RIVER RESEARCH AND APPLICATIONS
River. Res. Applic. **23**: 247–267 (2007)
Published online in Wiley InterScience
(www.interscience.wiley.com) DOI: 10.1002/rra.978

INSTREAM FLOWS AND THE DECLINE OF RIPARIAN COTTONWOODS ALONG THE YAKIMA RIVER, WASHINGTON, USA

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ABSTRACT

Under pre-settlement conditions the Yakima River in Washington state, USA was characterized by multiple channels, complex aquifers and extensive riparian cottonwood forests. Subsequent implementation of headwater dams to supply irrigation water has altered river and floodplain processes critical to the cottonwoods and associated riparian vegetation. In this study, we analysed hydrology and floodplain forests and especially the dominant black cottonwoods (*Populus trichocarpa*) along sequential reaches of the Yakima River. Elevations were surveyed and vegetation inventoried along cross-sectional belt transects, and cottonwood tree ring interpretations investigated historic associations between river hydrology and cottonwood establishment and growth. We analysed hydrographs relative to the apparent episodes of cottonwood recruitment and applied a quantitative model for seedling colonization that required: (1) floods, disturbance flows to produce barren nursery sites, and subsequent flows for seedling (2) establishment and (3) survival. In contrast to earlier conditions, flow patterns after the 1960s have generally been unfavourable for cottonwood recruitment although some cottonwood colonization has occurred in association with physical disturbance from gravel mining. With recent flow regimes, regulated flows along upper reaches maintain the river near bank-full throughout the growing season, thus inundating suitable seedling recruitment sites. Downstream, irrigation withdrawals reduce the river stage, resulting in seedling establishment at low elevations that are lethally scoured by subsequent high flows. These regulated flow regimes have not hindered growth of established trees, but have reduced the recruitment of cottonwoods, and particularly disfavoured females, thus altering sex ratios and producing skewed cottonwood population age and gender structures. The cottonwood decline has also been associated with other changes in riparian plant community composition, including the encroachment of invasive weeds. Based on this ecohydrologic analysis we discuss flow adjustments that could rejuvenate cottonwood forests along the Yakima River.
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KEY WORDS: age-structure; black cottonwood; *Populus trichocarpa*; recruitment box model; regulated flows; seedlings; sex-ratios

Received 23 August 2006; Accepted 13 September 2006

INTRODUCTION

Research along the rivers of western North America has documented widespread decline in riparian cottonwood forests (Fenner *et al*., 1985; Bradley and Smith, 1986; Baker, 1990; Rood and Mahoney, 1990; Braatne *et al*., 1996; Cordes *et al*., 1997; Merritt and Cooper, 2000). The primary causes of decline have included woodland clearing, livestock production, and impacts due to river damming and water diversion (Smith *et al*., 1991; Busch and Smith, 1995; Rood *et al*., 1995; Williams and Cooper, 2005). With respect to impacts of damming and diversion, flow reductions have led to mortality of established cottonwoods and willows (reviewed in Rood *et al*., 2003a). Cottonwood and willow seedlings are small and particularly vulnerable to drought stress and consequently altered flow regimes often severely suppress seedling recruitment and this provides a predominant factor impacting riparian cottonwood forests (Rood and Mahoney, 1995; Cooper *et al*., 1999; Polzin and Rood, 2000). Since cottonwoods are relatively short-lived trees, typically dying within a century and seldom surviving beyond two centuries ongoing reproduction is essential to provide continuity of riparian cottonwood forests (Braatne *et al*.,

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1996; Rood *et al*., 2003b, 2005). While woodland clearing and mortality have led to substantial losses of cottonwood galley forests over the past century across western North America and elsewhere in the Northern Hemisphere, the long-term losses of riparian cottonwood forests due to the deficiency of reproduction could be more extensive. Thus, an understanding of the association between river hydrology and cottonwood seedling establishment is essential.

The recruitment of cottonwood seedlings is dependent on dynamic fluvial and geomorphic processes (Braatne *et al*., 1996; Scott *et al*., 1996; Mahoney and Rood, 1998; Johnson, 2000; Lorang *et al*., 2005). Seasonal flow patterns including periodic spring flooding produce moist and barren substrates that are required for seedling recruitment (Bradley and Smith, 1986; Scott *et al*., 1996; Mahoney and Rood, 1998). After germination, the roots of young seedlings must keep pace with the receding soil moisture that is closely coordinated with the declining river stage (Mahoney and Rood, 1992, 1998). Thus, if river levels decline abruptly, young seedlings succumb to drought stress. Older cottonwoods also benefit from periodic flooding that recharges the alluvial groundwater table (Smith *et al*., 1991; Stromberg and Patten, 1991, 1996; Rood *et al*., 2003a). Dams that reduce summer flows often induce significant levels of drought stress among all age-classes, and thereby promote an older age-structure (Rood and Mahoney, 1995; Braatne *et al*., 1996; Rood *et al*., 2003a).

The Yakima River provides an ideal opportunity to analyze the influence of altered flow regimes on riparian cottonwoods. Recent historic flows have been regulated to maximize the supply of water for irrigation and this has resulted in artificial seasonal flow patterns along sequential river reaches. In the present study, we investigated how different flow regimes have influenced cottonwood recruitment and also considered the broader species composition and structure of these floodplain forests. This research particularly reveals the influences of regulated flows on black cottonwood, a species of the 'balsam poplar' type of trees within *Populus* section *Tacamahaca*. This cottonwood differs considerably in life history and ecophysiology relative to other *Populus* species and especially the section *Aigeiros* Fremont and prairie cottonwoods that are dominant in riparian forests of the drier regions of western North America and have been more widely studied (Braatne *et al*., 1992, 1996; Rood *et al*., 2003a).

Following from prior studies with section *Aigeiros* cottonwoods, we hypothesized that the successful seedling recruitment of black cottonwood would be dependent upon specific, seasonally varying hydrologic patterns (Mahoney and Rood, 1998). The cottonwood population responses along hydrologically distinct reaches of the Yakima River should further reveal the relative importance of different hydrograph components relative to black cottonwood colonization. This analysis extended the concept of the Recruitment Box Model that seeks to define the hydrogeomorphic requirements for cottonwood colonization (Mahoney and Rood, 1998) and also provided a test of the 'natural flow paradigm' an over-arching concept for fluvial systems in which the natural hydrograph pattern is regarded as the essential pattern for native river and riparian ecosystems (Poff *et al*., 1997).

