others 1993; Hanley and Hoel 1996) with the exception of Sitka spruce forests at Glacier Bay, Alaska (Bormann and Sidle 1990). Western hemlock has much lower stem densities and basal areas in the Queets River floodplain ($\bar{X} = 12.2$) stems/ha and 2.1 m^2/ha, respectively) than in similar-aged upland forests ($\bar{X} = 347$ stems/ha and $\bar{X} = 45.3$ m^2/ha). As a consequence, the mean standing biomass on the mature terraces of the Queets floodplain (541 Mg/ha) is lower than in upland forests (562–1,070 Mg/ha; Grier and Logan 1977, Harcombe and others 1990).

Productivity. Comparative data on riparian forest productivity in the PNW are scarce. Only two studies provide estimates of P and they refer only to mature forests dominated by Douglas-fir and western hemlock (Grier and Logan 1977; Means and others 1996). In the Queets River floodplain, older stands exhibit the greatest P (7.8–17.2 Mg/ha/y) with Sitka spruce contributing 72 to 86% of the total. Wood biomass production greater than 10 Mg/ha/y normally is found only in Florida or Louisiana swamps colonized by bald cypress (*Taxidium distichum*) or in mixed hardwood forests in North Carolina. Brinson and others (1980) report an average of 6.9 Mg/ha/y of wood biomass production for freshwater riparian forests in North America. The estimate of P in the Queets floodplain equals or exceeds this average in all stands older than 30 years. Temperate coastal rainforests are well known for their massive trees and seemingly high production rates but one might expect to find comparable rates in the lesser studied wet tropical forests.

Comparing Queets floodplain and upland forests P is made difficult by variability in measurement methods (that is, annual litterfall rates, diameter measurements, increment cores) and by inclusion of different tree components in the estimates (leaves, branches and stems). Zavitkovski and Stevens (1972) found a P of 10.6 Mg/ha/y for red alder in coastal Oregon, which is 56% higher than production of red alder stem in our 38 to 40-year-old young terrace plots ($\bar{X} = 6.8$ Mg/ha/y). Our estimate of stand-level P on the mature terrace (10.3 ± 1.6 Mg/ha/y) exceeds most stem production data from Douglas-fir dominated forests older than 100 years (2.2–5.4 Mg/ha/y) with the exception of western hemlock forests on the Oregon coast (6.3–10.1 Mg/ha/y; Fujimori 1977). Stem productivity by mature forests (100- and 630-years-old) dominated by Sitka spruce or western hemlock range from 3.5 to 11.4 Mg/ha/y, with an average of 7.0 Mg/ha/y. Highest P (11.4 Mg/ha/y) was for a 121-year-old western hemlock stand that included stems, branches, and foliage (Grier 1976). Our estimate of stand-level P (10.3 ± 1.6 Mg/ha/y)

