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Dynamic patch mosaics and channel movement in an unconfined river valley of the Olympic Mountains

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SUMMARY

1. River valleys resemble dynamic mosaics, composed of patches which are natural, transient features of the land surface produced by the joint action of a river and successional processes over years to centuries. They simultaneously regulate and reflect the distribution of stream energy and exchanges of sediment, wood and particulate organic matter between riparian and aquatic environments.
2. We determined the structure, composition, dynamics and origin of seven patch types at the reach scale in the Queets River valley in the temperate coastal forests of the Olympic Mountains, Washington (U.S.A.). Patch types included: (1) primary and (2) secondary channels; (3) pioneer bars; (4) developing and (5) established floodplains; and (6) transitional and (7) mature fluvial terraces.
3. Lateral channel movements strongly shape patch distribution, structure and dynamics. The primary channel moved laterally 13 m year^{-1}, on average from 1939 to 2002, but was highly variable among locations and over time. Mean lateral movement rates ranged from 1 to 59 m year^{-1} and moving averages (2 km) ranged from 3 to 28 m year^{-1} throughout the valley.
4. Each patch type exhibited characteristic vegetation, soil and accumulations of large wood. Pioneer bars contained peak stem density (69 778 stems ha^{-1}) and volume of large wood (289 m^3 ha^{-1}). Mature fluvial terraces contained the highest mean stem (1739 m^3 ha^{-1}) and canopy volume (158 587 m^3 ha^{-1}). These patches also contained the most soil nitrogen (537 kg ha^{-1}) and carbon (5972 kg ha^{-1}).
5. Patch half-life (the time required for half of the existing patches to be eroded) ranged from 21 to 401 years among forested patch types. Erosion rates were highest in pioneer bars (2.3% year^{-1}) and developing floodplains (3.3% year^{-1}), compared with only 0.17% year^{-1} in mature fluvial terraces. New forests formed continually, as pioneering vegetation colonised 50% of the channel system within 18 years, often unsuccessfully.
6. In the Queets River, the structure, composition, and dynamics of the patchy riparian forest depends on the interplay between channel movements and biophysical feedbacks between large wood, living vegetation and geomorphic processes. The cycle of patch development perpetuates a shifting-mosaic of habitats within the river valley capable of supporting diverse biotic assemblages.

Keywords: channel migration, floodplains, large woody debris, patch dynamics, riparian

Introduction

Riparian communities are dynamic mosaics of patches repeatedly dismantled by fluvial disturbances and reorganised by plant succession (Décamps, 1996). This

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interplay generates contrasting patches in shifting patterns (Wiens, 2002) in alluvial rivers. Well known and researched examples include the Tagliamento (Gurnell *et al.*, 2001), the Rhône (Bravard, 1987), the Ain (Marston *et al.*, 1995), the Drôme (Piégay, Thénevet & Citterio, 1999), the Middle Fork Flathead (Poole *et al.*, 2002) and the Queets River (Naiman, Bilby & Bisson, 2000). We consider riparian areas to be 'transitional semiterrestrial areas regularly influenced by fresh water, usually extending from the edges of water bodies to the edges of upland communities' (Naiman, Décamps & McClain, 2005b, p. 2).

Naturally functioning floodplain rivers are widely considered to be in a 'shifting-mosaic steady state' (e.g. Kollmann *et al.*, 1999; Arscott *et al.*, 2002; Ward, Malard & Tockner, 2002; Hauer & Lorang, 2004), a term describing ecosystems composed of a collection of patches in different developmental states (Bormann & Likens, 1979). The proportion in each state remains constant at large scales (e.g. an entire river valley), despite ongoing processes of vegetation succession, geomorphic development and erosion at smaller scales (e.g. a reach or patch). The magnitude of change is moderated across decades or centuries, though large, infrequent disturbances or climatic shifts may preclude a true steady state (e.g. see Bragg, 2000).

The most fundamental riparian patches are river landforms; natural, transient features of the land surface produced by the joint action of a river and plant successional processes. They consist of abiotic and biotic materials (alluvium, vegetation and large wood) assembled in stream reaches over years to centuries. They have varying structure (or quality), including vegetation age and size distribution, species composition, microclimate, soil characteristics and large wood deposits (Décamps *et al.*, 1988; Naiman *et al.*, 2005a,b; Van Pelt *et al.*, in press). They differ in geomorphology, susceptibility to disturbance and successional processes. These differences determine patch boundaries and create variation in internal structure. The pattern of patch distribution indicates the distribution of ecological processes (e.g. disturbance, aggradation, succession, N-fixation, wood production) within a river valley (Wiens, 2002).

River landforms (hereafter, patches) simultaneously regulate and reflect the distribution of energy and material exchange (e.g. water, sediment, wood, reproductive materials) between the riparian and aquatic environments (Swanson *et al.*, 1988). In alluvial rivers of the temperate coastal forests, logjams dissipate stream energy and form alluvial features (Abbe & Montgomery, 1996). This modifies patterns of water flux and the routing and distribution of sediments, organic matter and propagules (Fetherston, Naiman & Bilby, 1995). Together with stream flow variation, these fluxes shape dispersal patterns of plant propagules and the distribution of suitable habitat for germination and survival. Vegetation distribution reflects these factors within limits set by life history adaptations [see Gurnell (1997) and Bendix & Hupp (2000) for reviews]. Vegetation stabilises depositional features and promotes aggradation (Hupp & Osterkamp, 1996). Developing forests reduce light availability, moderate air and soil temperatures, and influence the cycling of carbon and nutrients, which may alter local community structure (Chen *et al.*, 1999). Plant succession is interrupted by channel movements, which entrain and redistribute large wood, sediment and plant propagules; the basic materials for building new patches.

Patch structure and dynamics reflect the distribution and variation in riparian processes over space and time (Naiman *et al.*, 2005b). An understanding of the spatial and temporal aspects of patch characteristics helps explain current conditions and informs our expectations of the future (Innis, Naiman & Elliott, 2000). Further, it reveals the relative or potential contribution of riparian areas to heterogeneity at the catchment scale (Wiens, 2002). The interdependence of vegetation and geomorphology underpins an understanding of the origins of heterogeneity in river valleys (Hupp, 2000). Further advances depend on quantification of landscape dynamics in addition to their spatial pattern (Poole, 2002).

Our goal was to determine the structure, composition, dynamics and origin of seven patch types, and the rate of lateral channel migration, in the Queets River valley, Olympic National Park, Washington, U.S.A. This river exemplifies conditions in Pacific coastal forests prior to human modification (Naiman *et al.*, 2000). Such reference systems inform the management and rehabilitation of comparable, impaired rivers (Karr & Dudley, 1981).

This investigation was guided by several specific, interrelated questions. First, what is the magnitude and longitudinal variation in the lateral channel migration rate of a pristine alluvial river? What fraction of the patches do not survive lateral movements, and does the erosion rate vary among patch types? How does the forest structure and composition vary among patch types and what are the implications for their potential contribution of large wood to the channel? Which patches contain the richest soils, and most abundant deposits of large wood? Finally, what is the origin or sequence of development of each patch type?

Answering these questions required an interdisciplinary approach that united several ongoing (1992–2005) studies on the characteristics of forests, soils, large wood and channel movements. Quantitative field surveys and retrospective analyses of aerial photography were used. Our working hypothesis was that variation in patch structure and dynamics reflects the influences of large wood and historic channel movements on initial site conditions and subsequent disturbance regimes.

Methods

Study area

The Queets River (basin area = 1153 km^2 at river kilometre 7.4 below the Clearwater River; Latitude 47 : 32 : 17 N, Longitude 124 : 18 : 52 W, Station 12040500, U.S. Geological Survey, 2005) flows west from the Olympic Mountains to the Pacific Ocean (Fig. 1). Much of the channel network lies within Olympic National Park. Small, steep, low-order tributaries intersect a large mainstem channel that winds through a >60 km long, U-shaped valley. The valley floor covers 4458 ha in the Park. Mountain glaciers descended the Queets valley at least six times in the past 50 000 years (Thackray, 2001). Ice advances formed large end moraines and broad outwash terraces. These formations flank the valley floor, which is comprised of undifferentiated terraces and alluvium (Thackray, 2001). The mainstem is a gravel-dominated, low-gradient (slope = 0.006; U.S. Geological Survey, 2005), laterally active channel (O'Connor, Jones & Haluska, 2003). Meander cutoffs and channel switching are common (Fig. 2). Debris flows from tributaries form deposits at the valley floor margins. Mean annual precipitation of 387 cm year^{-1} generates an annual mean stream flow of 124 m^3 s^{-1} (U.S. Geological Survey, 2005). Precipitation in the headwaters can exceed 600 cm year^{-1}, much in the form of snow at high altitude. Peak flows are driven by rainstorms or rain-on-snow events from November to April and range from 931 to 3764 m^3 s^{-1}, or roughly