MATERIALS AND METHODS

Study area

The Yakima River Basin is located in central Washington (Figure 1), encompassing an area of approximately 15 900 square km. The Yakima River originates near the crest of the Cascade Range and flows 344 km southeastward to its confluence with the Columbia River. Five major reservoirs in the headwaters of the Yakima and Naches basins are managed by the United States Bureau of Reclamation (USBR) and provide the primary storage for the Yakima Irrigation Project.

The Yakima is a gravel-bed river with its valley characterized by a series of long ridges extending eastward from the Cascades that are punctuated by extensive alluvial floodplains. Prior to European settlement, the alluvial floodplain reaches were dominated by complex geomorphic surfaces and extensive black cottonwood galley forests. Despite subsequent clearing and agricultural activity, cottonwoods still occupy significant portions of these alluvial reaches. Our field studies focused on the Cle Elum, Union Gap and Wapato reaches (Figures 1 and 2), in order to assess the influence of their varied flow regimes on the species composition and structure of floodplain forests.

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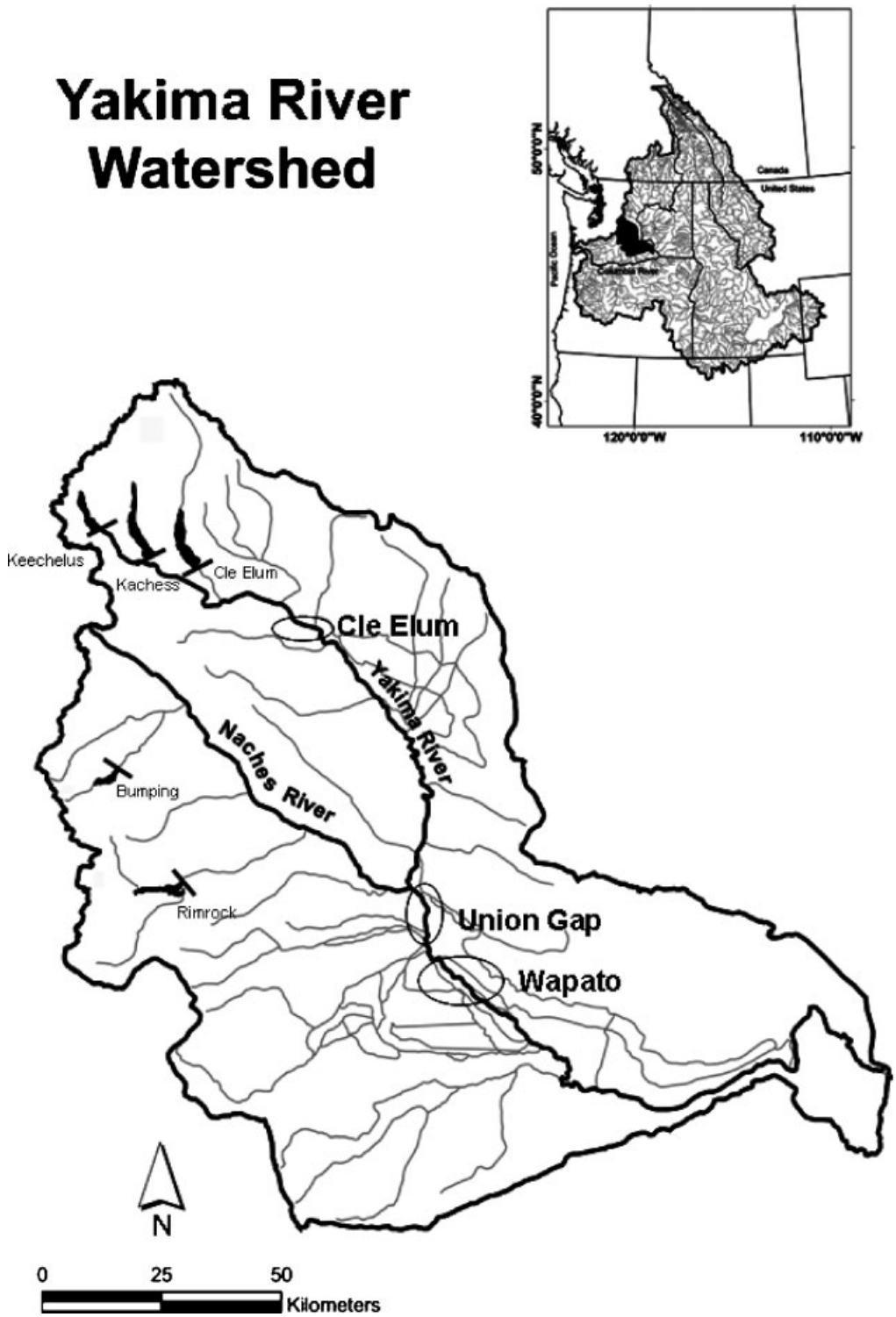

Figure 1. Map of the Yakima River and watershed showing study reaches and locations of dams

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A- Cle Elum Reach

B- Union Gap Reach

C- Wapato Reach

Figure 2. Photographs showing typical views of the riparian zones along the Yakima River along the Cle Elum (upstream), Union Gap (intermediate) and Wapato (downstream) reaches. Note the absence of younger cohorts of willow and cottonwood and the abundance of exotic woody and herbaceous species along the river margin. This figure is available in color online at www.interscience.wiley.com/journal/rra

Assessment of seasonal discharge and river stage

U.S. Geological Survey and USBR databases of mean daily discharge (Q_d) and associated river stage were used in our analyses of Yakima River flow patterns. Primary gauging stations were Cle Elum for the Cle Elum reach and Parker for the Wapato Reach. Flow data from gauges below Roza Dam and the lower Naches River was combined to estimate discharge for the Union Gap Reach. These data were used to characterize annual peak-flows and develop seasonal hydrographs for two time intervals: (a) 1908–1914, to represent natural flows prior to construction and

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operation of headwater dams in the Upper Yakima and Naches Rivers and (b) 1992–1998 to represent the flow manipulations including those initiated in 1981 to increase the supply of irrigable water for the lower Yakima Valley.

