

# A Process-Based View of Floodplain Forest Patterns in Coastal River Valleys of the Pacific Northwest

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## ABSTRACT

Floodplains in the Pacific Coastal Ecoregion (PCE) stem from steep eroding mountain landscapes in a rain forest environment, and sustain a rich array of natural resources. Like floodplains elsewhere, many of the approximately 200 coastal river valleys are profoundly altered by flow regulation and land conversion for agriculture and urban development, and these activities have contributed to widespread declines in anadromous fishes and environmental quality. Some of the coastal river valleys, however, still retain many of their natural features, thereby providing important reference sites. Understanding fundamental biophysical processes underpinning natural floodplain characteristics is essential for successfully protecting and restoring ecological integrity, including inherent goods and services. This article examines factors underpinning the ecological characteristics of PCE floodplains, particularly riparian soils and trees. Drawing on over

two decades of research and literature, we describe the spatial and temporal characteristics of physical features for alluvial PCE floodplains, examine the importance of sediment deposition and associated biogeochemical processes in floodplain soil formation, quantify vegetative succession and production dynamics of riparian trees, discuss how epiphytes, marine-derived nutrients, and soil processes contribute to tree production, describe the roles and importance of large dead wood in the system, the role of termites in its rapid decomposition, and show how large wood contributes to vegetative succession. These highly interconnected features and associated processes are summarized in a model of system-scale drivers and changes occurring over several centuries. Collectively, this integrated perspective has strong implications for floodplain rehabilitation, and we identify appropriate metrics for evaluating floodplain condition and functions. We draw heavily from our own experience on several well-studied rivers, recognizing additional studies are needed to evaluate the generality of concepts presented herein. As in any complex adaptive system, fundamental uncertainties remain and constraints imposed by the legacies of past human actions persist. Nevertheless, the evolving knowledge base is improving conservation strategies of lightly modified floodplains and is supporting the incorporation of emerging process-based perspectives into the rehabilitation of heavily modified systems.

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alluvial soils; epiphytes; large wood; Queets River.

## INTRODUCTION

Floodplains are highly complex, diverse, and productive systems of great ecological, social, and economic values. In our perspective, floodplains consist of valley floors and associated landforms created by fluvial sediment redistribution within the recent climate. These areas are well known for their important roles in sustaining regional biodiversity and water quality, and for their capacity to produce trees and fish (Tockner and others 2008). In many respects, floodplains are analogous to coral reefs and tropical forests in harboring regional diversity and sequestering carbon and nutrients (Naiman and others 2005b). In contrast to uplands they are subject to seasonal, and often extreme, variations in water flow and sediment flux. Concomitantly, they exhibit strong spatial gradients in moisture and in sediment texture, both of which are major controllers of ecological integrity (Naiman and others 2008). The concentration of biodiversity, the levels of carbon and nutrient sequestration, the spatial and temporal variability in moisture and sediment characteristics, and the social values they support make floodplains disproportionately important relative to other portions of river catchments. Nevertheless, floodplains are being transformed worldwide through land conversion, flow regulation, and flood abatement actions (Tockner and others 2008), often with low priority given to protecting underlying mechanisms sustaining their diversity and productivity.

It is a daunting challenge to describe the fundamental dynamics of active floodplains, to predict the outcome of human modifications to water, sediment, and nutrient flows, and to recommend self-sustaining restoration and conservation strategies. Increasingly, however, managers are expected to predict, achieve, and demonstrate significant, beneficial responses to restoration actions. Evaluating floodplains from a process-based perspective helps set realistic expectations and establish appropriate performance measures. Moreover, understanding whether floodplains exhibit equilibrium or non-equilibrium dynamics at the scale of interest (*sensu* Suding and Gross 2006) is crucial to both the design of appropriate restoration strategies and the ability to accurately predict restoration outcomes. Where floodplains are found to trend predictably toward a relatively stable pattern,

management strategies can focus on restoring underlying processes that drive the system toward an expected pattern while allowing for annual erosion and creation of floodplain patches. Alternatively, where floodplains exhibit multiple equilibria and transitions occur only when a threshold is reached, restoration strategies must allow for greater unpredictability in both rates of turnover and associated biological outcomes.

It is well appreciated that at the patch or sub-reach scale (10–1000 m<sup>2</sup>; defined as distinct substrates such as gravel bars or associated biotic communities), most alluvial floodplains may exhibit persistent non-equilibrium conditions determined by multiple disturbance types, biological legacies, and chance—resulting in divergent or cyclical trajectories that rarely arrive at true equilibria. However, when viewed at the scale of the reach, floodplains are often viewed as ‘pattern stable’, meaning that the proportions of channel, bars, islands, and floodplain are relatively constant through 100s to 1000s of years (Beechie and others 2006a). Focusing on key processes and disturbance regimes is especially critical where floodplains exhibit non-equilibrium dynamics and follow multiple pathways to similar (or different) endpoints.

Three basic questions underpin our synthesis of floodplains in the Pacific Coastal Ecoregion (PCE; Figure 1). They are: How can highly dynamic systems, subject to frequent and often powerful natural disturbances, remain so productive over the long-term? What are the underlying environmental drivers of the dynamic, yet consistent, vegetative patterns? How are high tree production rates sustained in spite of these apparently detrimental influences? These questions have implications that go far beyond floodplains, and the answers may lie in basic biophysical processes underpinning biodiversity and productivity. In the PCE there is a strong interaction, even a ‘tension’, between disturbance regimes and biotic patterns in streams (Naiman and Bilby 1998), riparian areas (Naiman and others 2005b), and uplands (Waring and Franklin 1979). Understanding fundamental processes shaping the intricate characteristics of natural and semi-natural floodplains establishes a foundation for successful rehabilitation and conservation programs.

In this article, we articulate the current understanding of processes contributing to patterns in



**Figure 1.** The Pacific Coastal Ecoregion (PCE) of North America, a region receiving from one to seven or more meters of annual precipitation, ranges over much of the West Coast from northern California to southeast Alaska. Major physiographic features and rivers mentioned in the text are highlighted.

riparian vegetation, provide a temporal model of the biophysical drivers creating and maintaining the ecological patterns of PCE floodplains, highlight process-based approaches to floodplain recovery, and suggest appropriate metrics for evaluating

floodplain condition and functions. Our perspectives focus primarily on ecological patterns and are most applicable to unregulated, laterally mobile alluvial rivers in the PCE that drain valleys with intact primary or secondary forests. This article synthesizes nearly two decades of research from Oregon, Washington, British Columbia and southeast Alaska. Collectively, this research suggests that ecological patterns in these forests are maintained by a dynamic self-regulating regime that balances disturbance intervals and scale-dependent processes with the rapid reorganization and growth of the floodplain community. We acknowledge that prevailing paradigms about floodplain ecology in the PCE are strongly influenced by a handful of well-studied river systems (for example, Queets River, Kadashan River). We look forward to further examinations of other rivers throughout the region, many of which remain ecologically intact, that promise new and deeper insights into key biophysical processes affecting broader ecological patterns.

## PACIFIC COASTAL FLOODPLAINS

### An Overview

The PCE is a geologically young region with a highly variable lithology. The geography is dominated by the Cascade Mountains and coast ranges (including the Olympic Mountains) in the northwestern USA and the Coast Mountains in western Canada and southeast Alaska. The mountains are comprised of continental rocks uplifted in the Late Cenozoic, which form peaks commonly exceeding 3000 m elevation (three peaks exceed 4000 m: Mt Waddington, Mt Shasta and Mt Rainier). In British Columbia and SE Alaska, the terrain drops steeply into the Pacific, creating a fjord-dominated coastline. In southern-most British Columbia, Washington and Oregon, many mountains are further from the coast and rivers flow west into a trough forming the Strait of Georgia, Puget Sound, the lower Columbia River, and the Willamette Valley. Other rivers in coastal Oregon, Washington, and southern British Columbia flow directly into the Pacific Ocean or into the Strait of Georgia. Glaciation prior to 16,000 YBP carved wide valleys and deposited till, outwash, and lake deposits in the trough and the main valleys (Booth and others 2003). This physical (that is, litho-topographic) template contains channel networks characterized by steep headwater streams on bedrock, moderate-gradient reaches in mid-basin where thick deposits of glacial sediments dominate, and wide floodplains

in low-gradient valleys approaching the coast (Beechie and others 2001).

The PCE receives 1–7 m/year of precipitation over a north–south gradient of around 2000 km (Naiman and Anderson 1997). Mountain ranges cause strong orographic effects, with mean annual precipitation increasing dramatically from coasts to headwaters, and generally higher precipitation on the western slopes (up to 7 m/year) and rain shadows on eastern slopes (as low as 45 cm/year). The approximately 200 rivers originating in the PCE have dynamic but predictable hydrologic regimes that vary with latitude. Unfortunately, to date there are no analyses of latitudinal gradients in flood frequency or intensity for the region. Most precipitation falls during discrete autumn and winter storms; less than 10% falls during summer (July–September). Hydrologic regimes are one of three types: snowmelt-dominated in high-elevation rivers (most runoff occurs during spring and summer snowmelt), rainfall-dominated in low-elevation rivers (most runoff occurs in fall and winter storms), and transitional in mid-elevation rivers (transient snow-zone—both winter and spring peaks occur; Beechie and others 2006b). The largest floods in all three hydrologic regimes occur during powerful fall and winter storms when rain falls on snow.

The PCE floodplains support high regional biodiversity and historically productive salmon (*Oncorhynchus* spp.) populations, yield abundant clean water, and are well known for large and rapidly growing endemic trees (Waring and Franklin 1979; Van Pelt 2001; Naiman and others 2005b). In general, the valley bottoms are dominated by mixed communities of willow (*Salix* sp.), red alder (*Alnus rubra*), black cottonwood (*Populus balsamifera trichocarpa*), bigleaf maple (*Acer macrophyllum*), Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*) and, in the southern-most regions, coast redwood (*Sequoia sempervirens*; Franklin and Dyrness 1973). Late-seral floodplain forests tend to be dominated by conifers, although black cottonwood also dominates mid-seral lowland rivers from Oregon to SE Alaska. The large sizes of the trees render them uniquely capable of shaping in-stream conditions as dead wood (Gregory and others 2003).

Plant community patterns and processes in PCE floodplains are well documented, but only in specific locations (for example, Fonda 1974; Hanley and Brady 1997; Van Pelt and others 2006). For example, it is known that vegetation composition in PCE floodplains varies considerably among

patches of different ages, and that PCE floodplain forests are among the most productive in the world (McKee and others 1982; Means and others 1996; Balian and Naiman 2005). However, the most complicated patterns and the highest tree production rates occur in environments where lateral river movements actively undercut streamside forests (for example, O'Connor and others 2003; Latterell and Naiman 2007) and rapid leaching of nutrients from soils is common (Bechtold and others 2003; Bechtold and Naiman 2009a).

## General PCE Floodplain Dynamics

Two defining characteristics of the alluvial floodplains are their distinct vegetative patterns, and the recurrent destruction and reformation of soils and vegetation as rivers move laterally within valley bottoms (Figure 2). Both characteristics are maintained by annually strong floods that erode some floodplain patches while depositing new sediments on other floodplain patches (Naiman and others 1992, 2005a, 2008). A key feature of floodplain formation is the rapid stabilization of new landforms, which is catalyzed by four interacting components and processes. They are: the presence of large wood (LW; Fetherston and others 1995; Abbe and Montgomery 1996; Latterell and others 2006); rapid development of fertile soils driven by the accumulation of organic matter (OM) through fine sediment deposition and sediment weathering (Bechtold and Naiman 2009b); variable disturbance return intervals for different-aged landforms that direct a successional sequence of species replacements (Balian and Naiman 2005; Van Pelt and others 2006); and a channel migration zone characterized by frequent oscillation, avulsion, and meander cutoffs, as opposed to the unidirectional sweep of a meandering channel across the valley bottom (O'Connor and others 2003). Collectively, these processes sustain inputs of LW-capable trees, which are potent agents of floodplain reorganization (Abbe and Montgomery 2003; Latterell and Naiman 2007).

This channel movement regime creates substantial environmental heterogeneity supporting the development of a heterogeneous plant community pattern (Pollock and others 1998; Naiman and others 2005a, b; Latterell and others 2006). Riverine landforms are strongly coupled to LW accumulations. The common landforms often progress from bars to floodplains to terraces as the associated succession of vegetation progresses from colonizing willow, alder, and cottonwoods to mixed-species mature forests to old-growth conifer



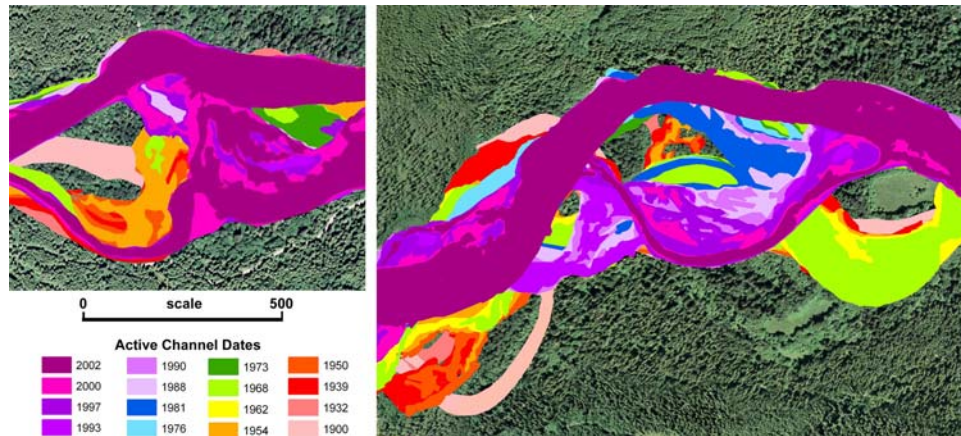


Figure 2. Twentieth century disturbance maps for two study reaches along the Queets River in the Olympic Mountains. The 16 dates represented are not necessarily specific years of major river action, simply the years for which accurate spatial data were available. The maps therefore represent a minimum of river activity; a complete coverage would undoubtedly show as of yet unmapped river movements. Adapted from Van Pelt and others (2006).