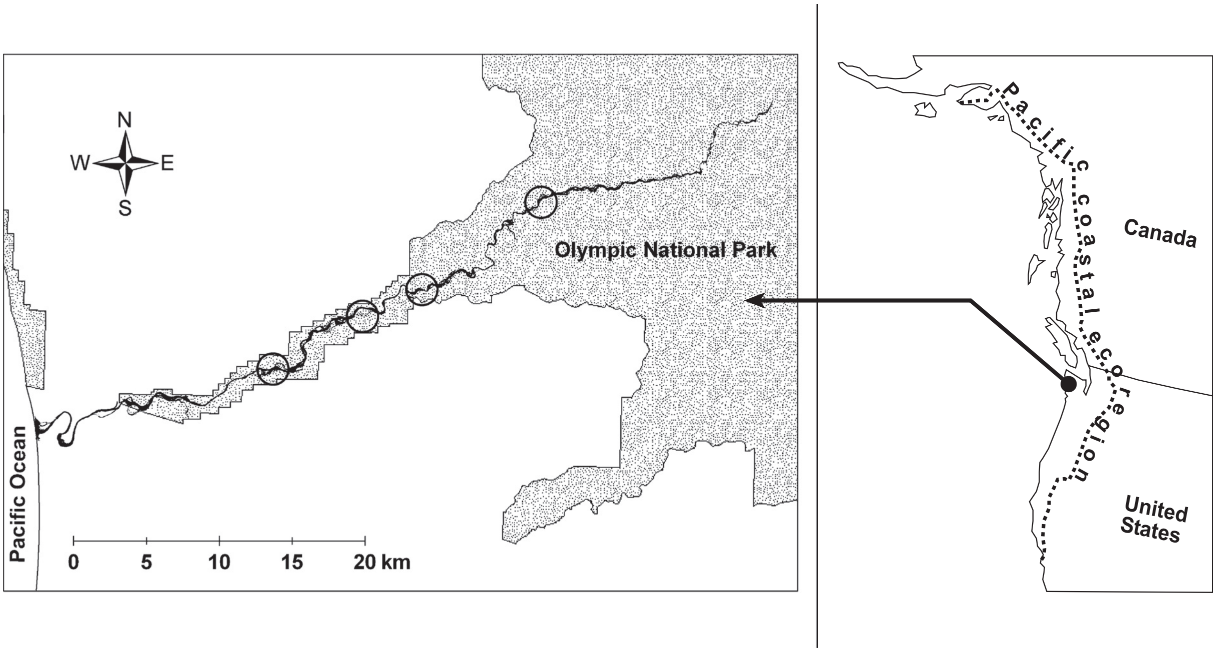
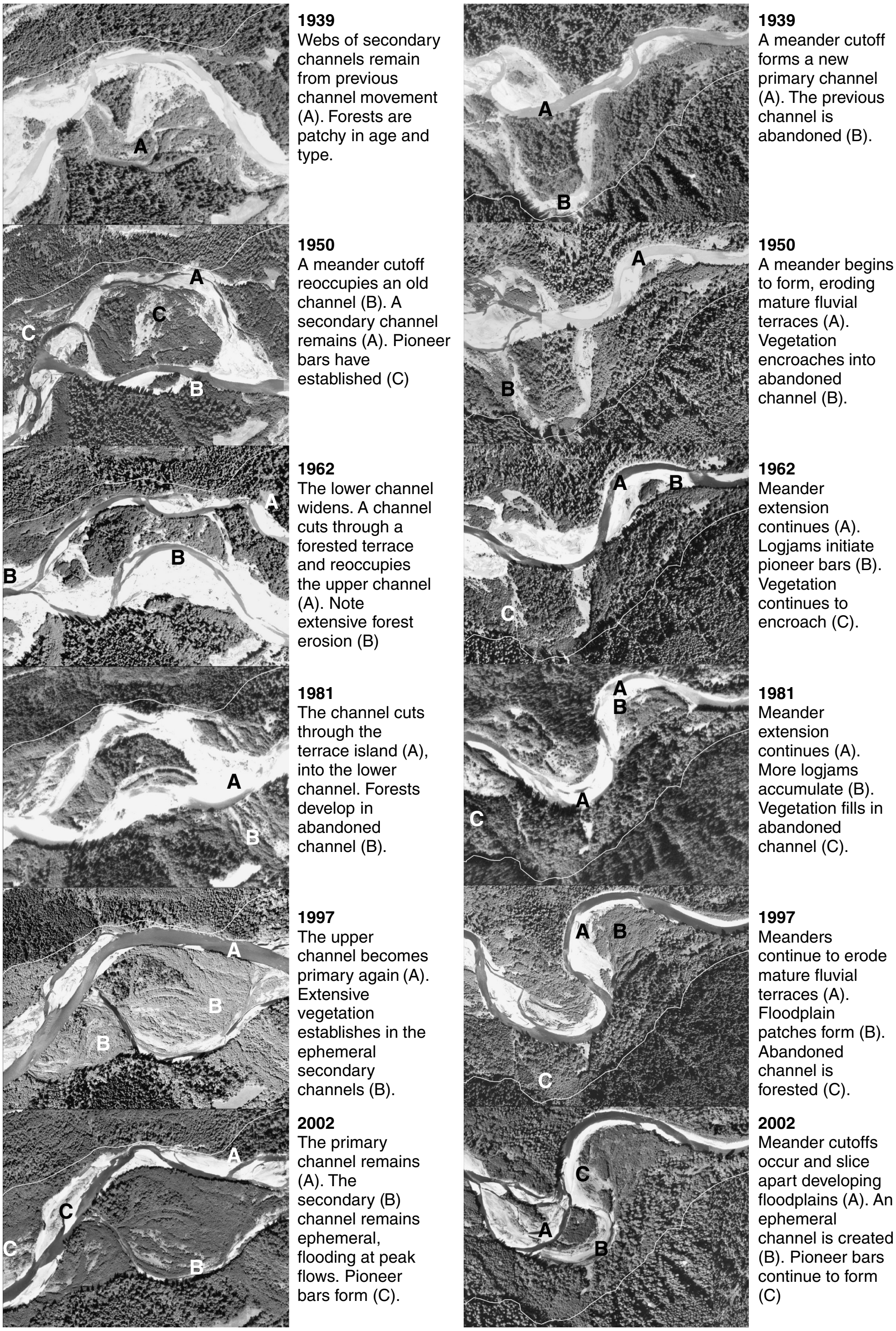


Fig. 1 A map of the Queets River mainstem (in black) within Olympic National Park, Washington, U.S.A. (stippled areas). The river valley extends >60 km from the Pacific Ocean to the headwaters. Field surveys were conducted within Park boundaries, at up to four locations (circles). Channel movements were measured in the entire portion of mainstem within the Park.



1939
Webs of secondary channels remain from previous channel movement (A). Forests are patchy in age and type.

1950
A meander cutoff reoccupies an old channel (B). A secondary channel remains (A). Pioneer bars have established (C)

1962
The lower channel widens. A channel cuts through a forested terrace and reoccupies the upper channel (A). Note extensive forest erosion (B)

1981
The channel cuts through the terrace island (A), into the lower channel. Forests develop in abandoned channel (B).

1997
The upper channel becomes primary again (A). Extensive vegetation establishes in the ephemeral secondary channels (B).

2002
The primary channel remains (A). The secondary (B) channel remains ephemeral, flooding at peak flows. Pioneer bars form (C).

1939
A meander cutoff forms a new primary channel (A). The previous channel is abandoned (B).

1950
A meander begins to form, eroding mature fluvial terraces (A). Vegetation encroaches into abandoned channel (B).

1962
Meander extension continues (A). Logjams initiate pioneer bars (B). Vegetation continues to encroach (C).

1981
Meander extension continues (A). More logjams accumulate (B). Vegetation fills in abandoned channel (C).

1997
Meanders continue to erode mature fluvial terraces (A). Floodplain patches form (B). Abandoned channel is forested (C).

2002
Meander cutoffs occur and slice apart developing floodplains (A). An ephemeral channel is created (B). Pioneer bars continue to form (C)

Fig. 2 Time sequence of aerial photographs (1939–2002) in two reaches on the Queets River, Washington, U.S.A. These photographs depict common patterns of channel movement and vegetation re-establishment. Photo position, scale and extent are identical throughout. A thin white line depicts the outer margin of the valley floor in each photo.

0.3–1.8 times the mean annual flood (2100 m^3 s^{-1}). Flow often declines to <30 m^3 s^{-1} by September, as <10% of the annual precipitation falls during the summer. The riparian forest consists of willow (*Salix* L.), red alder (*Alnus rubra* Bong.), Sitka spruce [*Picea sitchensis* (Bong.) Carr], black cottonwood (*Populus* *balsamifera trichocarpa* T. & G.), bigleaf maple (*Acer macrophyllum* Pursh), and vine maple (*Acer circinatum* Pursh) (Balian & Naiman, 2005). Western hemlock [*Tsuga heterophylla* (Raf.) Sarg.], Douglas-fir [*Pseudotsuga menziesii* (Mirbell) Franco], and Western redcedar (*Thuja plicata* Donn.) are occasionally present (Naiman *et al.*, 2005a; Van Pelt *et al.*, in press). Adjoining forests >400–500 years old on glacial terraces and hillslopes are dominated by western hemlock (Franklin & Dyrness, 1988).

Methods

Approach

The Queets River valley mosaic was subdivided at the valley and reach scales to facilitate systematic analyses of landscape patterns and dynamics (Fig. 3). Subdivisions reflect what we perceive to be fundamental units, differentiated by vitally important structures and processes. Valley-scale divisions distinguish between patches with contrasting geomorphology, vegetation and degree of connectivity with the river. Reach-scale patch types represent relatively distinct stages in biophysical development from fluvial deposits to conifer forests across a successional sequence. This approach expands and reinterprets some of the patterns first observed on the gravel bars, alder flats and first terraces described by Fonda (1974).

The channel system is subdivided into *primary* and *secondary channels*. This was to distinguish active channels from recently abandoned or seasonal channels. Primary channels actively cut into banks, form bars, and transport most of the flow and bedload (Richards, Chandra & Friend, 1993). Secondary channels form when a primary channel is abandoned, either abruptly or gradually (Fig. 2) Except where noted, observations from primary and secondary channels are collectively referred to as the 'channel system'. Numerous aquatic habitats exist within the channel system (e.g. instream pools, ephemeral channel and floodplain ponds). These features are dynamic (Arscott *et al.*, 2002; van der Nat *et al.*, 2002, 2003; Naiman & Latterell, 2005), shape patterns of species diversity (e.g. Dudgeon *et al.*, in press), and are also important elements of the riverine mosaic, but are not examined here.