River edge vegetation analysis

Riparian vegetation patterns along riverbanks and point bars were systematically sampled using cross-sectional belt-transects. Point and side-channel bars were especially sampled as these geomorphic surfaces typically display high probability for the recruitment of cottonwood seedlings (Braatne *et al*., 1996). Twelve transects were established and sampled within each study reach. Each belt-transect was perpendicular to the river edge and extended upslope into the mature cottonwood stand. Reflecting differences among floodplain features, belt-transects ranged from 50 m to 150 m in length. Areas along the riverbank dominated by herbaceous plants (both native and exotic species) were sampled using 1 m × 1 m quadrats placed at 1 m intervals along the transect. Larger quadrats were used to sample areas dominated by shrubs (2 m × 4 m quadrats) and trees (5 m × 20 m quadrats), with quadrats parallel to the river channel.

In each quadrat, percent leaf area cover was estimated for each plant species. Estimates of plant cover were converted to an octave scale for all subsequent analyses. This minimized sampling error, while preserving fine-scale differences at low values. Octave classes used in this study were: 0 (0% cover), 1 (1%), 2 (2–4%), 3 (5–9%), 4 (10–18%), 5 (19–35%), 6 (36–72%), 7 (73–100%); with mid-points of each coverage class used in subsequent analyses. For dominant trees and shrubs, stems were counted, diameters at 0.5 m measured and increment cores extracted for age-class determinations. The sex of mature trees was inventoried in early spring for 100 trees along four transects within each study reach ($n = 400$ trees/study reach). Species nomenclature follows Hitchcock and Cronquist (1991) and Whitson *et al*. (1996).

Surface substrates were classified into one of four categories: (1) fines—fine sediment (silt and sand 0.065–2.0 mm), (2) gravel—coarse surface (2.0–64.0 mm) with a subsurface of fines, (3) cobble—coarse surface (64–256 mm) without fines below the surface layer of rock and (4) boulders and bedrock (>512 mm). A visual classification of substrate class was recorded for each quadrat.

A laser level (Laser Alignment, Chicago, IL) was used to determine the relative elevation (±1 cm) of each quadrat. The bottom elevation of each transect was tied to the current water surface, with the date and specific time recorded for each measurement. GPS and elevation coordinates (Trimble ProXRS) of this benchmark were then linked with river stage data as derived from the nearest river gage (USGS/BOR river gage data) and/or survey benchmark data from the groundwater well networks of the Yakima Critical Reaches Project. This sampling regime allowed us to assess the structure and composition of riparian plant communities (trees, shrubs, forbs, both native and exotic species) and patterns of cottonwood seedling recruitment in relation to current and historic flow conditions.

Vegetation data analyses

Distribution patterns of major growth forms (trees, shrubs, forbs and grasses) along riverbanks were assessed relative to mean base-flow conditions (Figure 4), whereas multivariate relationships between plant species and key environmental variables were explored using detrended correspondence analysis (DCA, unconstrained ordination, Figure 6) and cannonical correspondence analysis (CCA, constrained ordination, Figure 7). Environmental variables analysed include: (1) quadrat elevation relative to mean base-flow elevation, (2) linear distance from the quadrat to mean base-flow elevation, (3) riverbank slope and (4) substrate conditions. These analyses were conducted using PC-ORD (Version 4.0, MJM Software, Gleneden Beach, OR), which is comprehensive software for multivariate analyses of vegetation and environmental data. Monte Carlo simulations were performed on all DCA and CCA analyses ($n = 100$, $P < 0.01$). In contrast to the unconstrained ordination (DCA), CCA groups species and study plots into distinctive clusters and spatially arrays these clusters in relation to environmental variables. As a result, CCA was useful in evaluating multivariate relationships within and between species, study plots, transects, river hydrology and other environmental data.

Dendrochronology

For the measurements of annual growth rings, the increment cores of black cottonwood were mounted on grooved planks and sanded to 320 grit. Annual radial increments (RI) were measured to 0.002 mm precision with a dissecting

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microscope, a Velmex stage and Acu-Rite encoder (Velmex Inc., Bloomfield, NY), and MeasureJ2X software (VoorTech Consulting, Holderness, NH). Annual basal area increments (BAI) were calculated from annual RI and corresponding wood diameters assuming a circular trunk cross-section (Willms *et al*., 2006). To reduce the influence of the increasing growth rate during the juvenile phase, the investigation of possible environment influence on the BAI pattern was restricted to the 40-year period prior to coring (1961–2000) for cottonwood trees older than 50 years. BAI plots from these individual mature trees were compared to consider possible correspondence of low or high-growth periods. Subsequently, for comparison across these trees, the proportional BAIs for the period 1961 to 2000 were calculated as the ratio of the specific year BAI versus the mean 1961–2000 BAI for that tree, low- or high-growth years are indicated by values $<$ or $>$ 1, respectively. Since some BAI plots displayed an apparent progressive increase, linear and quadratic regression were undertaken to investigate and quantify the trend. Following that, values from the regression function were calculated for each year and these were subtracted from the annual proportional BAI values from the individual trees to generate $+$ or $-$ for apparent high- or low-growth years, respectively. Since it is difficult to precisely assign specific growth year over a four-decade record, due to 'missing' and 'false' rings that are common in cottonwood cores, statistical comparison considered 3-year sequences and applied a χ^2 test with the null hypothesis being an equal likelihood of the proportional BAI values being $<$ or $>$ 1, or $+$ or $-$ after the regression extrapolation. For this and other statistical analyses, JMP 5.0 (SAS Institute Inc., Cary, North Carolina) was used.

Cottonwood forest population structure and hydrograph correspondence

The ring counts of the increment cores were used to the estimate the establishment year of each of the sampled cottonwood trees. The possible coordination between pulses of cottonwood establishment and major flood events was investigated in accordance with Samuelson and Rood (2004) whereby a χ^2 analysis was applied to detect non-random association. As with the growth analysis, correspondence was investigated within a 3-year interval to account for the imprecision of ageing of mature trees.