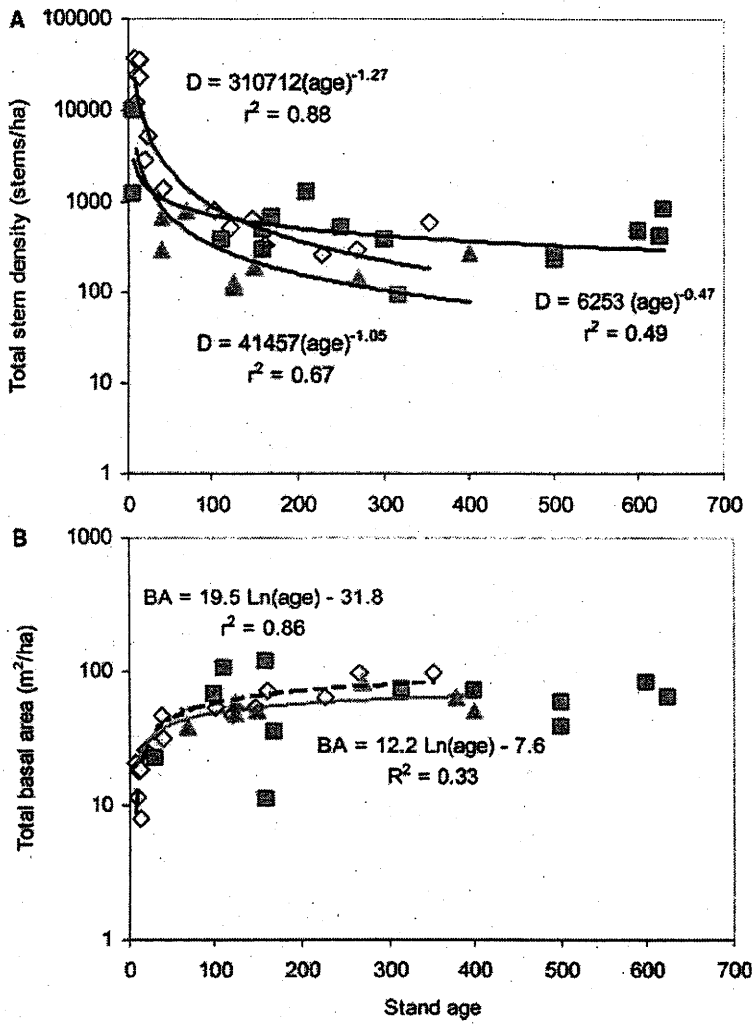

Figure 6. Comparison of total stem density (A) and total basal area (B) among riparian sites (▲), upland sites (■), and the Queets River sites (◇). Trend lines have been added except for basal area of upland sites for which $r^2 = 0.00$.

on the mature terrace is in the same range as upland estimates, but higher values were recorded in our two oldest plots (15.8 and 17.2 Mg/ha/y). If one considers only the Sitka spruce contribution to P in plots older than 150 years (4.9–13.9 Mg/ha/y), it is similar to maximum P by western hemlock in upland forests.

A Conceptual Model of Production Patterns

Stem production, shaped by riverine processes and local environmental conditions, influences vegetative community changes over decades (Figures 4A, B, and 5). High plant densities drive production on the active floodplain but total P remains low due to the small sizes of individual plants. In contrast, the rate of basal area growth is maximal on the active floodplain largely due to high densities of willow and occasionally red alder. The subsequent expansion of red alder within the community occurs over a wide time period depending on disturbance regime, sedimentation rate, and summer water availability. Red alder can colonize simultaneously with willow in the first pioneer assemblages, or can appear later in the vegetation sequence, slowly supplanting willow (Figure 4a). Red alder dominates the next phase with P and biomass increasing until the canopy closes. Eventually red alder is replaced by Sitka spruce and there is a rapid increase in young Sitka spruce biomass. The main difference between upland forests in the Pacific Coastal Rainforest and the lower Queets River riparian forest is the contribution of Sitka spruce to stem production. In our study, Sitka spruce maintains high productivity even after 300 years and grows larger, delaying the replacement phase by western hemlock.