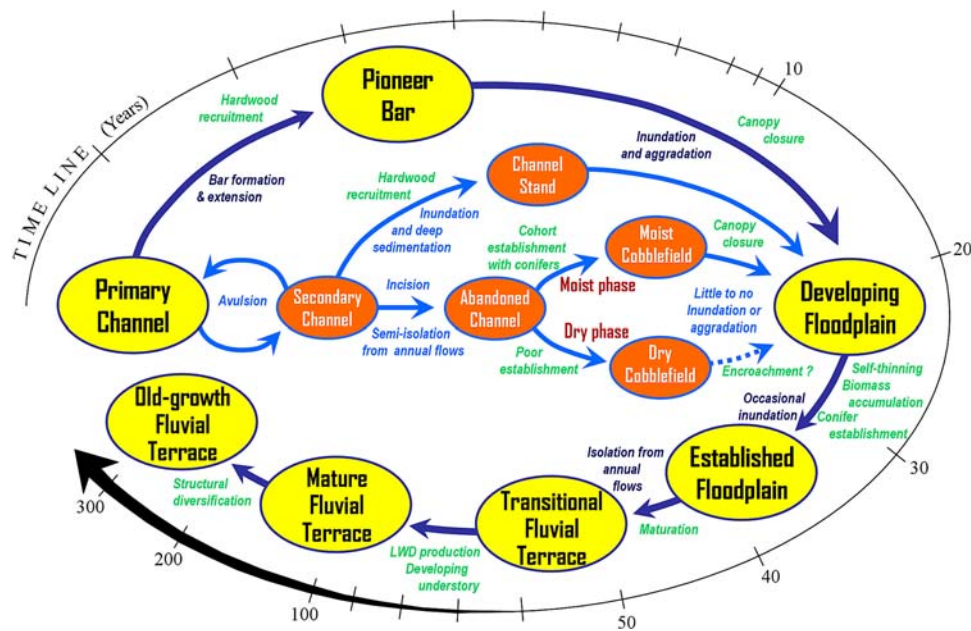


Figure 3. Biophysical model for the middle Queets Valley in the Olympic Mountains. *Purple arrows* indicate the primary biophysical pathway, whereas the *light blue arrows* indicate possible secondary pathways. *Yellow* is used to indicate the primary landforms along the primary biophysical pathway, whereas *orange* indicates landforms along secondary biophysical pathways. *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. Adapted from Van Pelt and others (2006).

forests (Figure 3). However, river-caused erosion can reset this process at any developmental stage, maintaining a distinctive mix of landforms and forest types through time. A key process driving this complex pattern is the initiation of bar and island formation by LW deposition, which helps sustain the mosaic of landforms and forest types

(Fetherston and others 1995; Abbe and Montgomery 1996). The resultant dissection of PCE floodplains creates a structurally complex environment with abundant edge length, facilitating the development of open, multi-storied canopies containing prolific and diverse epiphytic communities (Van Pelt and others 2006, unpublished

data). River-floodplain dynamics in PCE floodplains also drive key feedbacks from the floodplain to the aquatic environment, such as delivery of dissolved OM (DOM) to hyporheic zones (Clinton and others 2002), transfers of hyporheic P and N to surface channels (Fevold 1998), and movement of organic and sedimentary materials during floodplain erosion (Bechtold 2007).

This understanding of PCE floodplain dynamics establishes a foundation for a more comprehensive description of biophysical drivers and ecological responses over time. The basic information used to formulate a more comprehensive system-scale floodplain model is presented in the following two sections. First, we address key physical drivers (geomorphology, alluvial soils, subsurface water, and large wood) before addressing ecological processes (ecophysiology, vegetative succession, soil nutrient cycles, marine-derived nutrients, canopy epiphytes) underpinning floodplain patterns and tree productivity.

## PHYSICAL DRIVERS

Interaction of the PCE's complex geography with ecological processes—across broad spatial and temporal scales—is central in forming the emergent floodplain patterns and processes. Geophysical controls on structure and productivity can be hierarchically arranged at five scales (patch, reach, valley, catchment, and region), and these controls interact with four important ecological processes within individual patches (soil formation, nutrient dynamics, vegetative initiation, plant succession; Table 1). Collectively, they produce the diverse biophysical patterns exhibited by PCE floodplains (Figure 4). In such nested hierarchies, local environmental attributes (for example, nutrient fluxes, productivity) are controlled by soil and moisture characteristics at the site. However, these site characteristics are nested within and controlled by larger scale features, including patch-scale distur-

bance history, reach-scale channel dynamics, and valley or catchment-scale controls on channel pattern (Beechie and others 2008a).

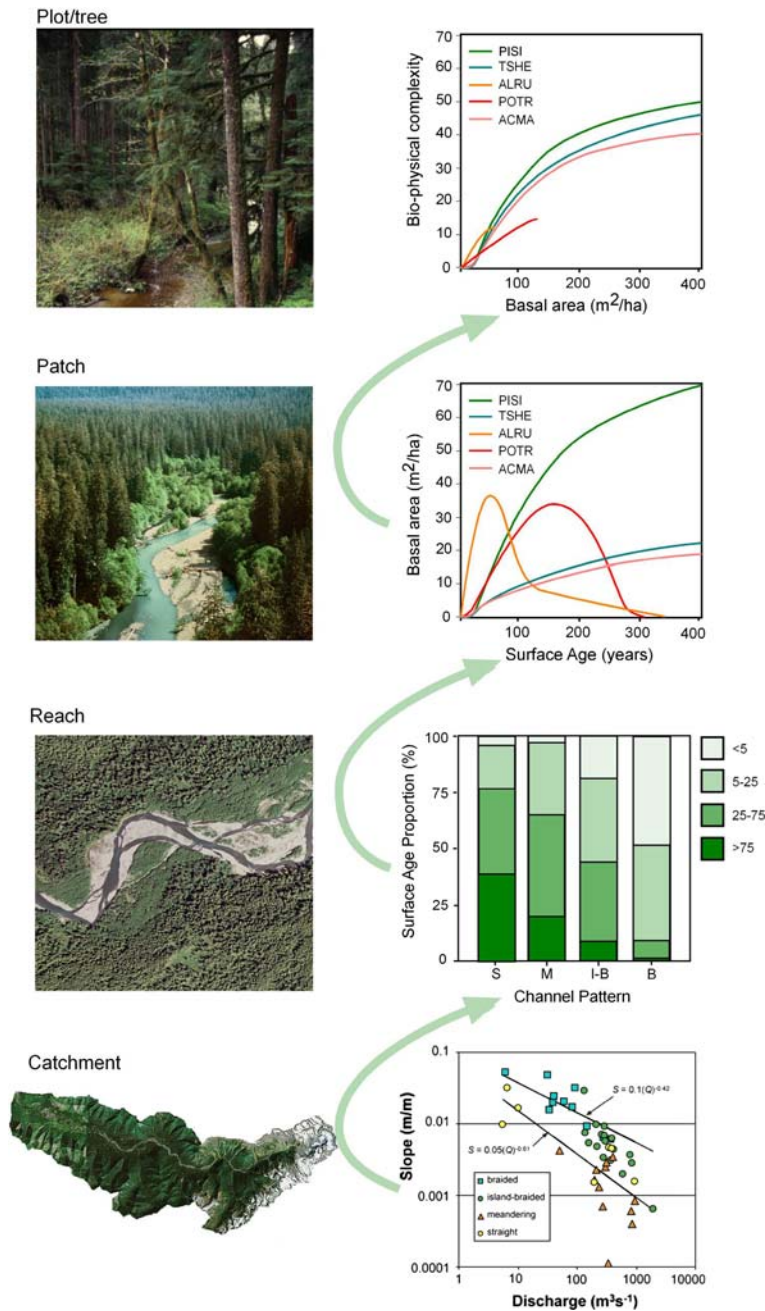
## The Geophysical Template

The hierarchical suite of physical influences creates riverscapes where downstream changes in channel pattern and floodplain dynamics are predictable (Naiman and Sedell 1979; Beechie and others 2006b). The geophysical (for example, litho-topographic) template controls downstream patterns of channel slope, width, and discharge, as well as locations of confined canyon reaches and unconstrained valleys (Figure 5). The uppermost reaches often have high bed load supply and relatively steep channel slopes, contributing to a braided channel. Downstream abundant LW and a decreasing bed load supply, combined with increasing plant root strength, promote a transition to a relatively dynamic, island-braided channel. The lowest reaches tend toward a slowly meandering channel pattern, characteristic of channels dominated by suspended sediment loads (that is, low bed load supply). In the PCE, meandering reaches tend to be in low gradient, lowland valleys (for example, Quinault River, O'Connor and others 2003; Snoqualmie River, Collins and others 2003).

Steep terrain, unstable geology, and high precipitation drive an active erosion regime with highly episodic sediment delivery to rivers and floodplains (Benda and Dunne 1997). Thus, headwater streams are sediment limited in most years but never fully depleted, with rare episodes of high sediment supply when landslides occur (for example, Martin and others 2002). Year-to-year variation in sediment supply decreases downstream, as increasing drainage area and desynchronization of tributary sediment fluxes integrate sediment pulses and dampen temporal variation in supply. In general, rivers and associated floodplains with drainages larger than 200 km<sup>2</sup> tend to trans-

**Table 1.** Dominant Processes Underpinning Floodplain Tree Productivity as a Function of Spatial Scale

Spatial scale	Key processes
Vegetative patch (10 <sup>1</sup> –10 <sup>3</sup> m <sup>2</sup> )	Water regime; hydraulic shear stress; herbivory; nitrogen fixation, weathering of sediment P and cations; nutrient retention; epiphytic influences; microclimate; microtopography
Catchment (10 <sup>2</sup> –10 <sup>4</sup> km <sup>2</sup> )	Local lithology; sediment deposition and erosion; sediment texture; deposition and patterns of LW; marine-derived nutrients; biophysical legacies
Regional (10 <sup>4</sup> –10 <sup>6</sup> km <sup>2</sup> )	Lithology; tectonic processes; topography; precipitation and temperature regimes; disturbance regimes; species assemblage; ocean proximity; biophysical history
Continental (>10 <sup>7</sup> km <sup>2</sup> )	El Niño, La Niña cycles



**Figure 4.** Biophysical complexity at the scale of individual trees or plots is ultimately controlled by a nested hierarchy of processes operating at larger scales. Illustrated here is but one of numerous examples that could demonstrate this principle. Starting at the top of the figure, the biophysical complexity of a single tree is a function of basal area through time, which is controlled by the age of the growing surface, which in turn is controlled by the reach-scale channel pattern and age structure of the floodplain, which is then a function of watershed-scale controls of valley slope and dominant discharge. *PISI* Sitka spruce (*Picea sitchensis*); *TSHE* Western hemlock (*Tsuga heterophylla*); *ALRU* Red alder (*Alnus rubra*); *POTR* Black cottonwood (*Populus balsamifera trichocarpa*); *ACMA* Bigleaf maple (*Acer macrophyllum*).

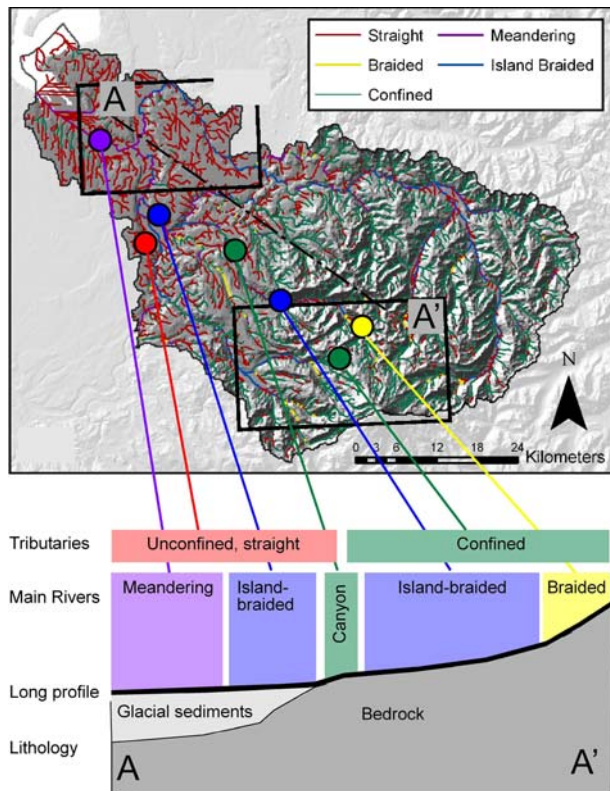
port relatively consistent bed loads. In these systems, the uppermost reaches tend to have low to moderate sediment supply and are therefore either straight reaches or island-braided reaches. The synergism between high precipitation and erosion can result in relatively large floodplains; catchments can have up to 25% of their ridge-to-ridge area occupied by floodplain (McKee and others 1982). It is conceivable that after major precipitation events the availability of new surfaces for colonization will be at a maximum for a few years post disturbance. However, the available evidence suggests that the floodplains and their forests ex-

hibit relatively stable habitat distribution patterns when the hydrologic regime is within long-term norms (Kloehn and others 2008; Latterell and others 2006).