Floodplains are subdivided into *pioneer bars*, *developing floodplains* and *established floodplains*, to distinguish areas with contrasting forest stand structure and connectivity with seasonal floods. Our working definition of a floodplain is a transitional semi-terrestrial environment (Junk, Bayley & Sparks, 1989; Naiman *et al.*, 2005b) formed by lateral and vertical accretion during modern climates (Leopold, 1994) and inundated at least once every 1–3 years (Hupp & Osterkamp, 1996). Pioneer bars are created by accretion of bedload and suspended sediments in low shear-stress areas downstream from logjams or pioneering vegetation (Fetherston *et al.*, 1995; Abbe & Montgomery, 1996; Edwards *et al.*, 1999; Gurnell *et al.*, 2000) and repeatedly inundated each year. Developing floodplains form from pioneer bars that grow and coalesce through lateral and vertical accretion enhanced by the presence of vegetation (Reinfields & Nanson, 1993; Osterkamp, 1998). They are inundated at least once in most years. As overflow channels and depressions are filled, they become established floodplains, where overbank flows are infrequent (e.g. once every few years). Geomorphic changes are limited to vertical accretion or lateral erosion (e.g. dissection; Gurnell *et al.*, 2001).

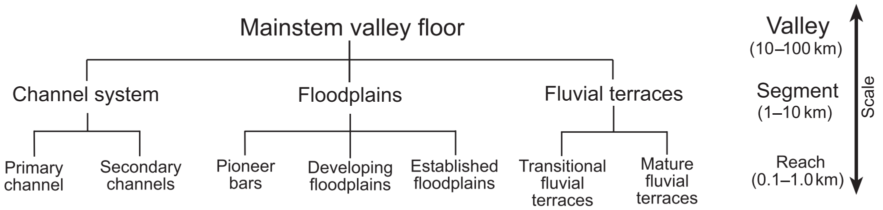


Fig. 3 Hierarchical relationships of patches comprising the mainstem valley floor of the Queets River, Washington, U.S.A. Terms represent the physical and biological stage of patch development. The mainstem valley floor is composed of the channel system, floodplains and terraces at the valley segment scale. At the reach scale, the valley floor is subdivided into primary and secondary channels, pioneer bars, developing and established floodplains, and transitional and mature fluvial terraces. At the habitat scale, each patch could be further subdivided according to microclimate and topography.

Fluvial terraces are subdivided into *transitional* and *mature fluvial terraces* to differentiate areas with vegetative contrasts in stand age and composition. Terraces form either from channels or floodplains abandoned by channel incision (Osterkamp, 1998). Terraces underscore the importance of the transition to a physical environment dominated by competition and gap formation rather than flooding. We focus on terraces formed by Holocene fluvial processes and the internal processes (e.g. logjam formation or channel movements). Some were probably formed during shifts in sediment supply, precipitation, or tectonic activity over centuries to millennia (Knighton, 1998; Hereford, 2002), or even by deposition of sediments at the mouths of tributaries, but these terraces are not considered here because they are relatively rare and typically lie at the extreme margins of the valley floor.

Lateral channel movement

Mean annual lateral movement rates were calculated for the entire primary low-flow mainstem channel within Olympic National Park. Our methodology followed O'Connor *et al.* (2003); we quantified movements in the whole valley over five intervals (i.e. 1939–1968, 1968–1993, 1993–1996, 1996–2000, 2000–2002). Changes in the position of the channel thalweg were measured at 266 transects at 0.2 km increments perpendicular to the valley axis (i.e. starting from 405204 E 5266867 N; NAD 1927 UTM Zone 10 N). Lateral movement distance was measured along each transect between the points of intersection (where the channel thalweg crossed the transect at the beginning and end of each interval), and divided by the interval duration. Mean annual lateral movement rates were estimated across intervals for each transect. Some changes in position cannot be detected when the interval between photos exceeds 1 year because the direction of movement may reverse (O'Connor *et al.*, 2003). Therefore, we used simple linear regression to model the observed relationship between annual channel movement rate (across transects) and the interval between photos. This relationship is given by the following equation:

$$y = mt + b$$

where y is the mean annual rate of channel movement, m is the slope of the regression line, t is the time elapsed between photos in years and b is the y-intercept. Solving for $t = 1$ yields an mean annual rate of channel movement for Queets River. We also calculated moving averages (i.e. over 10 transect or 2 km) to assess longitudinal variation in channel movement rate at the reach scale. This distance matched the length of our study sites. The coefficient of variation was calculated to evaluate the degree of temporal variation of channel migration rates at each transect and for 2 km moving averages.

Patch structure and composition

Stratified random sampling was used to quantify patch structure and composition. The goal was to disperse sampling in an unbiased manner to quantify the general characteristics of the valley, rather than compare individual reaches (except where noted). Strata were four valley segments between major confluences (Fig. 1). A single point (river kilometre; RK) was randomly selected from each segment and a 2-km study reach established immediately downstream. One-way ANOVA by ranks (i.e. Kruskal–Wallis test, Zar, 1999) was used to compare the mean rank of response variables among patch types. Dunn's test for non-parametric multiple comparisons of unequal sample sizes was used to evaluate the statistical significance of differences ($P < 0.10$) between individual patch types (Zar, 1999).

Forest characteristics were quantified by measuring species composition, size structure, stem density, and stem biomass of trees and shrubs in each patch type. Rectangular plots (0.0045–0.96 ha) were established in 19 stands (trees 8–330 years old) in two reaches (see Van Pelt *et al.*, in press for details). Plot length was scaled to ≥ twice the height of the average dominant tree, and plot width was approximately 1/5th of length, so they would fit within patchy, narrow stands and capture spatial variability without over-sampling (Van Pelt, 1995; Van Pelt & Nadkarni, 2004). Trees >5 cm diameter at breast height (dbh) were mapped and measured for species, dbh, height, crown height, and four cardinal crown radii. Canopy volume, an indicator of forest structure, was estimated with crown models using simple conic shapes (Van Pelt & North, 1996; Van Pelt & Franklin, 2000; Van Pelt & Nadkarni, 2004). Where trees <5 cm dbh dominated, all trees were measured, including those shorter than breast height. Variation in litterfall rates among patch types was measured in 15 of the plots using synthetic

0.1 mm mesh inside 0.23 or 0.19 m^2 plastic baskets ($n = 3$–5), depending on plot dimensions (T.C. O'Keefe and R.J. Naiman, unpublished data). Samples were collected over a single year at monthly or biweekly intervals.

Soil bulk density, horizons and nutrient concentrations were measured to characterise soils in each patch type. Three pits were excavated in each forest plot, and located mid-slope >4 m from tree stems. Soils were sampled in depth increments rather than by horizon because pedogenic features were generally absent. Although less precise than sampling by horizon, sampling by depth was intended to reduce subjectivity and quantify carbon and nutrient pools more accurately. Specifically, we used 10 cm increments to 50 cm depth. In non-rocky areas, bulk density was determined by extracting a known volume of soil using a 2.5 cm diameter steel tube. In rocky areas, fine earth bulk density was estimated by the excavation method (Blake & Hartge, 1986), after adjusting for the volume of >2 mm material removed. Soil C and N were determined by micro-Dumas dry combustion (Bremner, 1996) in a Carlo Erba C/H/N analyser.

Fluvial deposits of large wood (or large woody debris) were quantified (i.e. abundance, dimensions, species composition and state of decay) in all four study reaches with line-intersect sampling at 91 randomised field plots. Twenty-five per cent of the points in a 100-m dot grid overlain on each study reach were selected at random for sampling. Each plot was a cluster of four sub-plots of three equidistant 18 m transects. This design eliminates bias because of non-random orientation of wood pieces in rivers (Waddell, 2002). Plots were classified by patch type. Mature fluvial terraces were not sampled as fluvial deposits of large wood could not be distinguished from local deadfall. Each intersected log (≥10 cm diameter and ≥2 m in length) deposited by the river was measured. End diameters were measured (to 1 cm) with a caliper and length was measured (to 0.1 m) following protocols used by Waddell (2002). Large diameter was measured to 1.4 m above root base (dbh) if attached. Log volume was estimated using Smalian's formula (Waddell, 2002). Logs were classified by decay stage [i.e. 1–5; Waddell (2002), modified from Maser *et al.* (1979) and Sollins (1982)] and species, based on bark and ring structure. Wood abundance (m^3 ha^{-1} and logs ha^{-1}) was estimated for each plot according to Waddell (2002), and averaged among patch types.

Patch dynamics

We used aerial photography (Table 1) to measure the area, size structure and dynamics of each patch type. Photos were scanned (i.e. 0.4–1.5 m ground resolution), georeferenced, corrected for radiometric distortion, and converted to a common scale, coordinate system and projection with ERDAS Imagine (Leica Geosystems, Atlanta, GA, U.S.A.). Planform maps of patches in 2002 were created manually using non-overlapping polygons at a fixed (i.e. 1 : 3000) scale of magnification in ArcMap (ESRI, Inc., Redlands, CA, U.S.A.). Pathways of development were determined by reconstructing the physical development and disturbance history for patches of similar age, but different forest structure and soil characteristics.

Cumulative erosion rates were estimated for each patch type over a 63-year period by tracking erosion at 886 sampling points in airphotos spanning 1939–2002 (Table 1). A 100 m grid of sampling points was established across the valley floor at each study reach. The initial state (i.e. patch type in 1939) of each point was assessed. Each point was visually inspected in up to 14 subsequent years (Table 1) to estimate the year of erosion. Once a point was eroded, it was excluded. Similar to van der Nat *et al.* (2003), an exponential decay model was fitted to observed cumulative erosion of points in each patch type. Models intercepted the y-axis at 1.0 (or 100% of points). The form of the model is:

$$y_t = y_0 e^{-kt}$$

where, y_0 is the initial fraction (0.00–1.00) of the sampling points that have not been eroded by the river by year t, y_t is the fraction remaining at time t, k is the erosion rate constant, and t is time in years. Each model was used to calculate the length of time required for half of the initial points in a patch type to be destroyed by erosion (half-life; $t_{0.50} = 0.693/k$, 95% life, $t_{0.05} = 3/k$, Harmon *et al.*, 1986). Resulting estimates have a high level of uncertainty because the window of observation is relatively short (i.e. 63 years), and estimates may exceed the range of observations. In addition, fluvial processes are likely to change in response to anticipated changes in climate (see Nijssen *et al.*, 2001).

Table 1 Aerial photography used to determine the origin and developmental history of patches, and to map channel position and the extent of each patch type in the Queets River, Washington, U.S.A.