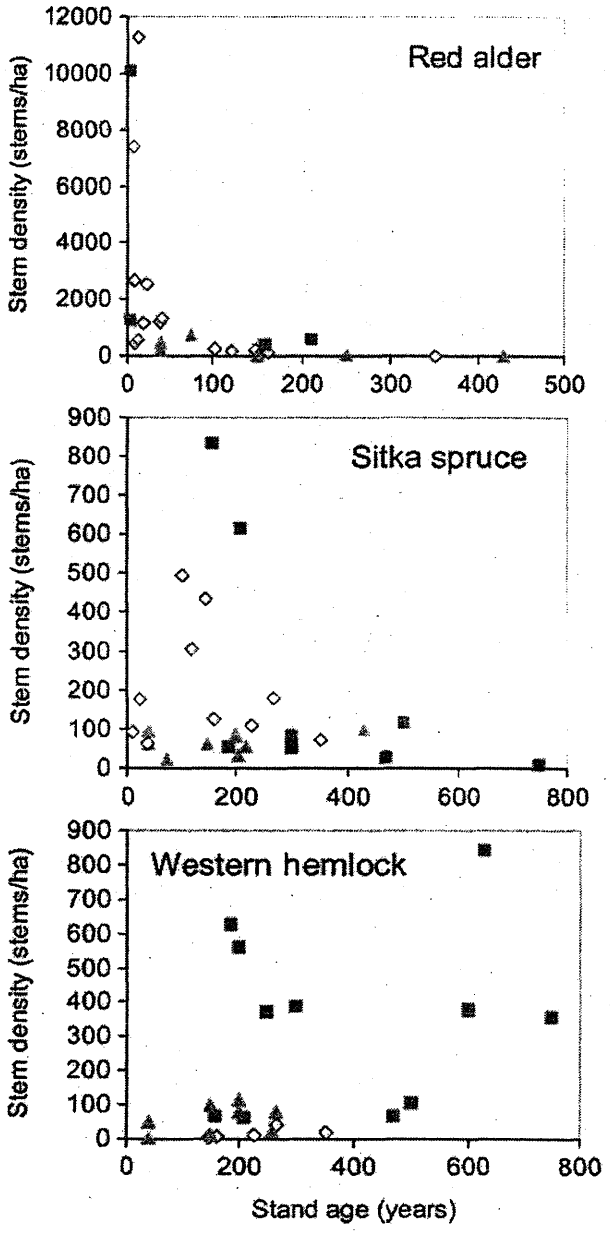

Figure 7. Comparison of total stem density for red alder, Sitka spruce, and western hemlock among riparian sites (▲), upland sites (■), and the Queets River sites (◇). Other riparian species did not have enough references for a meaningful comparison.

Stem Production and Implications for LWD Supply

The mature riparian terrace is the major contributor to total tree production of the entire floodplain. The annual tree production on mature terraces within the Queets floodplain reaches extraordinary values (~23,300 Mg/y; 81% of the total floodplain-scale stem production), suggesting that mature terraces contain abundant supplies of organic matter (and especially LWD). In contrast, red alder on the young terraces contribute a much smaller proportion of the annual floodplain-scale stem production (14% of total) despite relatively high production rates at the plot level.

The LWD is ecologically critical because it strongly affects aquatic as well as riparian forest dynamics (Maser and Sedell 1994; Bilby and Bisson 1998). Large trees captured from the riparian forest by the meandering river form prominent LWD jams that shape the next generation of riparian forest (Abbe and Montgomery 1996, 2003; Naiman and others 2005a, b). At meso-scales of space (for example, stream reaches) and time (for example, decades to centuries), LWD jams influence resource availability (for example, habitat quantity and quality) for aquatic and riparian organisms, and subsequently for riparian functions. Once LWD is in the active channel, pioneering red alder and willow colonize the moist alluvial deposits accumulating in the lee of logjams. When LWD jams establish mid-channel, the colonization and growth of pioneering vegetation enhances hydraulic roughness, also encouraging sediment deposition. Persistent bars accumulate sediments with successive floods – often burying much of the original logjam for centuries – and quickly become forested islands. Jams incorporated into riparian forest patches strengthen the landform against further erosion, providing refuge for patches of mature forest within a highly dynamic corridor (Abbe and Montgomery 1996; Naiman and others 2000, 2005a). Ultimately, conifers overtop alder and reach sizes that are able to initiate new LWD jams upon their death and delivery to the channel – starting the process of floodplain forest development anew (Fetherston and others 1995).

Basic to this process is having LWD of sufficient size to resist the river's erosive energy. In the Pacific Northwest, many rivers require large pieces (DBH > 50 to 60 cm and length > 5 m) for creating habitat (Sedell and others 1982; Bisson and others 1987; Sedell and others 1988; Robinson and Beschta 1990) even though smaller pieces still have critical roles in logjams initiated by the larger key pieces. Willow is unlikely to reach a diameter greater than 30 cm, therefore contributing only to accumulations in already existing logjams. Red alder needs at least 50 years to reach a diameter greater than 30 cm (but seldom reach 50 cm DBH). Sitka spruce reaches a diameter larger than 50 cm in 100 years but stem production keeps increasing with time so that between 100 and 200 years, individual Sitka spruce can reach a size sufficient to resist the river's

erosive power, and trigger formation of logjams. Mature stands located adjacent to the channel are thought to provide most of the LWD through windthrow or bank erosion; however, major flooding events or landslides result in channel migration and open new areas to LWD recruitment.

Collectively, this study and our companion studies are quantifying the complex interplay between species, biomass, productivity, LWD, and channel hydraulics. These are the foundation for the long-term vitality of river corridors in the Pacific coastal rainforest, with the production dynamics of riparian trees being a key component. Understanding the biophysical complexity – at the floodplain scale – illustrates how the interplay between the rapid lateral migrations of alluvial rivers and the riparian forests provide sustained supplies of organic matter (especially LWD) that, over decades to centuries, give coastal rivers in the Pacific Northwest their special characteristics.

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