Quantitative analysis of hydrograph requirements for seedling recruitment

Using the Recruitment Box Model as a conceptual foundation (Mahoney and Rood, 1998; Amlin and Rood, 2002), we analysed historic daily mean discharge (Q_d) and annual maximum mean daily discharge (Q_{max}) data from the Yakima River at the USBR Parker gage (PARW, Wapato reach). This gage is situated towards the lower end of the Yakima River and thus reflects the cumulative flow pattern. It must be recognized that reach-specific Q patterns differed considerably along the river and these would produce localized differences in cottonwood colonization.

We considered the full period of hydrometric record for PARW, but emphasize and present data for intervals with apparent pulses of cottonwood recruitment, as revealed in the population age structure analysis. We considered the essential sequential hydrograph components recognized by other researchers and expanded these to include other processes, especially winter flooding that is prevalent along the Yakima River.

Both discharge (Q) and stage hydrographs were analysed, with back-conversion of stage using the current PARW hydrometric site ratings function. While the local ratings function changes with changing channel geometry, our intent was to compare general hydrograph suitability along the river rather than at a particular cross-section and thus back-conversion from Q data using a 'typical' stage versus discharge function provided a sound approach for historic assessment. Flood recurrences were analysed with standard functions in accordance with DISTRIB2.12 (SMADA 6.0, University of Central Florida). From the discharge and stage hydrographs and recurrence estimates, quantitative ratings were developed for individual hydrograph criteria and then defined weightings across the criteria (Table IV). We applied an iterative approach that sought to best explain the observed results within the context of the previous literature analysing the hydrogeomorphic requirements for cottonwood colonization (Rood *et al*., 1995; Scott *et al*., 1996, 1997; Mahoney and Rood, 1998; Johnson, 2000; Karrenberg *et al*., 2002).

RESULTS

Physical and geomorphic features were similar between study reaches (Table I). Comparable levels of sinuosity and channel gradient strengthen our comparative analysis of regulated flows on riparian cottonwoods.

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Table I. Physical characteristics of three study reaches along the Yakima River, Washington

Characteristic	Cle Elum	Union Gap	Wapato
Sinuosity	1.35	1.32	1.36
Mean elevation (m)	569	306	284
Gradient (m/km)	2.4	2.6	2.3

Flow regimes

Variations in flow regime within and between-study reaches are related to peak-flow (Figure 5) and mean daily flow (Figure 3). Over the last century, the Yakima River has shown high levels of variation in peak-flow, with these flows unaltered by dam construction and irrigation withdrawals (Figure 5). Throughout the period of record (1908–1998), annual maxima ranged from lows of 200–650 $m^3 s^{-1}$ to highs of 1200–1575 $m^3 s^{-1}$ (Figure 5), with the largest flood on record occurring in 1996. The lack of dam-related effects appears related to their location in the upper basin and low reservoir storage capacity. Thus, major storm and snowmelt events still generate large peak-flows.

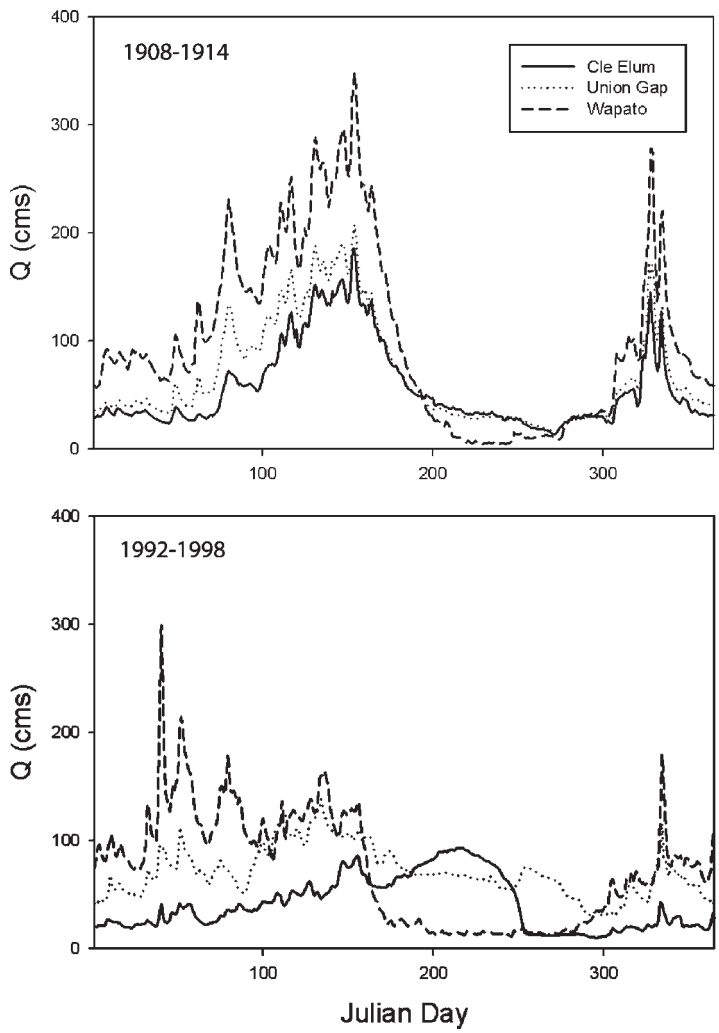

Figure 3. . Mean hydrographs for three reaches along the Yakima River for the pre-damming period (top) and recent, post-damming conditions (bottom)

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In the early 1900's, peak-flows associated with snowmelt were followed by progressive declines in discharge and stage over the summer months with periodic rain-driven storm-flows during the winter months (Figure 3, 1908–1914). These flow regimes, notably gradual stage declines during the seed dispersal periods, would have favoured the widespread establishment of riparian cottonwoods. In contrast, seasonal flow patterns were highly modified following construction of headwater dams and with flows specifically tailored to support the irrigation of agricultural crops within the Basin (Figure 3, 1992–1998). Recent flow management practices decrease springtime flows, yet discharge varies significantly between study reaches during the summer months. In both Cle Elum and Union Gap reaches, summer discharge is maintained at levels two to three times higher than historic flow regimes. Summer discharge in the Cle Elum reach is actually higher than springtime flows. By maintaining high summer discharges, seasonal stage fluctuations in the Union Gap reach are less than 1 meter. This lack of stage decline represents a highly unusual flow pattern when compared to other flow-regulated rivers. Collectively, these regulated flows inundate potential nursery sites for recruitment by cottonwood seedlings and other native riparian plants. In contrast, summer discharge declines abruptly to very low levels along the Wapato reach. These low summertime flows promotes seedling establishment by cottonwoods and other riparian species at lower river stages, which leaves them highly vulnerable to scour from winter and springtime flows.