### Alluvial Soil Development

Alluvial soils are a foundation for the expression of plant community traits. PCE floodplains are formed from the abundant sediments; legacies of Pleistocene glaciations (Figure 6). Although newly deposited sediments are ideal environments for hardy colonizing vegetation, fertile soils capable of





**Figure 5.** Illustration of typical downstream transitions in channel pattern for the Nisqually River in the Cascade Mountains, and lithological controls on transitions. Simplified geological cross-section A–A' shows bedrock underlayment in the steeper, upper reaches of the basin, and glacial sediments filling the lower reaches near the Puget Lowland. Resistant bedrock forces relatively steep main channels (braided and island-braided) and tributaries confined between valley walls, whereas erodible glacial sediments promote development of low gradient meandering channels and unconfined tributaries. Variants of this sequence of channel patterns are common throughout the PCE.

supporting more sensitive, late-seral, and highly productive floodplain forests develop within a few decades. Intense fluvial sorting results in a common pattern where there is often a less than 2 m “cap” of sand/silt/clay over cobble-sized bed sediments. Silts and clays, which play critical roles in retention of nutrients and water, tend to be concentrated in the uppermost part of the soil cap (Latterell and others 2006).

Four discrete stages of alluvial soil development are observed (Bechtold and Naiman 2009a); initially, sand is deposited over coarse bed sediments. This commonly occurs where colonizing willow and alder, and LW jams, create resistance to flow. Aggradation of floodplain landforms along point bars or abandoned channels occurs rapidly, with



**Figure 6.** A simplified, graphic model of a PCE floodplain depicting many stages of landform and forest development. Closest to the river are gravels and cobbles, which are the primary initial substrate in active mountain floodplains. Stability to these surfaces is usually provided by large wood, often in the form of jams. Fine sediments and OM (fines; less than 1 mm diameter) are deposited on top of these as brief inundations allow fines to fall out of suspension in slow-moving water. If not reworked by the river, colonization by shrubs (willows) and trees (alders) follows, which attract further fines and coarse wood deposition. If allowed to persist into a second century, mature conifer forests may develop. Due to the dynamic nature of rivers within the PCE, and the dramatic differences between summer low flows and flows following rain-on-snow events, evulsions, steep incisions, and anastomosing patterns are common. This can lead to below-ground sediments that are a mixture of many textures, including buried wood and other organic matter. The hyporheic flows (blue areas and arrows) are highly varied in both volume and velocity due to this below-ground mixture of sediment texture.

most physical floodplain construction taking place within the first decade or two. The aggradation of floodplain surfaces is caused by either free-formed deposits, or in association with LW, vegetation, or a combination of both. Rapidly growing seral forests usually develop during this period, and soils receive large inputs of OM, N from N-fixing red alder and rock-derived nutrients (P, cations) from sediment weathering. However, these sandy soils contain limited OM, have limited capacity to retain water, and nutrients are easily leached (Bechtold and others 2003).

Following this initial period of aggradation, there is a transition from bed load deposition to suspended sediment deposition within individual patches. Silt and clay deposited during this phase of floodplain development critically influence a soil's capacity to retain nutrients and water, as discussed later. The most fertile soils within these coarse-textured environments are the ones receiving the



greatest overbank deposition of suspended sediments. Eventually, sufficient deposition occurs that direct inundation of developing alluvial surfaces becomes infrequent. From this point forward, soils on terraces can be thought of as a nearly fixed physical template. Subsequent alteration of soil character and function is primarily by pedogenic processes, with little direct fluvial influence. Finally, soil destruction results from channel migration. Floodplains experience recurrent soil destruction and reformation faster than most of any terrestrial ecosystem. For example, floodplains on the Olympic Peninsula, Washington, have half-lives of only 200–500 years (O'Connor and others 2003), with internal turnover times varying greatly depending on the specific patch type (Latterell and others 2006). Rather than being an endpoint, floodplain destruction is best considered as one stage of a cyclic process during which floodplain soils undergo large changes in pattern and function.

At larger scales, differences in channel slope, valley constraint, and sediment supply lead to highly heterogeneous distributions of floodplain soils differing in sediment character and pedogenic development. These patterns of sediment deposition underpin soil fertility and plant production throughout stand development, and shape surface and subsurface water flows.

### Subsurface Water: The Hyporheic Zone

Hyporheic zones underlying floodplains are typically spatially extensive and hydraulically conductive due to abundant coarse glacial sediments and dynamic flow regimes (Edwards 1998). Locally, hyporheic-related ecological patterns may be exemplified by those of the Nyack floodplain of the Flathead River, Montana (Stanford and Ward 1993; Poole and others 2006). In that location hyporheic upwelling is an important source of nutrients in off-channel aquatic habitats, and hyporheic water provides important moisture and nutrient subsidies to some trees (Harner and Stanford 2003).

The relation between the overlying vegetation and the hyporheic zone is complicated, and the understanding of the interaction is far from complete. Our sense is that hyporheic zones are important water sources for colonizing vegetation but probably not for PCE vegetation on mature landforms. Survival of colonizing trees during the first decades depends on access to water (Naiman and others 2005b). In thin soils, alder survive only along banks and other low-lying areas with subsurface water sources, and this often results in narrow bands of alder along the banks of coarse-

textured terraces, where alder could not otherwise survive (Figure 7A). Hyporheic areas are generally not sources of water or nutrients to vegetation on older landforms, which are typically 3–4 m above the summer water table (Clinton 2001). In general, 2–3 m of coarse bed sediments eliminates any possibility of capillary movement of hyporheic water into the rooting zone. Roots in the mature conifer forest are normally directed toward the soil surface, with limited root penetration into cobbles.

### Large Wood: Sources and Dynamics

PCE rivers are renowned for LW accumulations (see reviews in Bilby and Bisson 1998; Gregory

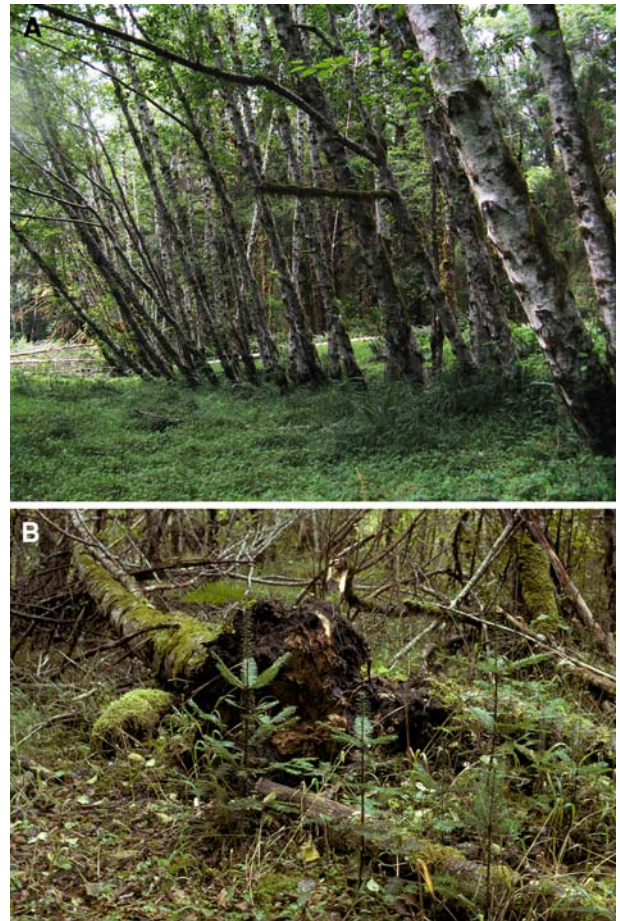


Figure 7. **A** A colonnade of red alder trees along bank of a floodplain terrace. Spatial variation in sedimentary landforms creates complex environments for establishment of floodplain vegetation. Here, red alder trees are able to colonize banks, where they can grow in full sun and access subsurface water. **B** During the primary biophysical pathway, small conifer seedlings are eliminated by burial during the primary shrub and hardwood tree colonization. Instead, they must wait for several decades until the short-lived hardwoods die and release growing space, as depicted here.

and others 2003), which contribute to habitat formation for Pacific salmon and the creation of stable forested landforms (Montgomery and Abbe 2006). The mass of LW varies greatly within a river as well as among rivers according to elevation, channel pattern, and forest composition (McHenry and others 1998; Abbe and Montgomery 2003; Beechie and others 2006a). Variation in patterns of LW accumulation, delivery, retention, and longevity have important feedbacks on the establishment and persistence of depositional landforms and the forests that grow on them (Abbe and Montgomery 1996; Gurnell and others 2005). In PCE floodplains, LW accumulates in logjams of many arrangements. Some form recognizable, distinctive structures, such as arrow-head-shaped 'bar apex' jams which often create perennial floodplain scour holes and forested islands, or 'meander jams' that can bend the river and elevate the streambed and the water surface (Abbe and Montgomery 1996; Brummer and others 2006). A single jam often contains a heterogeneous mixture of fresh whole trees, partial stems splintered and abraded by the river, and remnant boles made brittle by terrestrial decay (Latterell and Naiman 2007).

Large wood delivery to floodplain rivers has rarely been quantified, but a few studies indicate it is mainly supplied by lateral movements (meandering, avulsions, and cutoffs). This is especially so along unconstrained river reaches, which undercut and topple trees and redistribute the pieces into logjams during high flows (Benda and Sias 2003; Latterell and Naiman 2007). At other locations in a drainage network, wind throw, fire, or landslides may be the dominant delivery processes. Some primary channels also receive substantial inputs from local landslides (Reeves and others 2003).

All river-fringing forests provide LW to rivers, but old forests (for example, mature fluvial terraces) are the most important sources of large pieces of wood capable of initiating logjams (Abbe and Montgomery 1996; Montgomery and Abbe 2006; Van Pelt and others 2006; Latterell and Naiman 2007). LW from these mature forest patches influence channel form and floodplain processes in a manner that smaller pieces of wood typically cannot (Fetherston and others 1995; Montgomery and Abbe 2006). Though old forests may cover most of the floodplain, they may border only a minority of the active river channel. In island-braided and meandering portions of rivers, older floodplain forests commonly fringe the outside of eroding river bends, critical source areas for LW (Latterell and Naiman 2007). Mature trees on

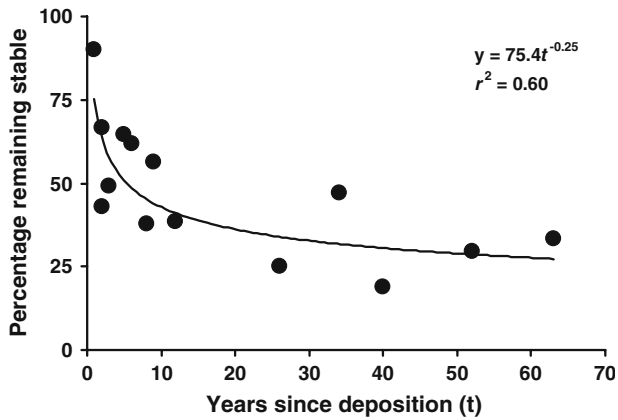
fluvial terraces are often lacking along modified rivers (Collins and others 2002).

Young forests often dominate banks and bars due to rapid channel migration and forest turnover rates, particularly in braided systems. When dense thickets erode, large numbers of pieces—usually red alder and cottonwood—are captured and amassed against more stable LW. These stands also contain remnant and buried logs deposited historically by the river and contributing to the establishment of contemporary vegetation on the site (Hyatt and Naiman 2001).

Many PCE rivers are physically capable of transporting stand-dominant trees to downstream reaches. Thus, LW loading reflects local and upstream sources (Swanson 2003; Latterell and Naiman 2007). For example, transport may be helpful in maintaining LW abundance in reaches where channel migration is very slow (that is, resulting in low rates of recruitment from local sources; Martin and Benda 2001) or very fast (that is, preventing the growth of large-diameter trees; Beechie and others 2006a). Once a tree falls into the river, it may remain on site forming a jam in situ or be transported downstream. Logs that remain stable for long periods tend to have large diameters relative to the bankfull depth, tend to retain their rootwads, and are long relative to the width of the channel (see Abbe and Montgomery 2003).