Year	Scale	Type	Project	Holdings
1939*	1 : 30 000	Black and white	GS-J	1
1950	1 : 12 000	Black and white	M49-13	2, 3
1952	1 : 60 000	Black and white	GS-WR	4
1954*	1 : 60 000	Black and white	GS-VFB	4
1962	1 : 12 000	Black and white	EJK-62	3
1968*	1 : 36 000	Black and white	OLYM	4
1973	1 : 58 000	Black and white	OL-H-73	3
1976	1 : 24 000	Colour	OL-C-1975	4
1981	1 : 40 000	Black and white	OSI-81	3
1988	1 : 63 360	Black and white	OL-H-88	3
1990	1 : 40 000	Black and white	NAPP-1990	3, 5
1993*	1 : 12 000	Colour Infrared	593-0813	6
1994	1 : 40 000	Black and white	NAPP-1994	3, 5
1996*	1 : 12 000	Colour	596-0923	7
1997	1 : 12 000	Black and white	OL-97	8
2000*	1 : 32 000	Black and white	OL-2000	9
2002*	1 : 15 480	Colour	S02013	4, 10

Holdings: 1, U.S. Department of Interior Geological Survey, Luis Fueste, Information Officer, USGS, Tacoma Field Office, 1201 Pacific Avenue, Suite 600, Tacoma WA. (Also Wallace Aerial Surveys, Spokane Washington U.S.A.); 2, Carl M. Berry Aerial Surveys, Boeing Field, Seattle; 3, University of Washington Maps Collection, Seattle, WA, U.S.A.; 4, Olympic National Park, Port Angeles, WA, U.S.A; 5, National Aerial Photography Program, Aerial Photography Field Office, PO Box 30010, Salt Lake City, UT, U.S.A.; 6, Photos and diapositives are held by RJ. Naiman, SAFS, University of Washington, Seattle, WA, U.S.A.; 7, Walker and Associates, Seattle, WA, and RJ. Naiman, SAFS, University of Washington, Seattle, WA, U.S.A.; 8, Washington Department of Transportation, Aerial Photo Section, 1655 S. Second Ave, Tumwater, WA 98152, U.S.A.; 9, Washington Department of Natural Resources, Photo and Map Sales, Olympia, WA, U.S.A; 10, Army Corps of Engineers, Prints at Olympic National Park, Port Angeles, WA, U.S.A.

*Photo series that cover the entire mainstem.

The cumulative rate of vegetation establishment in the channel system was determined by reversing this approach. Vegetation establishment was defined as the appearance of visible vegetation obscuring some substrata in aerial photographs. Once vegetation established at a point that had been channel in 1939, that point was excluded. The half-life of the channel indicates the time required for half of the initial channel to be colonised by pioneering vegetation at least once.

Temporal variation in the relative abundance of each patch type (i.e. % of all points) was determined for each study reach and, overall, by classifying the patch type at each sampling point in every year for which photos existed. The long-term average of the relative abundance of each patch type (across study reaches) was calculated, based on eight years between 1939 and 2002, in which photos were available for all four reaches. The coefficient of variation (hereafter, CV) in the mean relative abundance of each patch type was used as a metric of the temporal stability.

Results

Lateral channel movement

The mean annual rate of lateral channel movement was highly variable among transects and over time. Four highly unstable valley segments were interspersed by relatively stable segments (Fig. 4). Unstable segments contained pool-riffle reaches whereas stable segments contained plane-bed reaches (Montgomery & Buffington, 1997). The primary low-flow channel moved an average of 11 m year^{-1} (±9 SD) during the period of observation (1939–2002), although rates estimated in each photo interval were inversely related to the length of time elapsed between photos ($r^2 = 0.83$; $P = 0.03$). The relationship is described by the following equation:

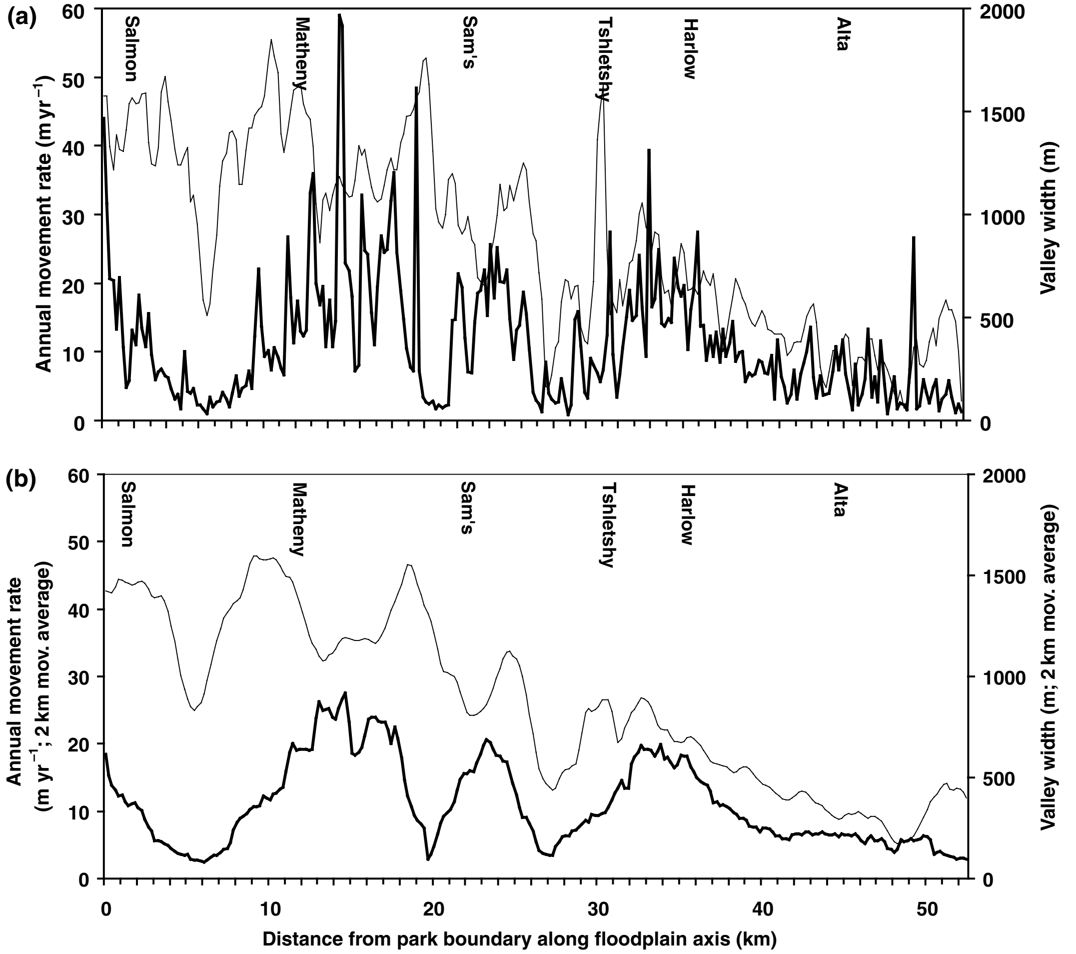


Fig. 4 Longitudinal variation in mean annual channel movement rates (thick lines) for the primary low-flow channel of the Queets River, Washington, U.S.A., and valley floor width (thin lines) on the secondary axis. Channel movement was determined from retrospective analysis of a time-sequence of airphotos spanning 63 years: (a) values estimated at 200 m increments, perpendicular to the valley axis at fixed transects, (b) the moving average of those data, calculated over 2 km (the length of our study reaches). The name and position of major river confluences is indicated along the top of each figure.

$$y = -0.403t + 13.694$$

where y is the mean annual rate of channel movement (in m year^{-1} over a given interval t between photos in years). Solving for $t = 1$ suggests that the mean annual channel movement rate for the Queets River was 13 m year^{-1}. Mean annual movement rates ranged from 1 to 59 m year^{-1} at individual transects, and averaged between 12 and 22 m year^{-1} among the four study reaches. Moving averages (2 km) ranged from 3 to 28 m year^{-1} across the valley. The CV (across years) averaged 115% (±36 SD) of the mean annual channel movement rate, or from 87% to 150% of the moving average.

Patch structure and composition

The valley floor was dominated by the channel system (i.e. 866 ha or 19%) and mature fluvial terraces (i.e. 2156 ha or 48%), although floodplain patches were most numerous, and generally increased in size from pioneer bars to established floodplains (Fig. 5). Pioneer bars were the smallest patches, averaging only 0.5 ha (±0.8 SD), ranging from <0.01 to 6.8 ha. Developing floodplains were over twice as large, on average (i.e. 1.2 ha, ±2.0 SD, range = >0.1 to 22.0 ha). Established floodplains patches averaged 2.8 ha (±3.9 SD), ranging from <0.1 to 19.8 ha. Floodplain patches collectively comprised 17% of the valley floor (e.g. pioneer bars = 160 ha or 4%; developing flood-

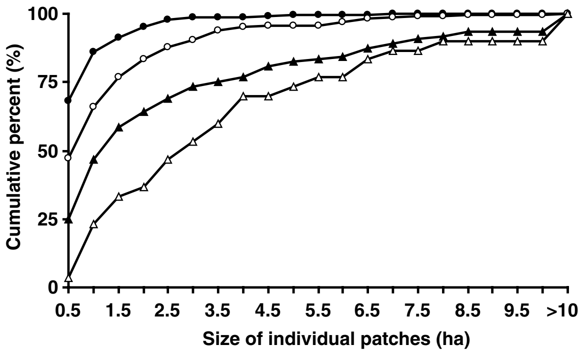


Fig. 5 Cumulative size distribution of individual patches, by patch type, for the Queets River, Washington, U.S.A. Symbols denote pioneer bars (●; $n = 303$), developing floodplains (○; $n = 222$), established floodplains (▲; $n = 109$), and transitional fluvial terraces (△; $n = 30$). Patches were manually digitised at 1 : 3000 scale from geocorrected aerial photos taken in 2002.

plains = 265 ha or 6% and established floodplains = 304 ha or 7%). Transitional fluvial terraces averaged 3.9 ha (±3.9 SD), ranging from 0.4 to 19.0 ha. Transitional fluvial terraces covered only 3% (116 ha) of the valley floor. The remaining area (592 ha or 13%) had been previously cleared and was excluded.