Composition and structure of riparian plant communities

Along the Cle Elum reach, riparian populations of cottonwoods and other native plants were largely composed of healthy and vigorous individuals. However, there was a lack of younger cottonwoods throughout the reach. Cottonwoods were more abundant at elevations of one meter or more above base-flow conditions (Figure 4). This pattern of distribution corresponded to those areas of the floodplain located above the elevated stage associated with the regulated flows in this alluvial reach (Figure 3). Similarly, grasses and forbs were more abundant at these higher floodplain elevations (Figure 4). Herbaceous life forms were dominated by perennial species, thus native grasses and forbs were more common than exotic species (Table II). However, invasive stands of reed canary grass dominated riverbanks throughout this study reach. The relative abundance of reed canary grass was indicative of the persistent elevated flows that favor its expansion via vegetative propagules during the summer months (a fairly common occurrence in many flow-regulated rivers of western North America).

Along the Union Gap reach, scattered stands of riparian cottonwood are interspersed with European willows (*Salix alba* and *Salix x. rubens*) and other exotic woody (i.e. silver maple and elm) and herbaceous species (Table II). Similar to other study reaches, younger ages classes of cottonwood were absent. Given the relative stability of regulated flows and lack of a significant stage declines (Figure 3), vegetation was growing closer to the river channel (Figure 4). Cottonwoods were primarily located at elevations of one metre or more above base-flow conditions (Figure 4), though clonal expansion via root suckers extended their distribution down to one-half metre above summer base-flow. Grasses and forbs were found at comparable elevations (Figure 4). Perennial grasses, such as reed canary grass, were more common than annual grasses. Invasive annual and perennial forbs were also common members of these riparian communities (Table II). The close proximity of this riparian corridor to the City of Yakima, fruit orchards, agricultural fields and major highway networks were also important factors in supporting the relative abundance of exotic species within this study reach.

Along the Wapato reach, remnant and fragmented stands of riparian cottonwood were composed of a mosaic of black cottonwood, European willow and Silver Maple (*Acer saccharinum*) along with other exotic woody and herbaceous species (Table II). With the exception of seedlings, juvenile age classes of cottonwood were absent from this reach. In response to low and relatively stable summer flows (Figure 3), riparian vegetation was found growing very close to the water's edge (Figure 4). Mature cottonwoods were located at elevations over one metre above base-flow conditions (Figure 4), yet young seedlings were commonly found at less than one-half metre above summer base-flows. Germination at these low elevations was the primary cause for their subsequent mortality as flows increase during the late fall and winter months. Grasses and forbs were found at comparable elevations (Figure 4), with exotic and invasive species dominating these riparian communities (Table II). Annual grasses and forbs were more abundant than perennial species. Reed canary grass was widespread, yet less dominant relative to other study reaches. The exceptionally low summer flows appear to be an important factor leading to the increases in exotic species.

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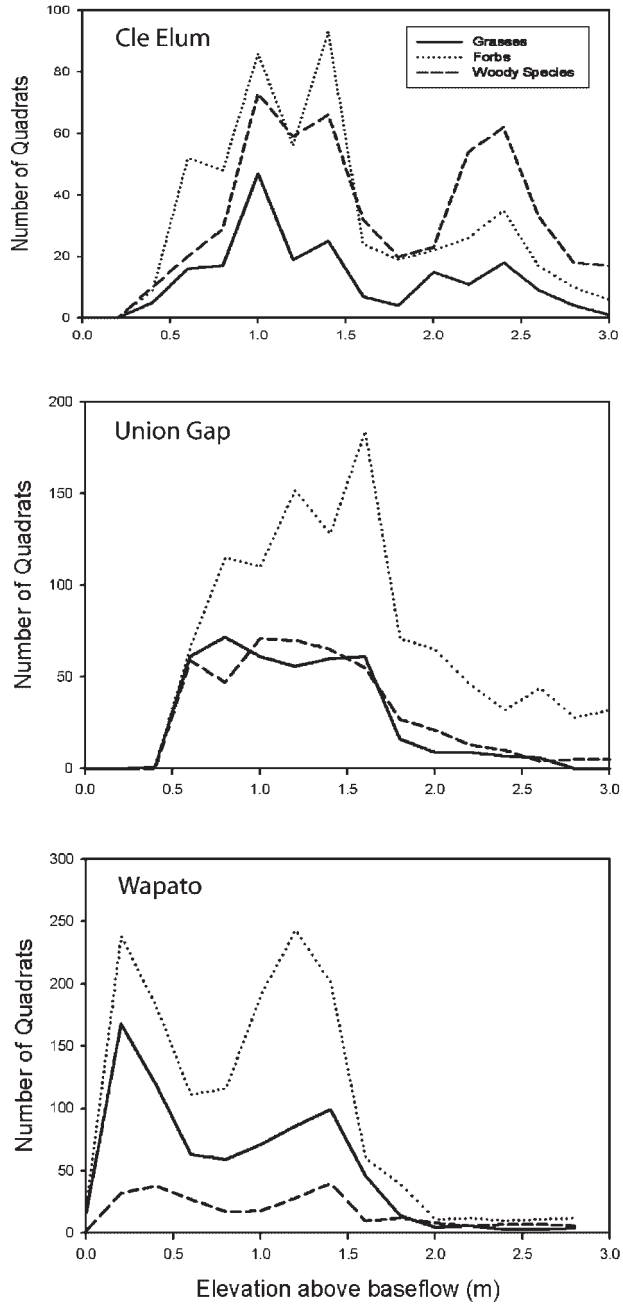