Case studies of the Queets River, Washington, provide insights into the dynamics of large wood in floodplain rivers. In one study, LW generally appeared to be most vulnerable to displacement 1–3 years after initial deposition (Figure 8; Latterell and Naiman 2007). Empirically based simulations suggested that many transported logs are eventually retained in locations where they remain stable long enough for floodplain vegetation to establish. As time progresses, the LW is less and less likely to move. An earlier study demonstrated that 98% of bar-apex jams associated with forested islands remained stable over a period of 8 years (Abbe and Montgomery 2003). Vegetation primarily helps to stabilize logs by adding root cohesion in the deposited sediments and by adding weight on top of the jam (Abbe and others 2003), as well as by dissipating stream energy and facilitating deposition of sediments.

The longevity—or residence time—of LW varies greatly within individual floodplains (Hyatt and Naiman 2001), among rivers across a gradient of size and elevation (Beechie and others 2006a) and among trees (Graham and Cromack 1982; Harmon and others 1986). Studies from the Queets River suggest that a minority of logs remain in the river



**Figure 8.** Relationship between large log retention (percentage of logs remaining stable) and the years elapsed (years) since the cohort was deposited in the active channel in the mainstem of the Queets River in the Olympic Mountains. Each point represents a different cohort ( $n = 14$ ). The average number of large logs in a cohort was 108, ranging from 12 to 361 logs. From Latterell and Naiman (2007).

for more than 50 years, but some important fraction is preserved—likely through burial—for many centuries (Hyatt and Naiman 2001; Abbe and Montgomery 2003; Montgomery and Abbe 2006).

Collectively, the patterns and processes in geomorphology, sediment origin and delivery, soil texture, hyporheic water flow, and LW provide the foundation for discussing key ecological processes contributing to tree production and for eventually providing a better understanding of system-scale floodplain dynamics.

## ECOLOGICAL PROCESSES UNDERPINNING FLOODPLAIN PATTERNS AND TREE PRODUCTION

Vegetative patterns on floodplains are strongly influenced by species-specific physiologies interacting with the temporally shifting combination of processes associated with sediments, nutrients, and LW (Swanson and others 1982; Tockner and others 2003). The nutrients have geologic, atmospheric, and oceanic sources—and the dominant source changes during succession. Nutrient location, delivery, and availability are mediated by soil organisms, anadromous fishes, and canopy epiphytes. The LW acts to spatially concentrate organic matter and nutrients, and also shape energy regimes, thereby providing habitat for plant development. Basic changes in plant community patterns

and ecological processes occur mainly through the shifting of their relative vertical position on the floodplain and the degree of annual flooding (Junk and others 1989). Further, the broad valley floors allow the development of a variety of backwater and seasonal channels, each of which offer contrasting micro-environments for biotic patterns and processes. In this section, we discuss key processes underpinning patterns in floodplain vegetation, their temporal dynamics and, collectively, their relation to tree production.

## Ecophysiology of Coastal Floodplain Trees

Several physiological characteristics of PCE floodplain plants are key to their success: formation of adventitious roots, symbiotic N-fixation, tolerance to abrasion when young, and tolerance to submersion in water for extended periods. Many of the adaptations are essential for survival, particularly in the earliest stages of succession. For example, even though seeds are generally widely dispersed, most willow and cottonwood germinate only in the moist zone near waterlines (McBride and Strahan 1984; Stettler 2009). Small-seeded species tend to exhibit successful germination sporadically as compared to larger-seeded species, which exhibit more consistent survivorship, though rates are lowered by the stresses of drought or flooding (Krasny 1986; Streng and others 1989; Stolnack and Naiman 2010).

The ability of willow and cottonwood to sprout roots from portions of their stem after being removed from the tree is well known (Carlson 1950). Root primordia develop in the stem and sprout from buds. Adventitious root formation begins after most of the primary tissues of the new shoot have formed and then become dormant by the end of the first growing season. Depending on stem age, primordia rapidly develop into roots when placed in water. This is an advantage when willow pieces broken off the main plant are buried in newly deposited river sediments. Riparian willows develop roots on all portions of submerged stems, whereas terrestrial willows do so only at basal ends of cuttings (Densmore and Zasada 1978). Conifers generally do not possess this capacity but western redcedars reproduce readily from branch layering (Schmidt 1955; Minore 1983). Like willow and cottonwood, Sitka spruce and western redcedar also maintain shallow root systems, enabling growth in areas with high-water tables. Sitka spruce and western hemlock have the added ability, particularly in shady environments, to suc-



cessfully colonize elevated organic substrates such as logs and root wads (Pojar and MacKinnon 1994).

Alder is the only tree in the PCE to develop a symbiotic relationship with nitrogen-fixing bacteria (Deal and Harrington 2006). Fresh sediment surfaces often lack much OM and are challenging places for tree seedlings seeking nutrients. Because nitrogen availability is a primary limitation to tree growth, once water needs are met, this symbiotic relationship affords alder a competitive advantage on fresh gravel bars. However, alder sprouting from seed on new gravel bars will not always have the mycorrhizal and actinomycete associates that are available on upland sites with well-developed soils (Walker and others 1986; Fisher 1990). There may be slow initial growth rates for several years compared to alder on upland sites while these associates are established (Van Pelt 1991).

Complete inundation of plants eventually results in mortality but the ability to tolerate inundation varies by species (Hosner and Boyce 1962; McBride and Strahan 1984). Also, partially inundated plants survive longer than those totally submerged. In general, willow are most tolerant of flooding but cottonwood are similarly tolerant (Stettler 2009). Western redcedar, Sitka spruce, and red alder have a fairly high tolerance of excess moisture, whereas western hemlock, grand fir, and Douglas-fir do poorly with excess water (Minore 1979). The net result is that vegetative patterns reflect interactions between the plants' physiological breadth and the spatial pattern of micro-environments, as well as the riverine disturbance regime.

## Vegetative Succession

There are several highly generalized successional pathways that vegetation can follow between germination on newly created surfaces to the time that floodplain forests reach maturity (Van Pelt and others 2006). Such pathways can be illustrated in simple heuristic models (Figures 3 and 4). In one of these pathways (Path 1), newly created surfaces are quickly colonized by vegetation. Subsequently, characteristics such as valley constraint, river size, local landform development, substrate texture, and herbivory strongly influence the development of the plant communities (Schreiner and others 1996; Rot and others 2000). In most situations, willow, alder, and cottonwood are often the first to establish (Figures 3 and 4). The physiological tolerance of these tree species to inundation is advantageous, as many of the newly created surfaces spend hours to weeks under water-saturated, light-limited

conditions in winter. Small seedlings of several conifer species also sprout on moist surfaces but few tolerate the frequent winter scouring, sediment deposition, and inundation. Mortality is high among early colonizers, as newly created surfaces shift in size and shape until stabilized and also become extremely hot and dry during summer low water (Stolnack and Naiman 2010). In addition, herbivory by beaver (*Castor canadensis*) and elk (*Cervus elaphus*) has a significant impact on plant communities (Schreiner and others 1996; Naiman and Rogers 1997; Beschta and Ripple 2008). These conditions also contribute to the high mortality of conifers in the young stands that follow this pathway, except those associated with LW accumulations.

As discussed earlier, the creation of new surfaces results from the destruction of older surfaces. The great dimensions of trees in older forests mean that sizeable accumulations of wood form in the river, and they interact with river flows (Abbe and Montgomery 2003). As water flows are diverted by log jams, quiet areas immediately downstream accumulate sediment and become bars (Abbe and Montgomery 1996). These jam-protected bars can be relatively stable surfaces for many years, allowing trees to thrive. At higher elevations, smaller high-energy floodplains are cobble-dominated, which favors early successional willow and alder (Van Pelt 1991). Bar surfaces of large rivers at lower elevations are generally composed of increasingly finer sediments that are ideal for cottonwood (Braatne and others 1996). Subsequent deposition of fine, soil-forming alluvial sediments is greatly enhanced by vegetative establishment, which increases resistance to water flow (Bennett and Simon 2004). These concurrent events elevate both the nutrient pool and soil moisture-holding capacity.

Rapid tree establishment and growth during the first few decades after colonization generally result in dense stands of alder and cottonwood overtopping and shading willow species (Van Pelt and others 2006). Although often dominant during the first two decades, willow is nearly eliminated within 30 years (Figure 4) and later replaced by alder. Alder roots quickly become colonized by *Frankia*, a filamentous bacterium converting atmospheric N<sub>2</sub> into ammonia—a form of nitrogen available to plants. The N-fixation quickly converts a nutrient-poor site into a nutrient-rich one, creating sites favoring ungulates (for example, elk, deer) who can maintain open understories through herbivory (Schreiner and others 1996). The stands also contain substantial hardwood decay fungi, and

soon (40–70 years) alder begin to die, opening the canopy and allowing greater penetration of light. Rich soils, partial shade, and more protection from annual floods provide ideal conditions for the establishment of shade-tolerant conifers.

At the northern end of the PCE, and at the extreme coastal portions of the southern end of the PCE, Sitka spruce is often dominant during the second century. In parts of the Cascade Mountains and in southern British Columbia, Douglas-fir or grand fir (*Abies grandis*) is often the main conifer species to establish (Van Pelt 1991; Figure 7B). However, in other parts of the Cascades and in the coastal mountains of Oregon and Washington (except close to the ocean), western hemlock is the most common conifer underneath older alder in riparian settings—especially floodplains (Villarin and others 2009). Rapid conifer growth quickly converts a hardwood stand into a conifer stand as alder dies. Understories of maturing conifer stands are colonized by other tree and shrub species, including maples (*Acer circinatum* and *A. macrophyllum*), western redcedar and western hemlock.

For floodplains where the channel is laterally dynamic, the river ultimately returns to destroy the forest, starting the process again. A well-studied example is the Queets River where much of the unconstrained valley floor has been reworked by the river during the 20th century (Figure 2), which sustains a diverse mix of landforms and forest types. In the context of the PCE, the Queets River exhibits an intermediate rate of floodplain turnover, which is characteristic of island-braided sites. However, many of the region's rivers have either braided (more rapid floodplain turnover) or straight or meandering (slower turnover) patterns. That is, the average length of time a patch of floodplain exists before the river returns to erode it (the erosion return interval) is commonly less than 10 years in braided channels, but more than 50 years in straight and meandering channels. Average erosion return intervals are estimated to be 100 years in the Queets (Montgomery and Abbe 2006), and even shorter intervals (for example, 30 years) have been observed in other island braided channel systems (Beechie and others 2006a). The broad range of turnover rates in the PCE can be classified by channel patterns that reflect the age structure of floodplain surfaces (Figure 9), and the arrangement of these channel patterns on the landscape is largely predictable from channel slope and discharge.

Many variations exist to successional Path 1 along unconstrained reaches of river floodplains. These variations depend on river size, elevation,

annual precipitation, geology and whether glaciers are present upstream (Naiman and others 2005a). For example, in some cases, a chute cutoff may result in the partial abandonment of the mainstem channel. If the cutoff channel deepens, flows may inundate the mainstem channel less frequently. Such scenarios allow early establishment and survival of conifers (Figure 3). Inundation may still occur during high flows, but overbank flows of water often lack the physical energy or duration to kill small conifers. This situation can also result in an abandoned channel becoming high and dry in which the water table drops, becoming inaccessible to colonizing vegetation. These sites are locally common in the centers of large physical patches and lead to extremely slow plant colonization. In less dynamic rivers, where channel shifts are rare or very slow, other disturbances such as fire or insects may be more important in directing forest structure than those caused by river movement.

There are three relatively recent human-driven impacts on vegetative succession, and ultimately to floodplain tree production, that require discussion. They are seed dispersal (hydrochory—dispersal of seeds by water—and seed banks), invasive plants, and the eradication of predators that historically controlled herbivory. Seed dispersal via hydrochory is important for maintaining the diversity and genetic continuity of riparian plant communities (Nilsson and others 1991). Dams, however, may reduce levels of hydrochory to downstream reaches by trapping seeds within their impoundments. Unfortunately, this subject has received little attention in the PCE because most trees (for example, alder, cottonwood, willow, as well as all of the riparian conifers) have tiny, wind-dispersed seeds. Seeds blanket the landscape and differences in establishment are often due to other factors (such as substrate texture, LW, light availability, inundation regime, and/or water level). Nevertheless, Brown and Chenoweth (2008) have shown a 90% reduction in seed abundance and 84% reduction in species richness below Glines Canyon Dam on the Elwha River, Washington, suggesting that this may be more important than previously thought.