Each forested patch type exhibited a characteristic species assemblage and stand structure (Fig. 6), though stand ages overlapped. Metrics of stand structure (i.e. canopy volume, stem and density) and litterfall rates were significantly different across forested patch types (Table 2; $P < 0.01$). Thickets of 1- to 5-year-old red alder and willow $\leq$2 m tall were typical of pioneer bars, which exhibited peak stem densities (Table 2). Developing floodplain forests consisted of 5- to 20-year-old closed-canopy thickets of 2–20 m willow and red alder. Red alder 15–40 years old were typical of established floodplains, although spruce was prominent in the understory. Transitional fluvial terraces were dominated by 25- to 70-year-old red alder, cottonwood and spruce that generated peak litterfall (Table 2). Mature fluvial terraces contained structurally complex (Franklin *et al.*, 2002) stands of 100- to 300-year-old Sitka spruce and western hemlock, with some secondary colonisers (i.e. bigleaf and vine maple). Canopy and stem volume peaked in mature fluvial terraces, which were the only patches that contained standing trees sufficiently large to initiate jams after they fell into the river [>100 cm diameter, Latterell (2005); Table 2].

Channel soils were thin and poor, but terrace soils were comparatively deep, organic, moist and nutrient-rich (Table 3). Soil carbon and nitrogen differed among patch types ($P < 0.01$), peaking in mature fluvial terraces. Pedogenic horizons were absent in most floodplain patches and weakly developed in transitional terraces. In contrast, soils of mature fluvial terraces [i.e. Typic Udifluvents (Huel and Hoh series)] contained advanced horizons underlain by cobble. These had diffuse boundaries and were too thin to sample for bulk density. Two or more 'C' soil layers could be resolved from textural discontinuities representing successive depositional events. However, all consisted of river sediments with no indications of soil alteration.

The abundance of large wood ($m^3\ ha^{-1}$ and logs ha^{-1}) differed significantly among patch types (Table 4; $P < 0.01$). Peak abundances of both conifers and hardwoods were observed in pioneer bars. Hardwoods outnumbered conifers in the channel and pioneer bars, but conifers dominated by volume (Table 4). Conifers outnumbered hardwoods in developing floodplains and in all subsequent patch types. In established floodplains $\sim$40% of the remaining logs were focal points for Sitka spruce regeneration. Only large logs were prominent, often partially buried and colonised by invertebrate decomposers.

Patch dynamics

The cumulative erosion of each patch type was strongly related to the time elapsed since 1939

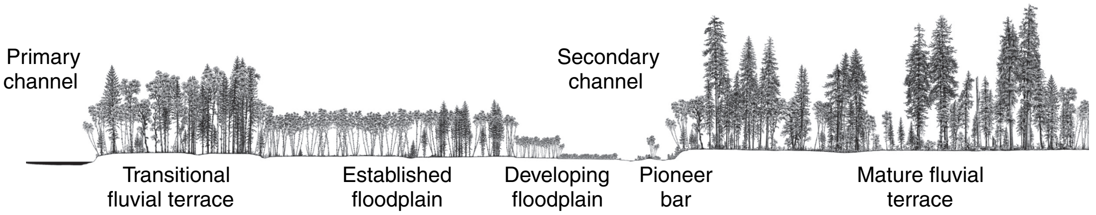


Fig. 6 Profile drawing of patch types in an actual (half) cross-section of the Queets River valley floor – Original artwork by R. Van Pelt. For simplicity, large wood, subsurface structure and variation in soil depth are not depicted. Pioneer bars and developing floodplains commonly occur near margins of the primary channel, as well.

Table 2 Selected characteristics of vegetation associated with patch types of the Queets River, Washington, U.S.A.

Variable	Units	Statistic	*P*-value	Patch type Pioneer Bar ($n = 1$)	Developing Floodplain ($n = 3$)	Established Floodplain ($n = 5$)	Transitional Fluvial Terrace ($n = 4$)	Mature Fluvial Terrace ($n = 6$)
Canopy volume	m^3 ha^{-1}	Mean ± SE (range)	<0.01	9032^{ab}	$42\,862^{ab} \pm 16\,257$ (23 491–75 163)	$33\,726^{a} \pm 4463$ (21 681–49 367)	$53\,298^{ab} \pm 6072$ (37 488–63 288)	$158\,587^{b} \pm 19\,455$ (105 827–222 809)
Stem volume	m^3 ha^{-1}	Mean ± SE (range)	<0.01	13^{ab}	$251^{a} \pm 65$ (135–358)	$380^{a} \pm 104$ (172–722)	$660^{ab} \pm 99$ (439–849)	$1739^{b} \pm 113$ (1289–2069)
Stem density	stems ha^{-1}	Mean ± SE (range)	<0.01	69778^{ab}	$15\,114^{a} \pm 1004$ (13 792–17 083)	$1697^{ab} \pm 513$ (544–3440)	$735^{ab} \pm 130$ (517–1107)	$322^{b} \pm 30$ (238–436)
Potential key pieces (>1 m dbh)	stems ha^{-1}	Mean ± SE (range)	<0.01	0^{ab}	$0^{a} \pm 0$ (0)	$0^{a} \pm 0$ (0)	$0^{a} \pm 0$ (0)	$35^{b} \pm 4$ (20–47)
Mean diameter at breast height	cm	Mean ± SE (range)	<0.01	1.3^{ab}	$6.1^{a} \pm 0.2$ (5.8–6.6)	$19.3^{ab} \pm 4.2$ (11.5–34.5)	$28.2^{ab} \pm 2.5$ (21.5–33.2)	$50.7^{b} \pm 4.1$ (35.1–60.5)
Conifer to hardwood ratio	By stem volume	Mean ± SE (range)	<0.01	$3.2{\cdot}10^{-7ab}$	$1.9{\cdot}10^{-3ab} \pm 1.9{\cdot}10^{-3}$ $(0–5.6{\cdot}10^{-3})$	$1.7{\cdot}10^{-3a} \pm 1.6{\cdot}10^{-3}$ $(0–8.1{\cdot}10^{-2})$	$1.7^{ab} \pm 0.8$ $(8.7{\cdot}10^{-3}$-3.4)	$2.7^{b} \pm 0.9$ (0.7–6.4)
Annual litterfall	kg ha^{-1} $year^{-1}$	Mean ± SE (range)	<0.05	847^{ab}	$3472^{a} \pm 1211$ (2174–5890)	$5952^{ab} \pm 74$ (5769–6129)	$8673^{b} \pm 811$ (7460–10 213)	$6227^{ab} \pm 567$ (5211–7847)
		n		1	3	4	3	4

Patch types with indistinguishable values ($P \le 0.10$; $Q = 2.576$) (homogeneous subsets) for a given variable are indicated by a shared letter (e.g. *a*, *b* and *c*). *P*-values indicate significance levels for Kruskal–Wallis *H*-tests. The channel system is generally unvegetated.

Table 3 Selected soil characteristics of patch types on the Queets River, Washington, U.S.A.

				Patch type					
Variable	Units	Statistic	*P*-value	Channel system ($n = 2$)	Pioneer bar ($n = 20$)	Developing floodplain ($n = 2$)	Established floodplain ($n = 7$)	Transitional fluvial terrace ($n = 6$)	Mature fluvial terrace ($n = 6$)
Particle size	Description			River cobbles w/interstitial sand	5–30 cm sand cap over cobbles	10–40 cm sand cap over cobbles	sand to loamy sand	loamy sand to sandy loam	sandy loam to loam
O Horizon	cm	Range		None	None	None	0–2	0–2	2–6
A Horizon	cm	Range		None	None	None	None	2–6	2–10
B Horizon	cm	Range		None	None	None	None	None	5–25
Bulk density	g cm^{-2} (fine earth fraction)	Mean ± SE (range)	>0.10	1.30 ± 0.05 (1.2–1.4)	1.20 ± 0.05 (1.1–1.3)	1.15 ± 0.15 (1.0–1.3)	1.03 ± 0.03 (1.0–1.1)	1.05 ± 0.05 (0.9–1.1)	0.98 ± 0.05 (0.8–1.0)
Soil C	kg ha^{-1} (50 cm depth)	Mean ± SE (range)	<0.01	311^{b} ± 60 (251–371)	2036^{b} ± 431 (1605–2466)	2381^{ab} ± 620 (1761–3001)	3704^{ab} ± 292 (2804–4962)	4105^{ab} ± 380 (2955–5699)	5972^{a} ± 157 (5575–6579)
Soil N	kg ha^{-1} (50 cm depth)	Mean ± SE (range)	<0.01	59^{b} ± 0 (59–60)	239^{b} ± 69 (170–309)	247^{ab} ± 67 (180–314)	388^{ab} ± 21 (309–446)	416^{ab} ± 37 (322–562)	537^{a} ± 16 (491–600)

Landforms with indistinguishable values ($P \le 0.10$; $Q = 2.713$) (homogeneous subsets) for a given variable are indicated by a shared letter (e.g. *a*, *b* and *c*). *P*-values indicate significance levels for Kruskal–Wallis *H*-tests.

Table 4 Selected characteristics of large wood in patch types of the Queets River, Washington, U.S.A.