Figure 4. Elevational distribution of different life history groups of riparian plants along three reaches of the Yakima River

Age-structure and sex-ratios of riparian cottonwood populations

In all study reaches, mature (and occasional juvenile) trees were cored ($n = 124$) to determine the age structure of local cottonwood populations (Figure 5). Since cottonwood establishment is generally correlated to peak flood events, these data correspond closely to peak flows from 1900 to 2000 (Figure 5). On the basis of these data, the following patterns were observed; (a) lack of correlation between peak flows and cottonwood recruitment following the initiation of regulated flows, (b) the relative abundance of 40–50 year old cohorts in relation to extensive river

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Table II. Common plant species by study reach along the Yakima River, Washington

Species	Cle Elum	Union Gap	Wapato
Grasses and sedges			
Agrostis Alba[*]	X		X
Bromus tectorum[*]			X
Carex rostrata	X		
Echinochloa crusgalii[*]		X	
Elymus glaucus	X		
Eleocharis palustris			X
Eragrostis hypnoides[*]			X
Juncus bufonius[*]			X
Juncus effuses[*]	X		
Phalaris arundinacea[*]	X	X	X
Poa compressa[*]			X
Scirpus microcarpus			X
Forbs			
Amaranthus retroflexus[*]			X
Bidens cernua			X
Centaurea diffusa[*]	X	X	
Epilobium paniculatum		X	
Hypericum perforatum[*]	X	X	
Linaria dalmatica[*]		X	
Linaria vulgaris[*]			X
Lythrum salicaria[*]		X	
Melilotus officinalis[*]	X	X	
Plantago lanceolata[*]		X	X
Polygonum persicaria[*]		X	X
Taraxacum officinale[*]			X
Tanacetum vulgare[*]	X	X	
Veronica americana	X	X	
Woody species			
Alnus incana	X		
Cornus nuttallii	X		X
Cornus stolonifera	X	X	
Populus trichocarpa	X	X	X
Rosa nutkana	X		X
Rosa woodsii	X	X	X
Salix exigua		X	
Salix lasiandra	X	X	
Salix monticola	X	X	
Salix ex. Rubra[*]		X	X
Salix sitchensis	X		
Symphoricarpos albus	X	X	
Ulmus pumila[*]			X

[*]Non-native, exotic or invasive species.

gravel mining during the 1960s, (c) lack of cottonwood recruitment over the last 20 years and (d) absence of cottonwood recruitment following the major flood events of 1996. These results highlight a skewed age-class structure, with the absence of cottonwood recruitment under current flow regimes limiting the long-term viability of these populations.

Sex-ratios varied between study reaches (Table III). In the Cle Elum reach, the ratio of males to females was 1:1, compared to 2:1 in the Union Gap reach. In contrast, the sex ratio was highly skewed toward males in the Upper Wapato reach (7:1). Sex could not be determined in 10–20% of the individuals encountered in each study reach.

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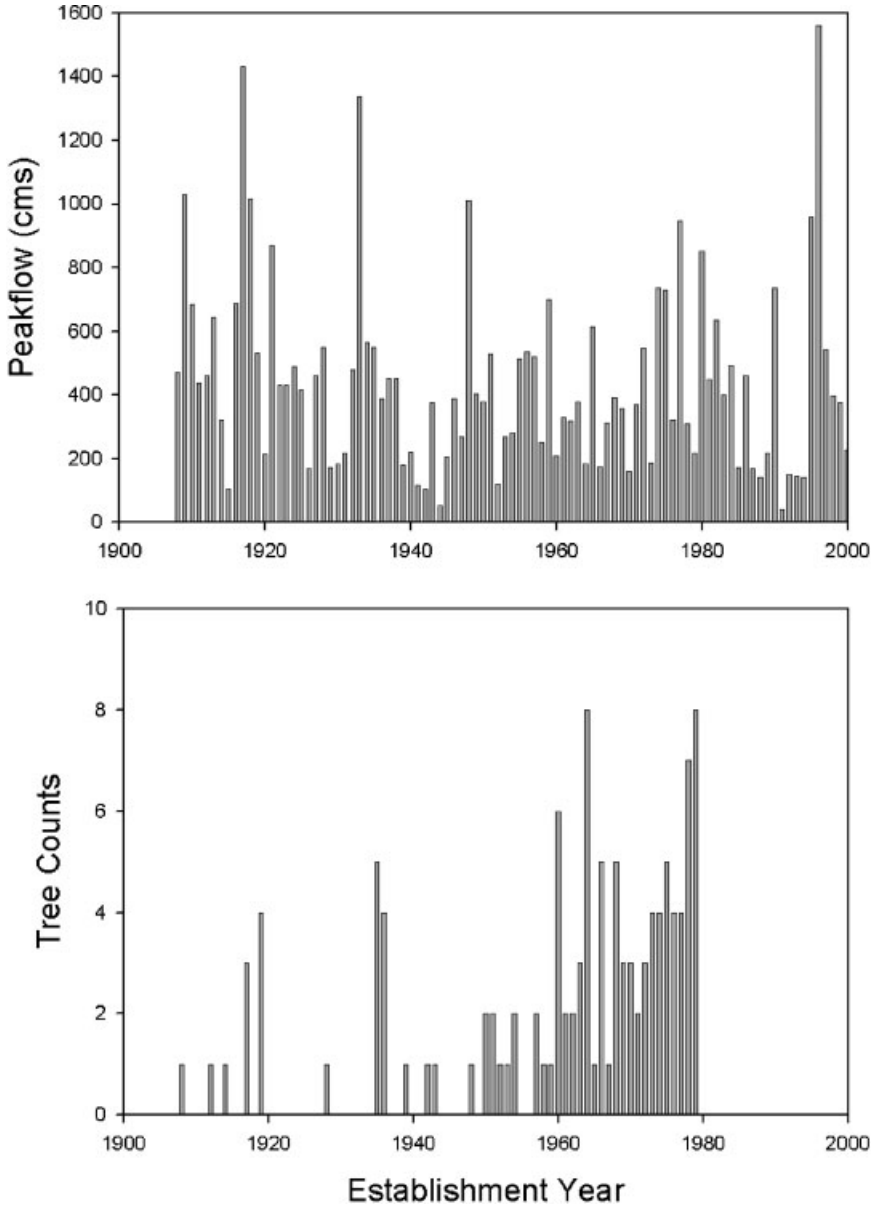