Further, vegetative succession and soil processes in PCE floodplains may be increasingly compromised by the proliferation of invasive plants. It has been known for over two decades that invasive plants are common on recently disturbed surfaces, such as gravel bars, but tend to disappear as light was limited by canopy closure at about 10 years of age (DeFerrari and Naiman 1994). The number of invasive species comprises about 25–30% of the

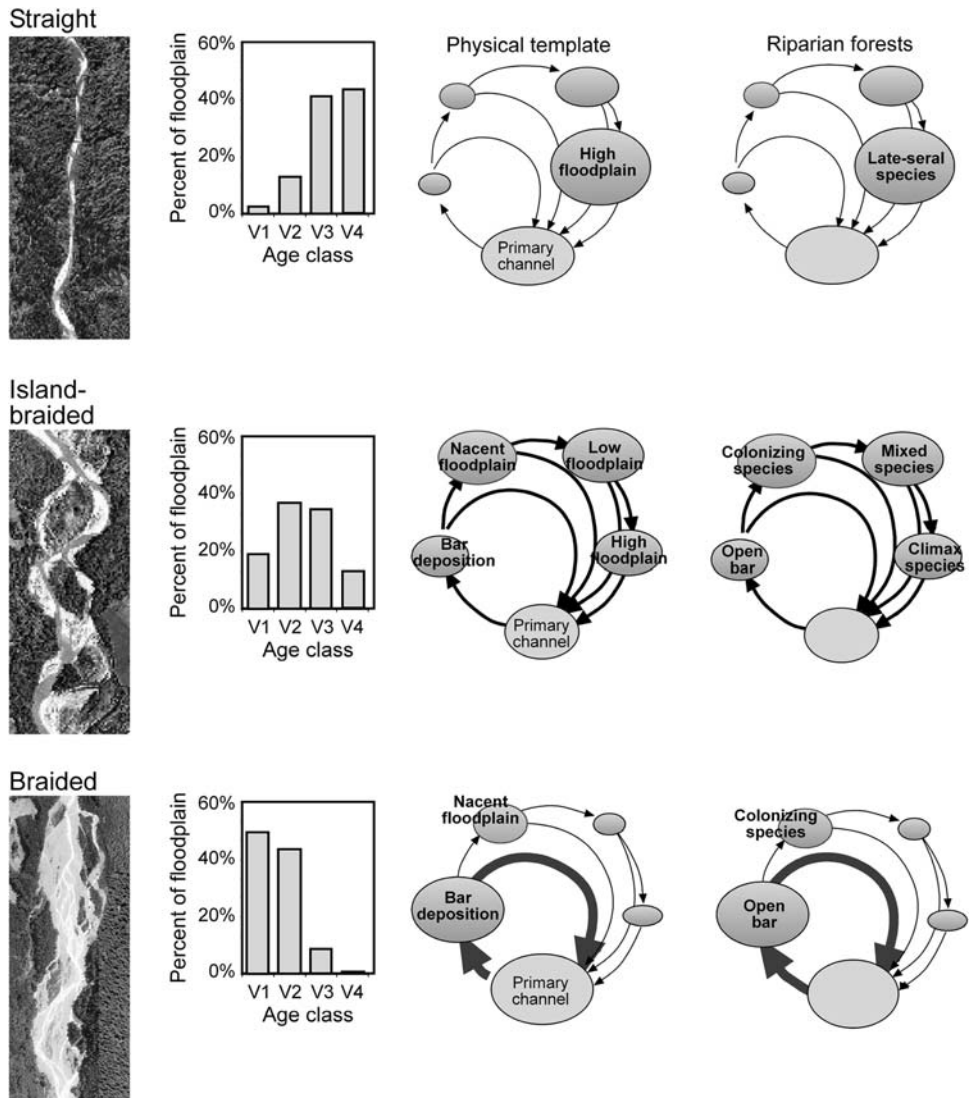


Figure 9. The generalized floodplain and forest development pathway in Figure 3 can be tailored to specific reach types to predict expected forest community structure. Throughout much of the PCE, straight channels have slow turnover rates (> 80 years), most of the floodplain consists of fluvial terraces, and forests are primarily late-seral (conifer) species. In contrast to this, braided channels have high turnover rates (< 10 years), most of the floodplain is channels and pioneer bars, and vegetation is typically early-seral (hardwood) seedlings. Finally, island-braided channels have an intermediate turnover rate (~30 years); a mix of bar, floodplain, and terrace surfaces, and a mixture of forest types.

native species richness, which is similar to that seen along alluvial rivers in other parts of the world (Hood and Naiman 2000). In general, the effects on successional processes and riparian soil formation have so far been minimal. However, with the proliferation of scotch broom (*Cytisus scoparius*) and knotweed (*Polygonu*) that is no longer the case. It is now known that giant knotweed (*P. sachalinense*) has profound effects on system-scale characteristics (Urgenson and others 2009). Richness and abundance (cover or density) of native herbs, shrubs, and juvenile trees are negatively correlated with knotweed density. Where knotweed is present (> 5 stems m<sup>-2</sup>), litter mass of native species is reduced by 70%. The carbon:nitrogen ratio of knotweed litter is 52:1, a value 38–58% higher than that of native red alder and willow. Resorption of foliar N prior to leaf drop is 76% in knotweed but only 5–33% among native woody species. By displacing

native species and reducing nutrient quality of litter inputs, knotweed invasion has the potential to cause long-term changes in the characteristics of riparian forests, their soils and the adjacent aquatic habitats. These effects are likely irreversible without a nearly complete eradication of knotweed.

Finally, the reduction of large predators, especially wolves (*Canis lupus*) and cougar (*Puma concolor*) throughout much of the PCE may have equally important effects on vegetative succession in the floodplains. It has been postulated that the age structure of black cottonwood and bigleaf maple in the western portion of Olympic National Park shows significantly decreased recruitment (growth of seedlings/sprouts into tall saplings and trees) as a result of intensive elk (*Cervus elaphus*) browsing in the decades following the loss of wolves (Beschta and Ripple 2008). Regular recruitment of black cottonwood and bigleaf maple occurred prior to the



extirpation of wolves. Following the removal of this apex predator, and in the absence of human hunting, the structure of the floodplain forests suggests that the recruitment of palatable trees and shrubs has declined. This outcome is consistent with trophic cascades theory (Ray and others 2005), whereby a loss or reduction of large carnivore predation may initiate changes in herbivore densities and altered foraging behavior that ‘cascade’ to lower trophic levels. We suspect that this phenomenon has occurred throughout the PCE wherever the population dynamics of apex predators and their prey have been altered.

## Soil Nutrient Cycling

Although initial nutrient availability may be low in newly deposited coarse sediments, most floodplains quickly develop fertile soils capable of supporting highly productive forests. Young floodplain soils (50–100 years old) typically receive large nutrient inputs from rapid sediment weathering and N-fixing plant species, but have poorly developed mechanisms for retention. They can be considered *open* systems as leaching losses are high due to coarse soil texture. The transition to *closed* systems, with much lower inputs but more efficient retention, is attained as plant community development augments the efficiency of plant-soil nutrient recycling through the accumulation of soil OM, which buffers nutrient and water transfers between soils and biota. Thus, the rapidity with which soils develop the capacity to support vegetation and accumulate soil OM influences nutrient availability to older forests. This is strongly mediated by sediment distribution patterns, with rapid soil OM accumulation occurring in newly deposited fine-textured soils.

A major source of nutrients to alluvial floodplains is associated with fine sediments. As sediments move from less-weathered upstream environments to downstream depositional areas (Carey and others 2005; Porder and others 2007), they expose ‘fresh’ surfaces as the sediments are abraded. However, chemical weathering, only weakly expressed in aquatic environments, is necessary to release biotically available nutrients in usable forms. Chemical weathering increases by 2–3 orders of magnitude following deposition as sediments are exposed to carbonic acid produced by respiring plant roots and decomposing OM (Bland and Rolls 1998; Schwartzman and Volk 1989). This process releases large amounts of available P, a nutrient often limiting primary productivity (Elser and others 2007), as well as base cations ( $K^+$ ,  $Na^+$ ,

$Mg^{2+}$ ,  $Ca^{2+}$ ). The base cations play important roles in buffering soil and aquatic pH, in addition to being ecologically important and occasionally limiting nutrients (McLaughlin and Wimmer 1999; Tripler and others 2006).

Phosphorus differs in solubility and weathering rate from the base cations, leading to differing catchment-scale patterns in its distribution and biological availability. Because P weathers more slowly and is far less soluble than the base cations, most P inputs to floodplains are from particulate matter deposition (Melack 1995). These particulate forms include P adsorbed to sediments, unweathered P within sediments, and P in organic debris. Because base cations have relatively high solubility and weathering rates, dissolved concentrations in soil water tend to be high. These can be transferred to soils through capillary movement—sometimes resulting in salt crusts where evaporation from bare floodplain surfaces is high, or via root uptake of subsurface water.

Marine aerosols are a secondary source of cations that may be important in some coastal floodplains. Amounts are greatest in forests immediately bordering on the ocean, with rainwater cation concentrations decreasing by half within the first 50 km inland (Blew and Edmonds 1995). These aerosols may be a significant source of base cations to older soils, where the original supply has been depleted by leaching, and to canopy epiphytes.

Of the several sources of nitrogen to PCE floodplains, by far the greatest is N-fixation by *Frankia* associated with red alder. N-fixation rates in alder forests may exceed 300 kg/ha/year (Binkley and others 1994)—high by even agricultural standards. N-fixation appears to greatly exceed biological demand during the first 50 to 100 years when red alder is the dominant floodplain tree. The resulting high nitrification rate of excess N has two consequences: it leads to leaching of excess N and it contributes greatly to soil acidification and weathering. Following the transition from alder to conifer forest N inputs are much lower, with free-living bacteria in soil and especially LW, forming the bulk of inputs in mature and old forests. In the southern parts of the PCE, cyanolichens, particularly the N-fixing lichen *Lobaria oregana*, supply up to 16 kg/ha/year of new N (Antoine 2004).

The apparent indifference of N-fixation to the available N supply raises the question: What controls N-fixation rates in floodplains? Several studies have found low N-fixation rates in early seral forests limited by P (Pearson and Vitousek 2002). In addition to directly benefiting vegetation, a high P supply may thus play an important enabling role in

the exceptionally high N-fixation rates often observed in PCE floodplain forests. Simulation modeling of fluvial deposition of OM suggests that N inputs from fluvial deposition of OM are minor in most rivers, accounting for less than 10% of the N accumulated during the first 100 years of floodplain development (Bechtold and Naiman 2009b).

Temporal patterns in retention and bioavailability of nutrients and organic matter during floodplain soil development are equally important in sustaining tree production. Although young PCE floodplains receive large nutrient inputs, sustaining high tree productivity on older surfaces with few new nutrient inputs requires efficient recycling mechanisms. Greater recycling efficiency is achieved largely through close coupling of physical (for example, adsorption) and biological (mineralization, microbial immobilization, and plant uptake) processes, as well as through the accumulation of soil OM. Soil OM accumulation, by incorporating nutrients within or adsorbed to external surfaces of OM, plays a fundamental role in providing temporary storage for almost all N, and increasingly for P, as it is weathered from sediments. Soil OM retention, in turn, is strongly influenced by sediment texture and mineralogy. Adsorption of OM to clays, and to aluminum and iron oxyhydroxide coatings on silt and clay, as well as incorporation within aggregates, enhances retention by reducing leaching and inhibiting decomposition (Sollins and others 1996)—thereby contributing to tree productivity.

The importance of nutrient and OM adsorption has been amply demonstrated in older upland soils but has an additional importance for floodplains. In floodplains, fluvial sorting creates complex patterns in sediment size distribution and biological retention mechanisms are initially poorly developed. Field, laboratory, and simulation studies on the Queets River floodplain demonstrate the far reaching influence of sediment texture in controlling OM and nutrient processes. There, soils accumulate carbon and nitrogen to plateaus during the first 100 years. This occurs as silt and clay-sized particles become highly enriched with adsorbed organic matter (Figure 10). Soil clay concentration, aluminum oxyhydroxides, and site age collectively account for 93% of the variation in (0–10 cm depth) soil carbon, with clay concentration being the single greatest predictor ( $r^2 = 0.74$ ) of soil carbon concentration (Bechtold 2007).

Sediment texture also influences the retention of organically bound nutrients. This is reflected most strongly for N, almost all of which is contained within OM. Soil OM establishes a sharply defined

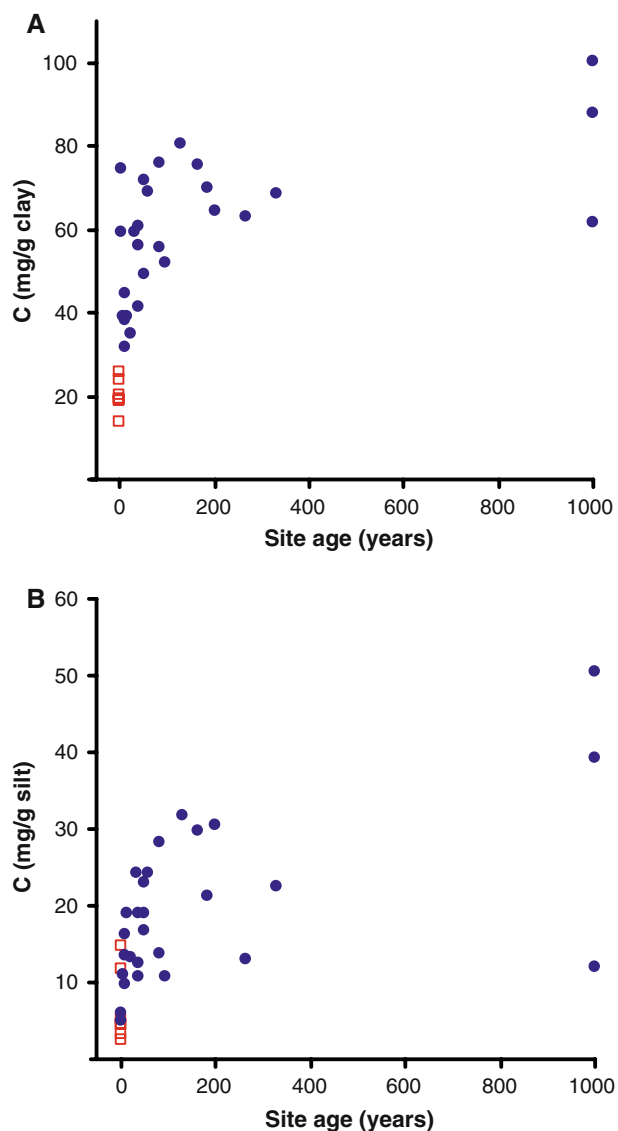


Figure 10. Concentrations of C adsorbed to clay (A) and silt (B) particles in flood deposits (rectangles) and soils (circles; 0–10 cm depth) from a 0–1000 year Queets River chronosequence. Adsorbed increased logarithmically for both clay ( $y = 6.24 * \ln(x) + 34.9$ ,  $r^2 = 0.72$ ,  $n = 35$ ) and silt ( $y = 3.56 * \ln(x) + 5.49$ ,  $r^2 = 0.53$ ,  $n = 35$ ). Soils were ultrasonically dispersed prior to particle size separation.

upper limit for N retention in alder forest soils at about 8% of soil C. Soil OM also becomes increasingly important over time for maintaining bioavailable P as it is increasingly weathered from sediments. Over 80% of the weatherable P is released from sediments during the first 1000 years of soil development, with the greatest portion being transferred to organic forms (Bechtold and Naiman 2009b, c).