				Patch type				
Variable	Units	*P*-value	Statistic	Channel system ($n = 38$)	Pioneer bar ($n = 11$)	Developing floodplain ($n = 20$)	Established floodplain ($n = 15$)	Transitional fluvial terrace ($n = 7$)
Overall abundance	m^3 ha^{-1}	<0.01	Mean ± SE (range)	165^{abc} ± 29 (0–843)	289^{a} ± 65 (3–779)	183^{ab} ± 45 (0–853)	88^{bc} ± 28 (0–325)	46^{c} ± 36 (0–260)
	logs ha^{-1}	<0.01	Mean ± SE (range)	191^{ab} ± 48 (0–1207)	347^{a} ± 99 (17–1123)	83^{ab} ± 17 (8–233)	33^{bc} ± 14 (0–171)	11^{c} ± 10 (0–70)
Conifers	m^3 ha^{-1}	0.03	Mean ± SE (range)	118^{ab} ± 22 (0–616)	213^{a} ± 53 (0–634)	168^{ab} ± 44 (0–816)	78^{b} ± 26 (0–322)	46^{b} ± 36 (0–260)
	logs ha^{-1}	<0.01	Mean ± SE (range)	45^{bc} ± 12 (0–327)	106^{a} ± 24 (0–246)	51^{ab} ± 11 (0–153)	22^{abc} ± 8 (0–102)	11^{ac} ± 10 (0–70)
Hardwoods	m^3 ha^{-1}	<0.01	Mean ± SE (range)	47^{b} ± 10 (0–227)	76^{a} ± 19 (3–205)	15^{bc} ± 5 (0–80)	10^{bcd} ± 6 (0–88)	0^{cd}
	logs ha^{-1}	<0.01	Mean ± SE (range)	141^{b} ± 36 (0–881)	242^{a} ± 77 (17–877)	28^{bc} ± 10 (0–158)	11^{bcd} ± 7 (0–108)	0^{cd}
New or undecayed	m^3 ha^{-1}	<0.01	Mean ± SE (range)	71^{a} ± 14 (0–355)	65^{a} ± 32 (0–279)	5^{b} ± 2 (0–39)	0^{b} ± 0 (0–1)	0^{b}
Partially decayed	m^3 ha^{-1}	<0.01	Mean ± SE (range)	37^{b} ± 9 (0–274)	140^{a} ± 33 (0–383)	15^{bc} ± 6 (0–98)	13^{bc} ± 9 (0–136)	0^{c}
Moderately decayed	m^3 ha^{-1}	0.05	Mean ± SE (range)	53^{bc} ± 13 (0–326)	73^{ab} ± 17 (0–169)	133^{a} ± 34 (0–560)	75^{abc} ± 25 (0–322)	37^{c} ± 34 (0–241)
Highly decayed	m^3 ha^{-1}	0.07	Mean ± SE (range)	0^{b} ± 0 (0–35)	11^{a} ± 10 (0–156)	25^{a} ± 15 (0–95)	0^{b}	9^{a} ± 7 (0–22)

Landforms with indistinguishable values ($P \le 0.10$; $Q = 2.576$) (homogeneous subsets) for a given variable are indicated by a shared letter (e.g. *a*, *b* and *c*).
P-values indicate significance levels for Kruskal–Wallis *H*-tests. Wood was not surveyed in mature fluvial terraces since it was indistinguishable from *in situ* mortality. Estimates of unidentified wood are not included in comparisons of hardwood and conifer abundance, but represented a minor fraction of the total. Categories of decay are based on Waddell (2002) and represent categories 1–4.

($P < 0.01$; $r^2 = 0.98$–0.99) (Fig. 7). Pioneer bars and developing floodplains were the most short-lived, excluding the channel system (Table 5). Half-lives ranged from 21 to 68 years among floodplain patch types and 62 to 401 years for terraces. These observations suggest that 95% of the points that fell within pioneer bars in 1939 will be eroded by 2070 (131 years). In contrast, model extrapolation suggests that 95% of the mature fluvial terraces will eroded in 1730 years. Our calculations indicate that 95% of the channel system in unconfined alluvial reaches is colonised by vegetation at least once in 78 years.

The relative abundance of each patch type (i.e. % of the valley floor area) fluctuated asynchronously among reaches and over time (Fig. 8), but remained relatively stable overall. On average (across years), 56% (±1.6 SD) of the area at the study reaches was mature fluvial terrace, 15% (±1.4 SD) was primary channel and 4% (±0. 9 SD) was secondary channel. Pioneer bars, developing and established floodplains, and transitional terraces covered an average of 4% (±1.3 SD), 5% (±0. 8 SD), 8 (±1.9 SD) and 7% (±1.3 SD) of the valley floor, respectively. The average CV was 18% among patch types. The relative abundance of mature fluvial terraces was least variable over time

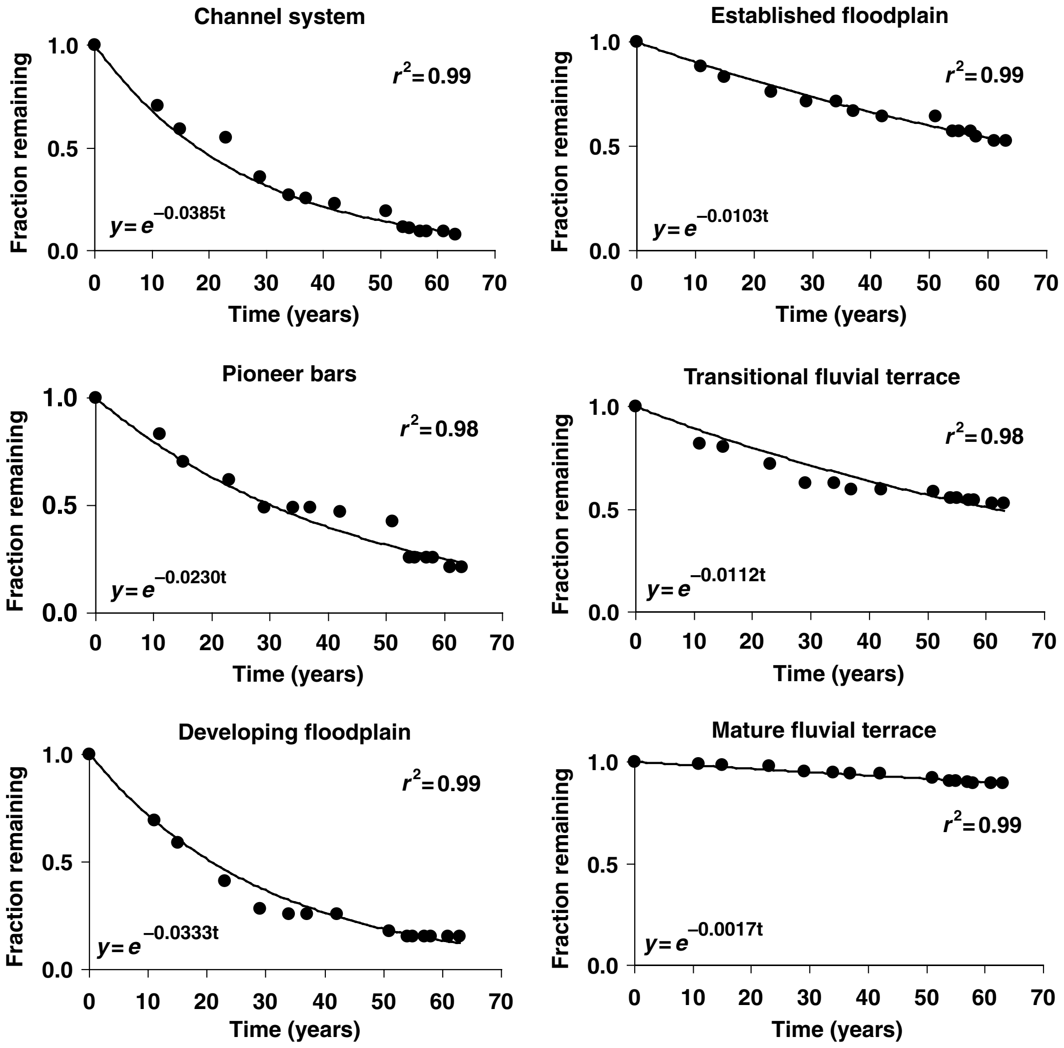


Fig. 7 Cumulative erosion of patch types in the Queets River, Washington, U.S.A. Exponential models quantify the fraction of initial (i.e. 1939) sampling points remaining in subsequent years (through 2002). In the case of the channel system, values represent the rate of colonisation by pioneering vegetation. Values for the coefficient of determination (r^2) for each model are overstated since models were forced through the intercept.

Table 5 Exponential erosion rates for patch types in the Queets River, Washington, U.S.A., where t is time in years

River landform	Erosion rate (k)	SE	r^2	Half-life; $t_{0.50}$ (years)	95% Loss; $t_{0.05}$ (years)
Channel system	0.0385	0.000849	0.99	18	78
Pioneer bar	0.0230	0.000765	0.98	30	131
Developing floodplain	0.0333	0.000810	0.99	21	90
Established floodplain	0.0103	0.000176	0.99	68	291
Transitional fluvial terrace	0.0112	0.000399	0.98	62	265
Mature fluvial terrace	0.00173	0.000050	0.99	401	1730

The erosion rate constant k and its standard error (SE) are given. In the case of the channel system, k represents the converse of the erosion rate; it is the rate of colonisation by pioneering vegetation. Coefficients of determination provided here probably overestimate true model performance, since the intercept was set at 1.0. Patch half-life, or the time required for channel erosion to destroy half the existing patches of that type, is given as $t_{0.50}$. Similarly, $t_{0.05}$ indicates the time required for the erosion of 95% of the existing patches. Estimates extrapolated beyond the range of observations (63 years) should be used with suitable caution.

(i.e. CV = 3%), whereas pioneer bars were most variable (i.e. CV = 29%).

Discussion

Our observations corroborate the importance of biophysical feedbacks in structure, composition and dynamics of river valley forests (Fetherston *et al.*, 1995; Abbe & Montgomery, 1996; Hupp & Osterkamp, 1996; Gurnell *et al.*, 2001). In the Pacific coastal forest, fluvial disturbances leave an obvious structural and biological legacy (*sensu* Franklin *et al.*, 2002) manifested in residual vegetation, seed banks, logjams, old channels and depositional features. This weaves together past and present, promoting continuity in the structure and composition of river valley forests (Scott, Friedman & Auble, 1996).