Figure 5. Peak flows (top) and apparent establishment years for black cottonwoods along the Yakima (bottom)

Unconstrained and constrained ordinations of community structure

Unconstrained Ordination (DCA): There were no significant trends between reaches arising from the unconstrained ordination of herbaceous species. Despite significant shifts in species composition towards exotics, this finding suggests a regular distribution pattern for herbaceous species among study reaches. In contrast, the unconstrained ordination of woody species showed significant differences between study reaches. Axis 1 was correlated with quadrat elevation relative to base-flow conditions, with a broader range of elevations corresponding to the top and lower elevations to the bottom of the graph (Figure 6). Axis 2 was correlated with distance to the water surface as well as longitudinal trends between study reaches. The higher elevation and cooler seasonal temperatures of the Cle Elum reach provide a different range of environmental conditions relative to the warmer

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Table III. Sex-ratios of riparian cottonwood populations along the Yakima River

Study reach	Males	Females	Unknown	Sex ratio (M:F)
Cle Elum	156	158	86	1:1
Union Gap	222	110	78	2:1
Wapato	292	42	66	7:1

and drier Union Gap and Wapato reaches. As a result, Cle Elum quadrats clustered towards the top with progressive clusters for Union Gap and Wapato downward along Axis 2 (Figure 6). The overlap observed among study reaches reveals the shared attributes of quadrats dominated by black cottonwood. This pattern of quadrat clusters reflects the distinct flow regimes and environmental conditions of these study reaches.

Constrained Ordination (CCA): There were significant trends between reaches arising from the constrained ordination for woody species (Figure 7), but not grasses and forbs. The distribution of woody plants was correlated with hydrologic variables. Distribution patterns of woody plants were strongly correlated with: (1) summer base-flow conditions ($r = -0.978$), (2) elevation above current water surface ($r = -0.963$), and distance to water surface ($r = 0.853$). Correlations for substrate conditions were non-significant ($r = 0.358$). The variance associated with Axis 1 accounted for 40% of the total variance observed (Pearson's Correlation, $r^2 = 0.658$). Elevation relative to summer base-flow and current water surface were both correlated with Axis 1, whereas distance to water surface was correlated with Axis 2 (Figure 7). Cottonwood-dominated plots were more common at higher elevations than riparian shrubs. These distribution patterns closely correspond to findings presented in Figure 4.

Dendrochronology

Among sampled cottonwoods, there was a moderate association between tree size (diameter) versus age (Figure 8). The relationship was better described by a quadratic ($r^2 = 0.46$) than linear ($r^2 = 0.44$) function that

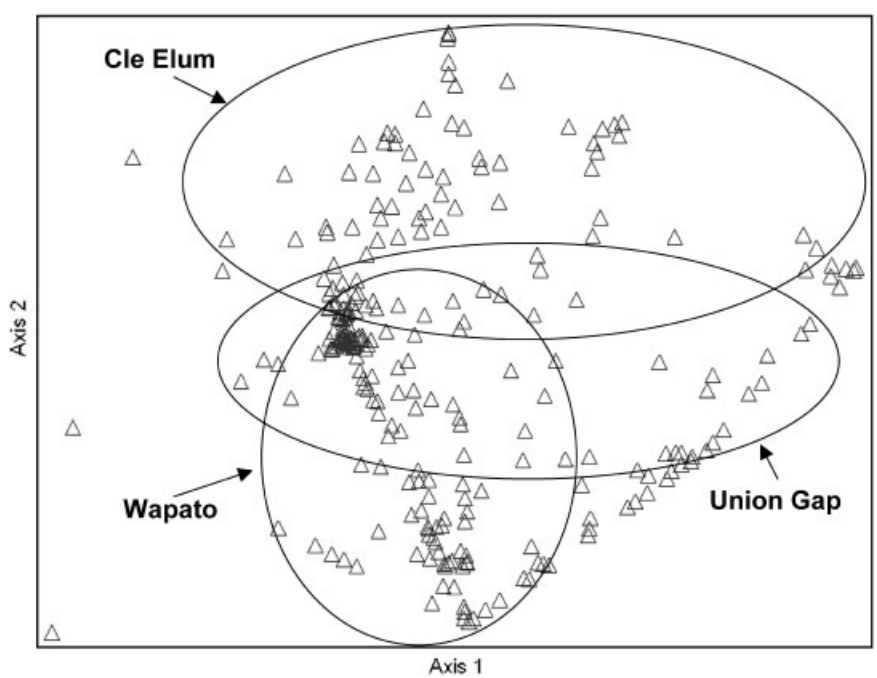

Figure 6. DCA ordination of woody species along three reaches of the Yakima River