The supply of bioavailable nutrients in floodplain soils is maximized by the relatively short turnover times of soil OM—further contributing to tree production. Respiration per unit soil C increases over the first decade or so as rapidly decomposing litter from the developing forest reaches a maximum, and then declines as soil OM increasingly becomes dominated by the recalcitrant OM pools. This results in a soil C turnover of about 10 years in mature conifer forests (Bechtold and Naiman 2009b); slightly faster than the 12-year turnover reported during secondary succession of forests on abandoned agricultural land, and much faster than the greater than 25 year turnover times in mature upland forests (Harrison and others 1995).

In contrast to N and P, the highest base cation concentrations are observed during the first few decades of soil development, adding an additional temporal aspect to nutrient processes. Base cation retention is strongly influenced by the intense leaching environment and by biological demand (Bechtold and Naiman 2009c). Base cations leach quickly under humid conditions (Bockheim 1980), especially where decay of coniferous forest OM or high nitrification rates in N-fixing forests contribute acids to soils (Johnson and Cole 1977; Van Miegroet and Cole 1984). In the PCE, this leads to rapid loss of calcium which is initially abundant in river water and soils. Potassium, in contrast, displays a striking pattern of translocation to the upper soil profile over time, with only small overall losses, suggesting intense recycling of  $K^+$  by vegetation (Bechtold 2007). A weaker pattern of upwards translocation is also observed for  $Mg^{2+}$ . Collectively, quantification of soil-nutrient processes in PCE floodplains reveals their fundamental controls on water quality as well as their importance in underpinning tree production.

### Marine-Derived Nutrients

Another important nutrient source for floodplain trees is marine-derived nutrients (MDN) carried by spawning Pacific salmon. Alluvial PCE rivers are essential habitat for five species of semelparous salmon, which return to spawn and die in natal streams (Quinn 2005). Where abundant salmon remain, annual spawning migrations transport substantial quantities of MDN from the fertile North Pacific Ocean to relatively nutrient-poor, coastal rivers and floodplains (Gende and others 2002; Naiman and others 2002, 2009). The salmon-borne MDN play important roles in shaping and maintaining plant communities and soils. When salmon are abundant, tree growth by most riparian species

(for example, Sitka spruce, Douglas-fir) is enhanced, whereas when salmon are removed, tree growth declines (Helfield and Naiman 2001; Drake and Naiman 2007). MDN effects vary by dominant salmon species (for example, mass spawners, or not), population abundance, distribution of spawning areas, river geomorphology, background nutrient loading, and the type and abundance of biotic vectors responsible for spreading MDN throughout riparian areas (Naiman and others 2009). People have been long aware of the importance of salmon-borne MDN for the productivity of freshwater ecosystems in western North America, and the rapidly increasing body of knowledge on this topic supports this notion. Nevertheless, many details associated with nutrient pathways, cycling processes, and the ecosystem-scale consequences of the MDN transfer remain a mystery.

The collective data suggest that the freshwater portions of the salmon production system, as well as the dynamics of local terrestrial plant and animal communities, are intimately linked to MDN in complex ways. At the same time, the ecological importance of MDN, relative to other major nutrient sources, is temporally and spatially dependent, and influenced by the specific life histories and the abundances of individual salmon stocks. For example, mass spawners (*O. gorbuscha*, *O. keta*, *O. nerka*; pink, chum, and sockeye, respectively) appear to have strong system-scale effects. Although interactions among climate cycles, salmon, vegetation, predators, and MDN flowpaths and feedbacks are complex, they also form an integrated ecological system with a high degree of resilience and productivity (Naiman and others 2009). This complex system, and its inherent temporal and spatial variability, encompasses important interactions among salmon life cycles and the physical setting, as well as numerous linkages to other ecosystem components. For example, within northern sections of the PCE where coastal brown bear (*Ursus arctos*) are abundant, there are positive synergistic interactions between bear, salmon, floodplain tree growth, and fish habitat (Helfield and Naiman 2006). Further, the removal of trees (for example, Teigs and others 2008) or salmon predators and scavengers negatively impact salmon and the ecological importance of MDN to floodplain communities.

### Canopy Development and the Roles of Epiphytes

Large trees on floodplains support abundant epiphytes—plants that live on other plants—and they



also play important roles in supporting tree productivity. Often noticeable in moist forests, epiphyte accumulations only reach massive biomasses in rain forests (Sillett and Antoine 2004; Williams and Sillett 2007). In general, epiphytes serve at least two important nutrient-related functions: they contribute to the nutrient-gathering capacity of the forest by greatly expanding tree surfaces and increasing atmospheric deposition of nutrients (Knops and others 1996; Nadkarni 1986), and some fix N (for example, cyanolichens) supplying up to  $16 \text{ kg N ha}^{-1} \text{ y}^{-1}$  (Pike 1978; Antoine 2004). Cyanolichens become dominant in old forests of the less humid sections of the PCE, especially in the southern Washington and Oregon Cascades.

Epiphytic bryophytes are major contributors to canopy soils that develop on branches in coastal rainforests (Ingram and Nadkarni 1993). These sponge-like accumulations store water in the canopy (Veneklaas and others 1990), allowing desiccation-sensitive organisms to flourish high above the ground. Throughout the PCE, most of the epiphytic biomass occurs as either lichens or bryophytes. Bryophytes become dominant in the wetter portions of the PCE, especially in the coastal mountains from the Oregon Coast Range northward. The dry mass of epiphytes and associated dead organic matter held in the crowns of individual trees can exceed 100 kg (Hofstede and others 1993; Nadkarni 1984; Ellyson and Sillett 2003). On the Queets River floodplain large individual trees can have in excess of 500 kg of epiphytic dry mass from bryophytes alone (Van Pelt and others, unpublished data). Vascular plants also occur as canopy epiphytes, especially on large trees in coastal floodplains (Sillett 1999; Clement and others 2001; Sawyer and others 2000). Recent work in PCE redwood canopies indicates that individual trees also can have more than 500 kg of epiphytic dry mass and associated soil from a single species—the leatherleaf fern (*Polypodium scoleri*; Sillett and Van Pelt 2007).

Large accumulations of bryophytes need large structures to support them. As a result, young stands support relatively little bryophyte biomass. Cottonwood, common in many of the river valleys, grows rapidly and produces large structures during the first century. Epiphytic dry mass values exceeding 10 Mg/ha have been recorded in stands as young as 120 years (Van Pelt and others, unpublished data). Slower-growing conifers do not develop sufficient structural features to support high bryophyte biomass until late in the second century. Cottonwood plays a crucial role in allowing this biodiverse community to develop early.

The vertical distribution of epiphytic biomass is strongly related to the structures present in the canopy and is also influenced by light availability (Sillett and Van Pelt 2007). As floodplain forests advance from mature to old-growth, the peak in the vertical distribution of biomass shifts upward, while the peak in foliage distribution shifts downward. The deep soils derived from epiphytes on large limbs and in crotches are favorable sites for adventitious rooting from the host tree—further contributing to productivity. First noted on bigleaf maple (Nadkarni 1981), adventitious roots are now known to be common in Sitka spruce, black cottonwood, vine maple, western redcedar, and coast redwood, wherever epiphytic soils are abundant (Sillett and Van Pelt 2007; Van Pelt and others, unpublished data).

Canopy epiphyte communities contain many species. The epiphytic communities contain over 100 species of bryophytes, lichens, and vascular plants—many only found in old-growth forest canopies (Nadkarni 1984; Ellyson and Sillett 2003; Williams and Sillett 2007). In addition, canopy epiphytes provide habitat to threatened or endangered animals, such as the marbled murrelet (*Brachyramphus marmoratus*). In some parts of their range, murrelet nest on thick bryophyte mats that form on tree limbs. Epiphytes also harbor many smaller animals. Bryophyte mats in the Sitka spruce/western redcedar rainforests on Vancouver Island, British Columbia, contain more than 150 species of microarthropods. At least 50 species were new to science and were found neither on the forest floor nor in nearby younger forest canopies (Winchester and Ring 1999).

## Production Dynamics of Floodplain Trees

Collectively, the physiologies of individual species, as well as the nutrients and OM from soil processes and from the ocean and from canopy epiphytes, contribute synergistically to tree production. Even though older PCE floodplain forests are patchy, they contain some of the fastest-growing and tallest trees known (Van Pelt 2001). Unlike other temperate or tropical alluvial forests, the long-lived conifer forests of the PCE maintain high productivity into the second and even third centuries of forest succession, accumulating impressive biomass (Table 2). Nevertheless, floodplain trees exhibit strong temporal and spatial variation in litterfall and productivity rates.

In a typical example from the Queets River, annual litterfall increases rapidly through the first

100 years of successional development, a period characterized by rapid hardwood colonization and growth (O'Keefe and Naiman 2006). For very young sites dominated by willow and alder (<50 years old), annual litterfall averages only about 3 Mg ha<sup>-1</sup> y<sup>-1</sup>; however, peak litterfall rates of around 10 Mg ha<sup>-1</sup> y<sup>-1</sup> are reached quickly as sites approximately 50–70 years old become dominated by mature alder. During the first century of forest development, but not thereafter, annual litterfall is significantly correlated with canopy volume, stem volume, and total basal area. After the first century, total litterfall declines by about 40%. During this transition, the

forest undergoes a compositional shift from hardwoods to conifers; this is reflected in conifer/hardwood stem density ratios of less than 0.01 on active channel surfaces but 1.7 and 2.7 on transitional terraces and mature terraces, respectively. Concomitant with changes in patterns of forest structure, litter production along the Queets River declines to about 5 Mg ha<sup>-1</sup> y<sup>-1</sup> in the second and third centuries commensurate with rates observed in other regional riparian zones dominated by conifers (about 7–9 Mg ha<sup>-1</sup> y<sup>-1</sup>; Sedell and others 1974; Neaves 1978) and in uplands (about 2–3 Mg ha<sup>-1</sup> y<sup>-1</sup>; Edmonds and Murray 2002; Gessel and Turner 1976).

**Table 2.** Structural Characteristics of Vegetation of Some Alluvial Forests from the Pacific Coastal Ecoregion

Location	Age (years)	Species	Canopy volume (m <sup>3</sup> /ha)	Stems (#/ha)	Basal area (m <sup>2</sup> /ha)	Stem volume (m <sup>3</sup> /ha)	Max. height (m)
ONP—Queets River <sup>1</sup>	130	<i>Picea sitchensis</i>	103,970	136	49.9	1065	56.8
		<i>Populus balsamifera trichocarpa</i>	50,549	50	34.7	615	51.8
		<i>Acer macrophyllum</i>	30,344	36	8.3	142	38.7
		Total	211,369	316	100.1	1907	
	~265	<i>Picea sitchensis</i>	77,427	267	70.1	1541	76.7
		<i>Tsuga heterophylla</i>	14,381	33	5.6	93	51.7
		<i>Acer macrophyllum</i>	36,585	69	17.1	318	39.7
		Total	148,081	650	99.8	2069	
	~330	<i>Picea sitchensis</i>	116,637	177	59.5	1268	81.5
		<i>Tsuga heterophylla</i>	48,729	174	20.5	329	59.2
		<i>Acer macrophyllum</i>	26,152	17	10.8	200	38.6
		Total	222,809	556	98.1	1899	
WNF—Middle Santiam River <sup>2</sup>	~450	<i>Pseudotsuga menziesii</i>	113,447	72	96.5	2198	81.3
		<i>Tsuga heterophylla</i>	84,959	286	22.4	388	50.3
		Total	200,331	359	119.8	2606	
MRNP—Carbon River <sup>3</sup>	~500	<i>Pseudotsuga menziesii</i>	45,106	17	45.0	825	81.4
		<i>Tsuga heterophylla</i>	102,774	254	36.0	778	75.5
		<i>Thuja plicata</i>	22,583	23	27.2	386	69.7
		Total	172,795	310	109.5	1989	
MSHNVP—Muddy River <sup>3</sup>	~650	<i>Pseudotsuga menziesii</i>	85,418	23	74.6	1575	90.3
		<i>Tsuga heterophylla</i>	65,228	157	19.1	308	62.5
		<i>Thuja plicata</i>	34,447	32	49.5	650	69.7
		Total	189,089	226	144.1	2550	
HRSP—Bull Creek <sup>4</sup>	1500+	<i>Sequoia sempervirens</i>	229,266	152	265.2	8071	111.6
		<i>Umbellularia californica</i>	839	4	0.2	1	41.5
		Total	230,105	157	265.4	8072	
PCRSP—Prairie Creek <sup>5</sup>	2000+	<i>Sequoia sempervirens</i>	312,917	113	363.2	9456	101.0
		<i>Pseudotsuga menziesii</i>	8,726	7	10.9	302	82.2
		Total	338,881	164	379.1	9837	

Only the stand dominant vegetation is listed; totals include all tree species present.