A cycle of change

We propose that the geomorphic and biotic transformation of fluvial surfaces into dynamic patch mosaics (Fig. 9) is a cycle of change operating at the reach to segment scale over decades to centuries (Fig. 10). The erosion of mature fluvial terraces perpetuates a shifting-mosaic condition (*sensu* Bormann & Likens, 1979) in the river valley forest by contributing pieces of wood large enough to remain stable during bed mobilising flows and trap other floating wood (i.e. key pieces; Nakamura & Swanson, 1994; Abbe & Montgomery, 1996). Resulting logjams are capable of initiating new patches in the channel (Abbe & Montgomery, 2003). The distribution, arrangement and longevity of patches vary in time and space, but their relative abundance remains relatively constant across decades at the scale of the entire valley floor. Heterogeneity arises in the valley floor as the cycle is interrupted at a variety of developmental stages and locations by the return of the active channel. Early patch development depends, at least in part, on channel behaviour. Similar patches can originate through contrasting pathways, depending on initial conditions established after disturbances (also see Van Pelt *et al.*, in press).

Lateral movement of the primary channel is a prerequisite of a complex valley forest. As erosion disassembles forested patches, accumulated sediment, nutrients and organic matter are redistributed. These materials mix with living vegetation and propagules from upstream and build new patches. In primary channels with meandering or braided morphology, patches are initiated by logjams. Jams alter the energy environment of the river (Abbe & Montgomery, 2003), which influences the rate and pattern of floodplain formation, in concert with sediment supply and the frequency of inundation (Knighton, 1998). By initiating sediment deposition and trapping floating propagules, jam formation triggers the transformation of the primary channel into forested patches.

Secondary channels create opportunities for alternative pathways of patch development. Secondary channels typically form where channel switching and meander cutoffs dominate and may remain active, ephemeral, or become abandoned. The degree of connectivity between the primary and secondary channels may dictate inundation frequency, flow

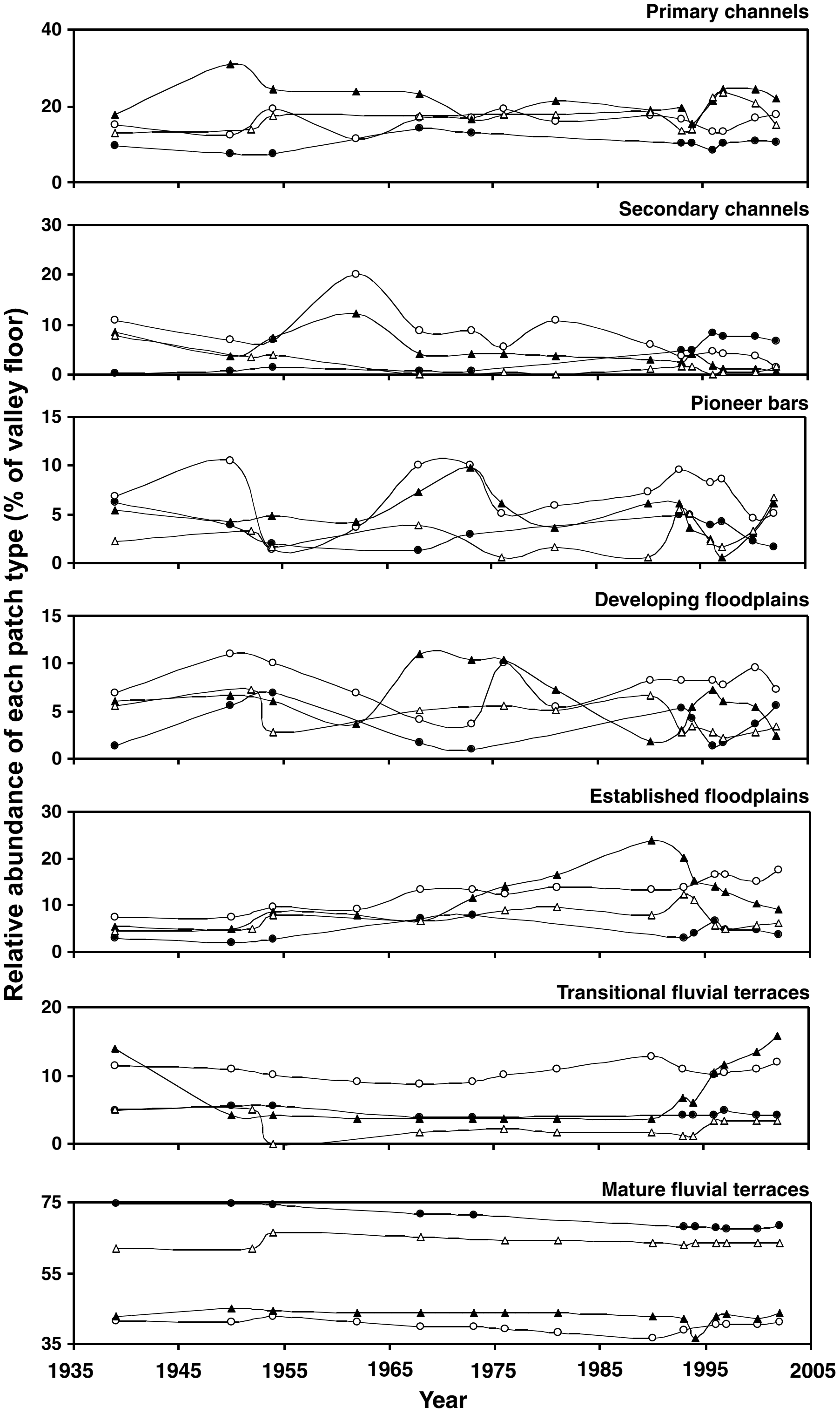


Fig. 8 Temporal variation in the relative abundance of seven patch types at four study reaches of the Queets River mainstem, Washington, U.S.A. Each chart illustrates changes in the per cent of the valley floor occupied by a given patch type in study reaches RK (river kilometre) 26 (○), 33 (●), 42(△) and 55(▲). Lines connecting points are only visual aids.

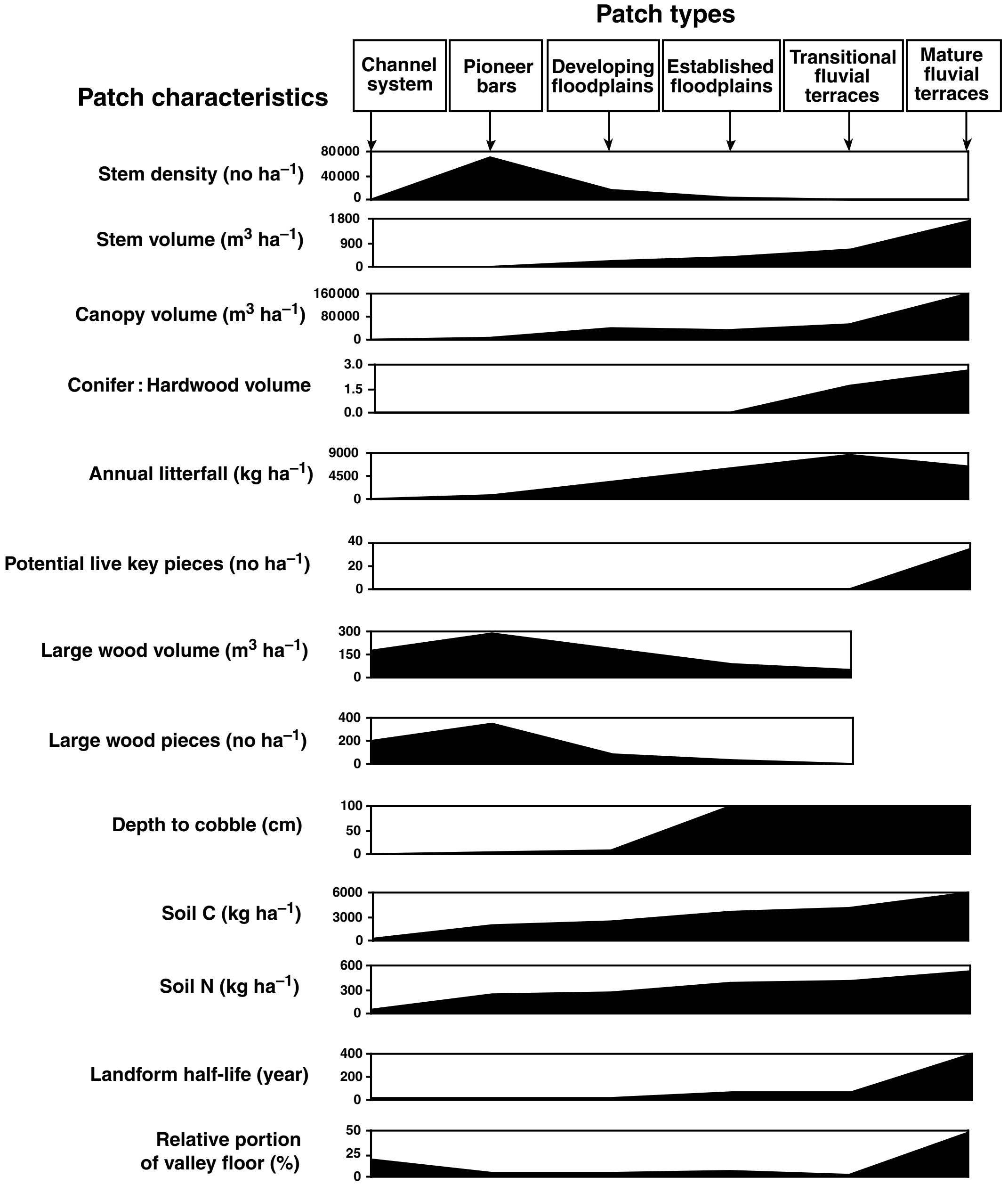


Fig. 9 Summary of general trends in the characteristics of patch types, from the channel to mature fluvial terraces, in the Queets River valley, Washington, U.S.A. Figures depict mean values from Tables 2–4. Units are given on each y-axis.

velocity and sediment transport dynamics (Piégay *et al.*, 2000) and, thus, soil depth and vegetation composition.