ONP Olympic National Park; WNF Willamette National Forest; MRNP Mount Rainier National Park; MSHNVM Mount Saint Helens National Volcanic Monument; HRSP Humboldt Redwoods State Park; PCRSP Prairie Creek Redwoods State Park.

<sup>1</sup>Van Pelt and others (2006).

<sup>2</sup>Van Pelt and Franklin (1999).

<sup>3</sup>Van Pelt and Nadkarni (2004).

<sup>4</sup>Van Pelt and Franklin (2000).

<sup>5</sup>Sillett and Van Pelt (2007).

\*Muddy River stand is on alluvium from a wet upper terrace, not a current floodplain.

Floodplain plant density, biomass, and production drive variation in litterfall rates over time. The few studies of floodplain tree production suggest that trees grow quickly with mature forests on floodplain terraces being the main contributors to production for at least 350 years after stand initiation (Balian and Naiman 2005). On the Queets River, tree density is highest on recently disturbed portions of the active floodplain (~27,000 stems/ha), declining exponentially to approximately 500 stems/ha in stands older than 250 years. Basal area and total stem biomass are lowest in the active floodplain (about 16 m<sup>2</sup>/ha and about 18 Mg dry weight/ha, respectively), greater on terraces with young forests (about 32 m<sup>2</sup>/ha and about 134 Mg dry weight/ha) and greatest on terraces with mature forests (about 69 m<sup>2</sup>/ha and about 540 Mg dry weight/ha). Surprisingly, at the plot scale, growth rates measured as annual increases in total basal area are not significantly different among differently aged physical surfaces—meaning that growth rates appear to level off as indicated by basal area alone—with mean values ranging from approximately 1.4 (low terrace) to approximately 2.8 m<sup>2</sup>/ha/year (active floodplain). In contrast, annual bole production is significantly higher on terraces with mature forests (10.3 Mg/ha) than on the active floodplain (3.2 Mg/ha); terraces with young forests are intermediate (6.5 Mg/ha). The high production rates on the terraces with mature forests are attributed to a rapid increase in conifer height on surfaces more than 250 years old.

These production rates are comparable to those in regional upland forests and are much greater than rates in many other parts of the world. At the floodplain scale (57 km<sup>2</sup> over 77 km of river length for the Queets River), mature terraces contribute around 80% of the total annual tree production (28,764 Mg), whereas the active floodplain and young terrace surfaces account only for 5 and 14%, respectively. If findings from the Queets River can be extrapolated to the region, this suggests that, in combination with the rapid lateral migrations of many alluvial PCE rivers, the older forests on terraces sustain OM inputs (especially LW). It is the LW that, over decades to centuries, largely shapes the character of rivers in the PCE and, as described below, provides a positive feedback to support further tree production.

### Forest Productivity and Large Wood

Even after the large trees die, they continue to influence forest productivity and stand structure in ways complementary to nutrient delivery processes.

They do so as LW by encouraging the growth of newly established trees early in stand development (Stolnack and Naiman 2010). For example, Sitka spruce distribution reflects—in part—the distribution of remnant logs. Sitka spruce establishes at much higher densities on remnant logs than on soils immediately adjacent to the log and, despite crowded conditions, grows at similar rates to trees in adjacent soils (Latterell and Naiman, unpublished data). Spruce growing on remnant logs on Olympic Peninsula rivers reach heights of 10 m in just 24 years; 14% taller than spruce of the same age in managed riparian areas along small streams without LW (Beach and Halpern 2001).

In addition to providing a more stable, sheltered growth substrate than alluvial sediments, many logs offer a moist, fragmented organic layer immediately below the exterior, which is the result of dampwood termite (*Zootermopsis*) activity. By excavating tunnels and generating frass, termites contribute to a fertile substrate for root growth and potentially hasten the establishment and frequency of spruce colonnades in recently disturbed floodplains (Latterell and Naiman, unpublished data). Early establishment provides more time to grow before the river reoccupies the location and captures the trees for the instream LW pool. LW appears much less important for conifer establishment where Douglas-fir occurs on floodplains, such as in drier inland areas (Stolnack and Naiman 2010).

In addition to direct effects, LW indirectly influences forest productivity by affecting the longevity of individual forest stands (Montgomery and Abbe 2006), and thereby the reach-scale age structure of the floodplain forest. LW-jams create erosion resistant areas or 'hard points' (Montgomery and Abbe 2006); as a result, trees growing on landforms created by and/or protected from erosion by logjams are more likely to survive to maturity than if the logjams were absent. Thus, logjams increase the extent of mature forest patches within a river reach. Older floodplain forests are more productive than young stands—as previously described for the Queets River (Balian and Naiman 2005)—with the presence of LW presumably contributing to higher overall forest productivity.

### Floodplain Complexity and Production Dynamics: A System-Scale Model

The ecological processes underpinning floodplain tree production—ecophysiology, soil development, large pieces of dead wood, salmon-borne MDN, canopy epiphytes, herbivory, invasive spe-



cies—exhibit extensive heterogeneity in space and time (Table 3). Further, the biophysical complexity is evident on several spatial and temporal scales (Table 1). This complexity is a product of floodplain history—shaped by variation in the pattern and sequence of erosion and inundation, the underlying physical template and the biotic (community) drivers and processes. More importantly, the environmental drivers are sequenced in time in terms of their maximum effectiveness, having synergistic effects over the entire 300–400 year chronosequence (Figure 11). As coastal floodplains mature they are largely influenced during the first few decades by more terrestrial processes—such as legacies of past disturbances and sediment texture and abundance—and later on by more oceanic drivers—such as marine-derived nutrients and marine aerosols. Internally they are highly influenced by herbivory, sediment trapping, and N-fixation in the early decades and by LW and abundant epiphytes in the 2nd and 3rd centuries. In combination, the sequence of environmental drivers shapes floodplain characteristics and vegetative productivity.

The high production rate of floodplain trees is supported by a combination of sediment fluxes, salmon-borne MDN, canopy epiphytes, alder, and the ability to trap and hold nutrients from precipitation and fog. In essence, the dynamic floodplain environment provides a diversity of sedimentary substrates, as well as nutrient and moisture sources, driving the productivity. Further, the existence of large, old trees—adding the dimensions of diameter and height—also is essential to overall system diversity and productivity in a number of ways. The trees harbor massive amounts of diverse epiphytes after the first century, condense fog into usable moisture, filter micro-nutrients from oceanic sources, provide LW for in-stream habitat, stabilize surface sediments, produce annually abundant litter, and share nutrients and moisture over wider areas via root grafting or mycorrhizae. Further, the large trees and the LW create habitat for additional species.

The relative importance of each ecological component underpinning floodplain characteristics and tree production varies in three dimensions. It varies laterally from the active channel to the edge of the valley, longitudinally along the river from uplands to the ocean, and latitudinally (N-S) throughout the PCE in response to the biophysical characteristics of specific floodplains and river valleys. Locally, spatial complexity in sediment texture, moisture, and disturbance regimes are well appreciated, and are manifest in the biotic communities

and processes (Naiman and others 2005a, b). Additionally, there are strong latitudinal patterns in lithology, climate, and elevation affecting the relative roles of epiphytes, invasives, MDN, litterfall, and herbivory in shaping plant communities and driving productivity. Although the complexity of these drivers hinders development of a detailed model that can be applied with confidence to local situations, the general system-scale model (Figure 11) can be a guide to ecological understanding and resource decisions considered in a local context.

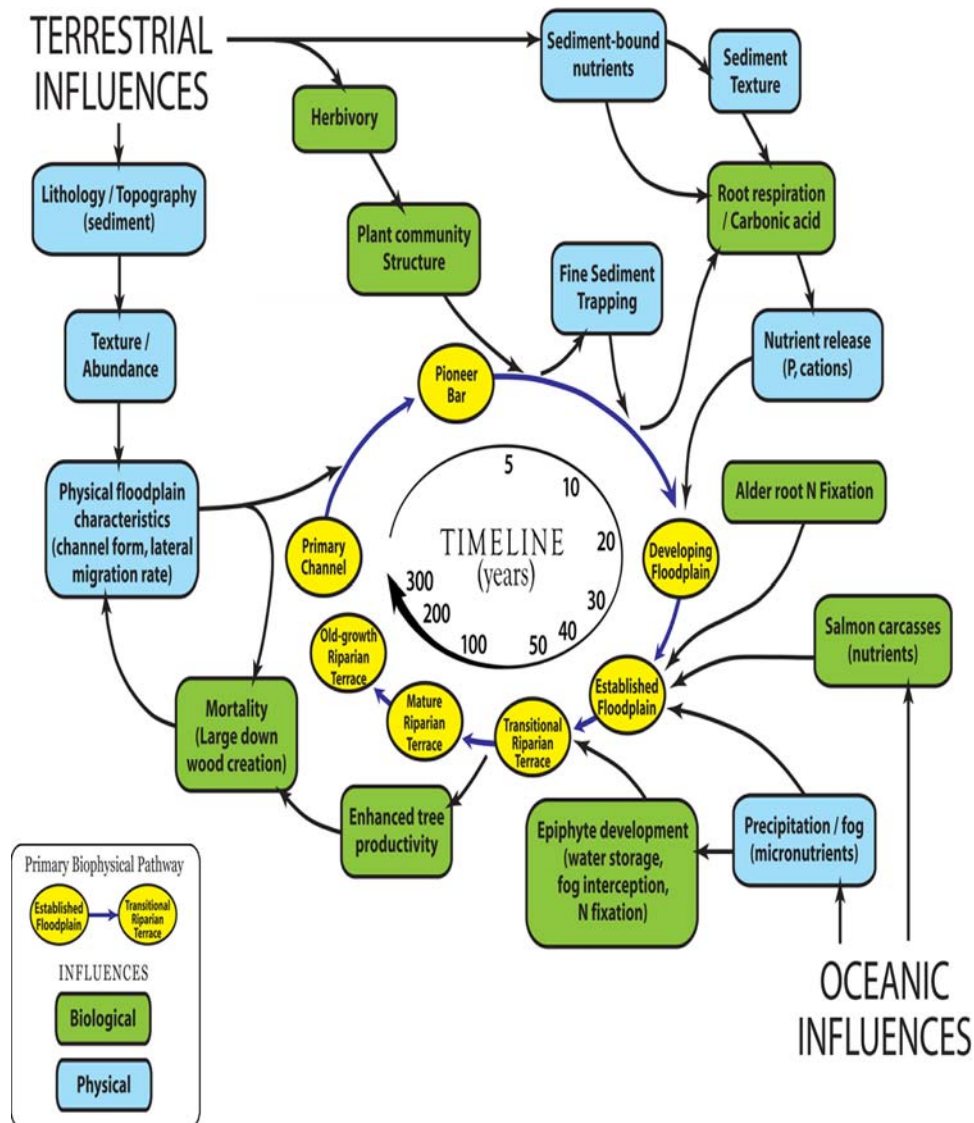
## IMPLICATIONS AND APPLICATIONS FOR FLOODPLAIN MANAGEMENT

The structures and processes associated with channel geomorphology, soil development, large wood, nutrient cycling, and plant succession are closely aligned with those described for alluvial floodplains in other temperate regions. For example, the alluvial Tagliamento River (Italy)—possibly the most natural remaining river in central Europe—exhibits much of the biophysical complexity and many nearly identical attributes related to channel migration patterns, soil development, woody accumulations, and plant succession (for example, Ward and others 1999; Tockner and others 2003). The Garonne River (France)—flowing through a more human-modified landscape—exhibits strong similarities in controls on nutrient cycling, in some physical processes, and in vegetative succession (Décamps 1996). Further afield in the savanna regions of South Africa, we have found sediment texture, large wood, and herbivory to be important in successional processes—but operating at very different time scales than in the PCE (for example, Bechtold and Naiman 2006; Pettit and Naiman 2005). In contrast, controls on floodplain nutrient cycling there respond to strong environmental drivers shaping the upland vegetative patterns, such as fire and herbivory, to enhance nitrogen, phosphorus and sediment fluxes to riparian zones (Pettit and Naiman 2007; Jacobs and others 2007a, b). Overall, the fundamental structures and processes described for the PCE are similar to many other rivers, but variation in climate, successional pathways, and disturbance regimes result in very different forest productivities and dynamics (Naiman and others 2005b).

Floodplains throughout the world are undergoing extensive modification, and those in the PCE are no exception. Many PCE floodplains, especially those south of central British Columbia, have been modified by forest harvest, farming, log storage,

**Table 3.** Processes and Drivers Contributing to the Productivity of Floodplain Forests in the PCE

Processes	Segment-scale drivers	Reach or patch-scale drivers	Consequences	References
Vegetated patch erosion and initiation	<ul style="list-style-type: none"> <li>Valley constraint</li> <li>Sediment supply</li> <li>Discharge patterns</li> <li>Forest types</li> <li>Wood supply</li> </ul>	<ul style="list-style-type: none"> <li>Channel dynamics</li> <li>Substrate texture</li> <li>Vegetation colonization</li> <li>Logjams</li> </ul>	<ul style="list-style-type: none"> <li>Material transfers from forest to river</li> <li>Complex floodplains</li> <li>Forested islands</li> <li>Dissipation of stream power</li> <li>Hyporheic flowpaths</li> </ul>	Abbe and Montgomery (1996), Beechie and others (2006a), Latterell and others (2006), Montgomery and Abbe (2006)
Soil formation	<ul style="list-style-type: none"> <li>Basin geology</li> <li>Valley constraint</li> <li>Sediment supply</li> <li>Discharge</li> </ul>	<ul style="list-style-type: none"> <li>Inundation</li> <li>Sand deposition</li> <li>Vegetation colonization</li> <li>Suspended sediment deposition</li> </ul>	<ul style="list-style-type: none"> <li>Formation of fertile soils</li> <li>Forest regeneration</li> <li>Organic matter production</li> <li>Denitrification</li> </ul>	Bechtold and Naiman (2009a, b), Bechtold and others (2003), Pinay and others (2003)
Plant succession	<ul style="list-style-type: none"> <li>Flood inundation and burial</li> <li>Ecophysiology of plant species (seed size, adventitious roots, shade tolerance, symbiosis with N-fixers, tolerance of submersion and abrasion, drought resistance)</li> <li>Invasive species</li> </ul>	<ul style="list-style-type: none"> <li>Microtopography</li> <li>Biological legacies</li> <li>Soil fertility</li> <li>Light availability</li> <li>Propagule dispersal</li> <li>Herbivory</li> <li>Decay fungi</li> </ul>	<ul style="list-style-type: none"> <li>Structurally diverse forests</li> <li>Diverse forest communities</li> <li>Microclimatic variation</li> <li>Variation in litterfall</li> <li>Development of canopy soils</li> <li>Biomass accumulation</li> <li>Suppression of native species</li> </ul>	Hood and Naiman (2000), Pollock and others (1998), Balian and Naiman (2005), Van Pelt and others (2006), DeFerrari and Naiman (1994), Urgenson and others (2009)
Nutrient dynamics	<ul style="list-style-type: none"> <li>Chemical rock weathering</li> <li>Deposition of marine aerosols</li> <li>Marine derived nutrients</li> <li>Deposition of atmospheric particles</li> <li>Epiphytic bryophytes</li> </ul>	<ul style="list-style-type: none"> <li>Bacterial N-fixers</li> <li>Soil OM</li> <li>Clay concentration</li> <li>Aluminum oxyhydroxides</li> <li>Carbonic acids from decay</li> <li>Moisture</li> <li>Forest composition</li> </ul>	<ul style="list-style-type: none"> <li>Plant-available P and base cations</li> <li>Soil buering</li> <li>Leaching of excess N</li> <li>Soil acidification and weathering</li> <li>Bioavailable nutrients</li> <li>Nutrient gathering from canopy soils</li> <li>Retention of nutrients from atmospheric deposition</li> </ul>	Bechtold and Naiman (2009b, c), Schwartzman and Volk (1989)



**Figure 11.** A summary of the major terrestrial and oceanic influences affecting floodplains in the PCE. The various influences occur at specific time periods during floodplain succession, collectively driving the expression of system-scale characteristics over the approximately 350 year chronosequence. Herbivory and the deposition of sediment-bound nutrients are especially influential during the first several decades of floodplain development. Later, marine-derived nutrients from spawning salmon and contained in precipitation and fog become increasingly important, especially as tall, deep canopies develop in the maturing forests, and their epiphyte communities becomes fully functional into the 2nd century. Eventually LW derived from productive forests returns to the river and shapes channel dynamics and patterns of sediment texture and deposition.

water regulation, dredging, and residential and industrial development (Naiman and Bilby 1998; Burnett and others 2007). Urban development has encroached into many major floodplains, facilitated by the construction of flood control facilities decades ago. Further, they are experiencing changes due to climate shifts expressed as decreased summer precipitation, increased winter flooding, loss of spring snow mass and extent of glaciers, and rising temperatures (Littell and others 2009). The legacy

of past land-use conversion and river modification, as well as ongoing climate shifts, have profoundly affected the way many river floodplains now function. In the future, one can expect to see an increase in the frequency and severity of large floods and upland wildfires, both of which will have effects on the biotic characteristics of the rivers and their floodplains.

Fortunately, attempts are being made to implement science-based regulations conserving and



protecting floodplains (for example, King County, Washington; <http://www.kingcounty.gov/property/permits/codes/CAO.aspx#best>). Such regulations represent significant progress toward maintaining the process-based functions of floodplains and in aligning policy with the best available science. Over time, improved regulations should result in substantial gains in floodplain function. However, for many rivers, much has already been lost; therefore, the key challenges lie in designing process-based approaches for system recovery that are effective now and into the future (Beechie and others 2009). Based on a contemporary understanding of natural PCE floodplains, what strategies would be effective in re-establishing self-sustaining systems within existing constraints?

### Process-Based Approaches to Floodplain Recovery

Some restoration techniques rely on static designs that are antithetical to natural functions (Beechie and Bolton 1999). That is, many restoration actions attempt to control natural dynamics and, as a result, eventually cease to function properly because they cannot evolve to changing conditions. Admittedly, many PCE floodplains are now urban and industrial areas where the legacy of past floodplain management policies severely constrains restoration options. There, techniques such as rehabilitation and substitution of structures for processes are among the only feasible options (for example, see Simenstad and others 2005; Simenstad 2006). Nevertheless, it is still common practice to implement static restoration designs and structures even in relatively low-risk situations (for example, public natural areas, sparsely inhabited areas). In low-risk situations, process-based restoration is a more effective and long-lived approach to restoring floodplain ecosystems. In general, a process-based approach focuses on understanding how driving processes have been changed by human activities and how they can be restored—thereby leading to a semi-natural recovery of floodplain dynamics and riparian complexity (Goodwin and others 1997; Beechie and others 2010; Kondolf and others 2006).

Five standards have been proposed for achieving successful river restoration (Palmer and others 2005): (1) a design based on a specified guiding image of a dynamic, healthy system; (2) an ecological condition to be measurably improved; (3) a self-sustaining system that is resilient to external perturbations so that only minimal follow-up maintenance is needed; (4) no lasting harm

inflicted during the construction phase; and (5) both pre- and post-assessments completed and data made publicly available. Two good examples of restoration techniques consistent with these standards include establishing environmental flow regimes that address the suite of flows required to maintain processes supporting riverine ecosystems (Whiting 2002; Richter and others 2006; Poff and others 2009), and removing bank armor and levees (or levee setbacks) to allow channel movements and increase channel–floodplain interactions (Collins and Montgomery 2002; Rohde and others 2004; Konrad and others 2008).

Successful restoration strategies initially assess local habitat characteristics as well as historical and contemporary driving processes (Beechie and others 2008b). However, even with the increased understanding that PCE floodplains and riparian zones are highly dynamic systems, major uncertainties and great research challenges remain (Naiman and others 2005a). These uncertainties and challenges need not delay recovery actions. The first steps are to identify those aspects known with various levels of certainty, paying particular attention to uncertainties and assumptions (for example, Marcot and others 2001; McCann and others 2006). Key uncertainties require special attention because important decisions require adequate and factual information (Williams 2006; Venter and others 2008). In the PCE, and elsewhere, chief uncertainties relate to determining what aspects of biophysical complexity are most ecologically meaningful as well as predicting how complexity and productivity will respond to changes in system characteristics. Major challenges relate to setting meaningful spatial and temporal scales on biotic responses and processes, and to focusing on multiple factors as drivers of system vitality. Identifying meaningful scales is important because intellectual paradigms or management guidelines are often based on acceptable minimums, which lead to system simplification if operative scales are not clearly identified. Finally, complexity and the responses of floodplain and riparian systems arise from many factors, some of which may dominate at particular scales of space and time. Employing this perspective helps achieve predictable understandings.

Despite the scientific advancements, the greatest obstacles to effective floodplain restoration remain—the social, legal, and economic constraints. Most medium and large-sized floodplains in the PCE are privately owned, regulated by multiple jurisdictions, in fragmented or discontinuous ownerships, and often support important economic activities. Landowners are understandably reluctant to

undertake activities that reduce land values or deny economic opportunities. Even where land is publicly owned, managers must comply with flood control obligations and respond to the concerns of local stakeholders whose interests may conflict with proposed restoration measures. Organizations such as the Cascade Land Conservancy (<http://www.cascadeland.org>) and Western Rivers Conservancy (<http://www.westernrivers.org>), in collaboration with various public agencies, have been highly successful in buying land and negotiating conservations easements throughout the PCE. Such efforts may represent an important advance in protecting floodplain and riparian habitats along large rivers. However, land acquisition is expensive, often involves complex negotiations and constitutes a new and largely unregulated form of land tenure (Fairfax and others 2005).

### Appropriate Measures of Recovery

Process-based river restoration focuses on restoring natural processes that shape floodplains; therefore, monitoring protocols should also track those processes. More specifically, assessing process-based indicators related to floodplain forest productivity is essential for restoration. Metrics may include channel dynamics (for example, disturbance return interval or comparisons with historical rates and mechanisms; Montgomery and Abbe 2006; O'Connor and others 2003), patch turnover rates (Beechie and others 2006a; Latterell and others 2006), tree regeneration rates, LW recruitment, and sediment accretion on floodplain surfaces (Pess and others 2005; Latterell 2008). Some of these metrics will require continued monitoring to obtain reliable estimates while others can be readily obtained from existing series of aerial photos. In addition, channel–floodplain restoration actions may be designed to meet both ecological and societal criteria for success, including species richness of aquatic and floodplain dependent species and the amount of land needed to maintain fluvial processes (Larsen and others 2006). Where this is the case, additional socio-economic monitoring metrics allow for balancing ecological benefits against the cost of allowing rivers to naturally modify their floodplains and the river valley.

The need for such comprehensive monitoring strategies poses unique scientific challenges. Monitoring becomes prohibitively expensive when comprehensive suites of monitoring metrics are compiled (Beechie and others 2009). We suggest that measures of process are generally better than structural indicators. This is because they are more

likely to promote sustained recovery by discouraging static solutions where they are not dictated by risk factors—thereby discouraging over-engineering—and by encouraging remediation of driving processes rather than by treating symptoms. In other words, where floodplain dynamics are considered to be reasonably intact and process rates are measured as criteria for success, restoration using process-based approaches is more effective. A key issue is that time will be required to accumulate enough information for some of these process-based measures to be meaningful. For example, channel movement is clearly a fundamental process for many systems in the PCE but much of the channel movement may occur during high-intensity, low-frequency flood events. How many of these events need to be included in the data set before a defensible conclusion about system behavior can be drawn?

A second challenge in monitoring floodplain restoration is that the approaches must explicitly account for time lags between restoration treatments and responses (Beechie and others 2009). A few very simple metrics of floodplain dynamics should be sufficient to evaluate whether the dynamics are recovering as expected, even though changes may occur gradually over many decades. Foremost, is the age structure of floodplain patches, from which patch turnover rates can be calculated (Beechie and others 2006a). Age structure of floodplain forests has been used to track gradual reduction in river dynamics and increasing floodplain stability after installation of dams, and the same procedures can be used to monitor recovery of river-floodplain dynamics (Kloehn and others 2008). A few good early indicators of restoration success—in cases where floodplain connectivity and channel migration is improved—are newly formed depositional features, newly established pioneering vegetation (both deciduous and coniferous), and the new accumulations of LW or the growth and retention rate of existing trees. Evaluations such as these integrate both remotely acquired and field data to evaluate project effectiveness (Konrad and others 2008).

### CONCLUSIONS

Although the biophysical complexity underpinning the ecological patterns of PCE floodplains is substantial, ongoing research and monitoring continually strengthens our understanding of processes contributing to observed patterns in vegetation as well as those that will speed floodplain recovery. Collectively, the dynamic processes contributing to

floodplain integrity present enormous challenges for effective management and restoration in the PCE. Fortunately, our current understanding of these systems, in association with appropriate metrics for evaluating floodplain condition and functions, provides process-based approaches to management and restoration, thereby sustaining long-term system-scale integrity. This ongoing exercise requires the insights and skills of diverse disciplines, as well as the on-going support of the public and their decision-makers. We submit that these ecological systems are so environmentally and socially important to the PCE that the efforts, although expensive and time consuming, are justified.

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