For example, patch development differs in active and ephemeral secondary channels. Active secondary channels transport substantial flow and sediment. Thus, vegetation establishes in patterns similar to primary channels. Ephemeral channels are inundated only during seasonal floods and may fill with or become blocked by alluvium until surface flow diminishes. Hardwoods and conifers can then establish simultaneously in these thick alluvial deposits, perhaps these areas are relatively sheltered (Asplund & Gooch, 1984). Vegetation establishes throughout, forming even-aged and uniformly distributed oxbow-shaped stands, or developing floodplains, without a pioneer bar precursor.

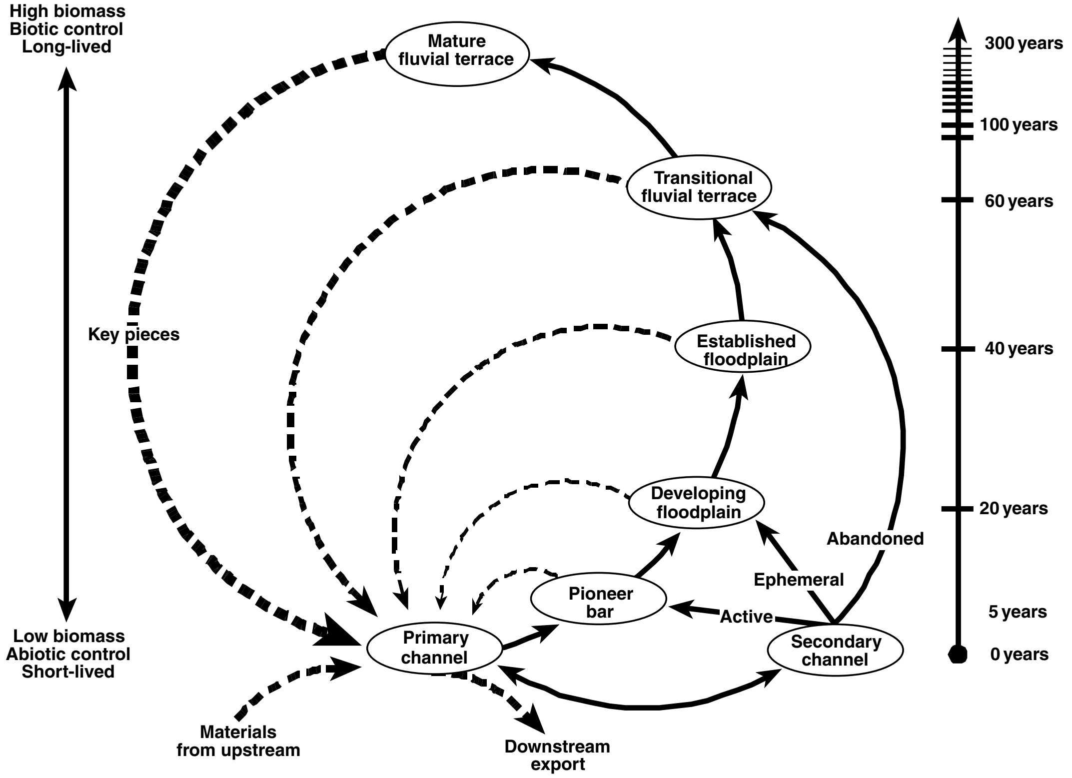


Fig. 10 A cycle of patch development and destruction in unconfined alluvial reaches of the Queets River, Washington, U.S.A. Patches undergo biophysical development from a simple and young state to a more complex and mature state through multiple pathways (solid lines). The vertical bar (left) refers to the relative importance of abiotic and biotic controls on patch development, vegetative biomass and patch longevity. The segmented bar (right) indicates the approximate time required to replace each patch type from unvegetated alluvial deposits. Patch development is interrupted at any point by the return of the channel, resulting in fluxes (dotted lines) of wood, sediment, and propagules to (or within) the channel system. Pioneer bars are quickly formed and destroyed, whereas mature fluvial terraces are formed over a long time and destroyed at a slower rate. The size of the dotted lines corresponds to the relative magnitude of the potential geomorphic impact resulting from erosion of a similar area from each patch type. New key pieces primarily originate from the erosion of mature fluvial terraces, although early patch types (e.g. pioneer bars) also contain 'abandoned' key pieces at high densities, which are returned to the channel by erosion. Primary channels may become secondary channels or vice versa. The cycle may be influenced by materials from upstream, as well as contribute materials to downstream areas.

Abandoned channels form when flow is interrupted and their soil and vegetation reflects the history of deposition prior to abandonment. In channels abruptly disconnected from the river by incision of the primary channel (e.g. after a meander cutoff; Fig. 2), depositional processes cease, forming cobblefields with thin dry soils inhospitable to woody vegetation. These areas remain treeless for decades until soil conditions develop to the point where woody vegetation can encroach from stands along the margins (Fig. 3). Contrasting patterns are evident in channels that accumulated sediments prior to abandonment. In this case, hardwoods and conifers establish simultaneously, forming distinctive stands in moist deposits (such as levees) along old channel margins (i.e. moist cobblefields).

The vegetation in floodplain patches stabilises alluvium, increases retention of sediment and organic matter, and slows flood runoff, but these patches are relatively short-lived. Growth and composition of vegetation communities in pioneer bars are regulated by primarily abiotic factors. Periodic flooding delivers propagules, sediments and nutrients, promoting soil development and sorting the early vegetation community. Species successfully colonising alluvium exhibit structural and life history characteristics facilitating widespread establishment and persistence in harsh fluvial habitats (Karrenberg, Edwards & Kollman, 2002).

In developing and established floodplains, biotic feedbacks increasingly regulate community structure, leading to precipitous declines in stem density and shifts in species composition (Table 2). Successional processes, including competitive interactions among species, also drive changes in plant species composition (Balian & Naiman, 2005). Floodplain vegetation conditions mineral soils through fine roots, litter and nitrogen-fixation, but dense thickets may inhibit the growth of other species through root competition and shading (Walker & Chapin, 1986). Ultimately, the destruction of floodplain patches by the river provides a vital, continuous supply of relatively small wood that, when trapped by key pieces, amasses into large jams which sculpt habitats for both aquatic and riparian organisms.

Fluvial terraces are particularly vital components of the dynamic patch mosaic because they are a primary source of large conifers capable of initiating jams, and contain peak levels of stem biomass, nutrients and fine sediment (Table 4). Whereas available N tends to be increased under red alder stands, total N is controlled by the amount of organic matter (Walker, 1993) and sediment texture (S. Bechtold, unpublished data). In terraces, the formation of an organic layer increases N retention capacity, although much of it is tied up in resistant organic matter and inaccessible to plants (Walker, 1993). Vegetation with diverse vertical and horizontal structure (Franklin *et al*., 2002), moderates light and temperature. Stand structure is primarily regulated by biotic controls such as competition and gap formation (Table 4). In some rivers, hillslope processes and landslides are major sources of large wood (Reeves, Burnett & McGarry, 2003). However, in floodplain rivers with wide valleys, such as the Queets, sustained delivery of large logs to the channel through erosion of fluvial terraces is a vital step in the cycle and redistributes structural complexity downriver.

Generality of findings

We infer that the cyclic pattern and relative estimates of patch structure and dynamics are transferable to forested alluvial reaches in unconfined mountain rivers with similar geomorphology, flow regimes, species assemblages and disturbance history. In a strict sense, our inferences are limited to the Queets River. Relatively few intact rivers remain, although the pristine valleys of the northern portion of the Pacific coastal ecoregion (e.g. British Columbia and southeast Alaska) would provide a reasonable testing ground for evaluating the generality of our findings. We caution that patterns described here are scale-dependent. Thus, extrapolation of our observations to different scales of space or time is unadvisable (Wiens, 2002).

Further validation of this model is needed, but our observations are generally consistent with previous studies. Similar patterns of development have been observed in the South Fork Hoh River (Fonda, 1974), but also the Willamette (Dykaar & Wigington, 2000), the Squamish (Brierley & Hickin, 1992), and even small streams in parts of the Oregon Coast Range (Pabst & Spies, 1998). Interactions between large wood, pioneering vegetation, geomorphic features, sediment and fluvial disturbance are also considered to play a major role in riparian patch dynamics in the Fiume Tagliamento in the Italian Alps (Kollmann *et al*., 1999; Gurnell *et al*., 2001).

Contrasting patterns are evident in large rivers that have different riparian vegetation, flow regimes or rates of flow transitions, which can create fundamental differences in depositional processes and vegetation distribution (Church, 2002). For example, our model does not characterise accurately large rivers of the eastern coastal plain in North America, where prolonged seasonal inundation of the floodplain is a dominant factor (Hupp & Osterkamp, 1996). Our observations also differ from semi-arid rivers, in which vegetation distribution is strongly controlled by water availability (Hupp & Osterkamp, 1996; van Coller, Rogers & Heritage, 2000). These findings may not be applicable to boreal rivers, which often have relatively small riparian trees and freeze during winter (e.g. Helm & Collins, 1997), unlike temperate coastal rivers.

Implications

Restoring dynamic patch mosaics is a formidable challenge in developed and agricultural river valleys (Collins, Montgomery & Sheikh, 2003; Piégay, 2003; Tockner *et al*., in press), where flow regulation and bank hardening has truncated or arrested the cycle of patch development (Marston *et al*., 1995). By restricting floodplain development and fluvial terrace formation, we often constrain the capacity of rivers to produce and renew rich alluvial soils, complex forest structure, and patches of trees large enough to initiate logjams.

Successful rehabilitation will rely on the rhythm and force of the river to promote variety and change, rather than on hard engineering (Holling, 2001; Ward *et al.*, 2002). River patches are arranged over time and space in a shifting mosaic, reflecting a unique history of creative and destructive events; the ongoing influence of abiotic and biotic processes that vary in composition, sequence, magnitude and frequency (Parker & Pickett, 1998). Successful rehabilitation sustains this interplay. The net result, although elusive, is heterogeneous river valleys capable of supporting diverse assemblages of plants and animals.

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