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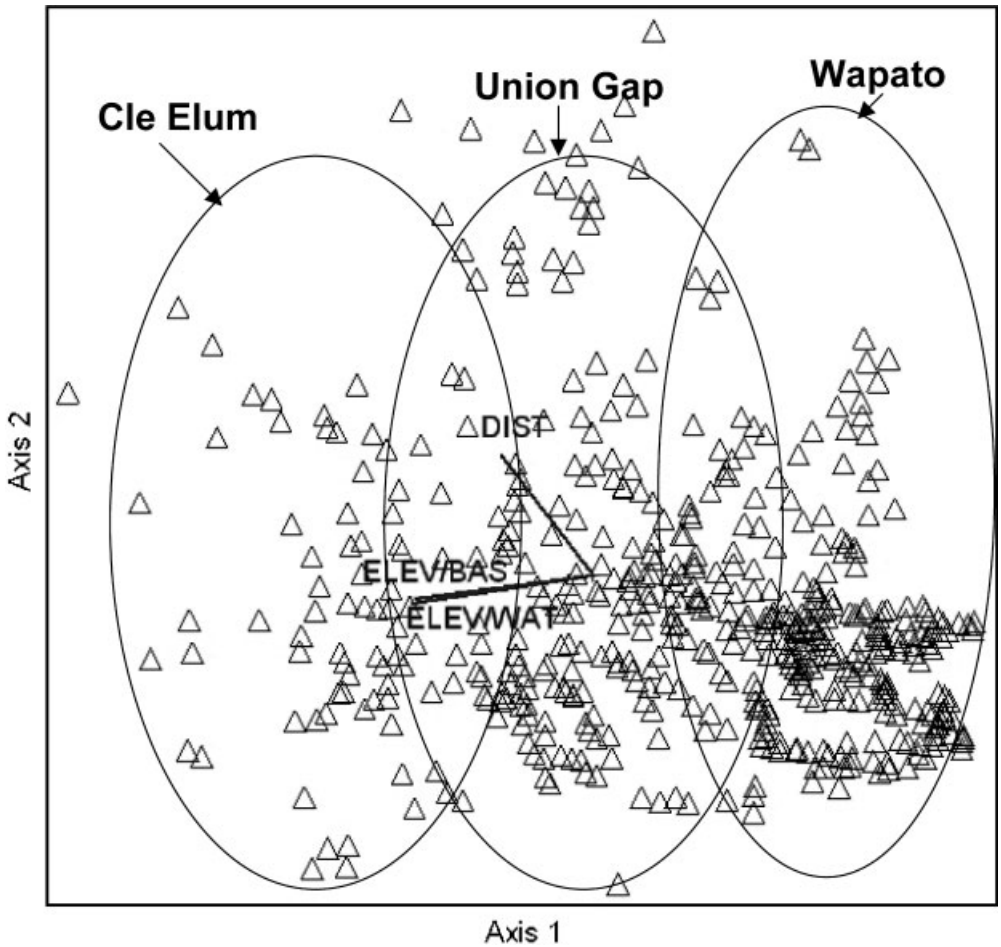

Figure 7. CCA ordination of woody species along three reaches of the Yakima River

accounted for almost one-half of the observed size variation. The scatter was probably due to genotypic variation, with individual fast- versus slow-growing trees, and our sampling at different sites along the river. Along other rivers, section Tacamahaca cottonwoods along lower reaches grow faster than those from higher reaches, probably due to the warmer climate (Kalischuk *et al*., 2001; Willms *et al*., 2006).

Due to the variation across the sampled trees, growth sequences were analysed for individual trees as well as for the aggregate sample population. Individuals demonstrated a developmental pattern consistent with patterns for black cottonwoods from other regions (Wilms *et al.*, 2006). The initial seedlings were small and growth rate as reflected in both annual radial increments and basal area increments (BAI), progressively increased as the saplings grew through the juvenile phase (Figure 9). After about two decades growth leveled-off and BAI were fairly consistent (Figure 9). This pattern is consistent with that of black and narrow leaf cottonwoods along Alberta's Oldman River (Willms *et al*., 2006).

During this mature growth phase, the more consistent BAI provides a baseline upon which environmental influences such as water supply are superimposed. For the Yakima trees the proportional BAI still provided a significant linear (Figure 8) or slightly higher fit quadratic ($r^2 = 0.25$, not shown) regression indicating a progressive increase in the BAI. This is consistent with expectations since these trees were as young as 50 years old and would have only been 10 years old for the start of the comparison data set and thus still in the juvenile phase with increasing BAI (Figure 8). There was also considerable interannual variation in BAI, but this was not coordinated across the sampled trees. Tree-specific low- or high-growth may reflect a range of influences, including insect pests

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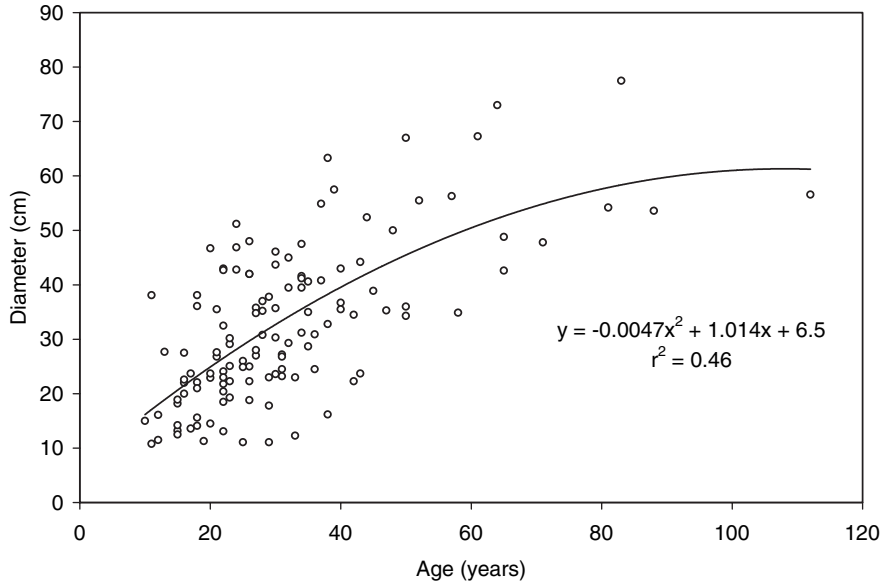

Figure 8. Relationship between basal diameter and the age of black cottonwoods along the Yakima River

or disease or physical factors, such as competition release as an adjacent tree experiences die-back. Growth responses that are associated with river flow should be more broadly coordinated across the cottonwoods and the BAI records did reveal a period in the early 1970's with reduced growth (Figure 9). This growth reduction was fairly consistent across the sampled trees indicating a broad-scale regional influence (Figure 9: for 1971–1973 data with comparison to regression plot, $\chi^2 = 10.9$, $P < 0.001$). However, the period of reduced growth was not associated with major variation in river hydrology since there was neither a natural nor regulation-based reduction in mean annual discharge during the low-growth interval (Figures 3, 5 and 9). Other than the period of reduced growth (early 1970's), there was little evidence for a coordinated reduction in growth over the interval from 1960 to 2000 (Figure 9). These data thus reveal relatively complacent growth, which suggest that environmental conditions were sufficient for the growth of black cottonwoods along the Yakima River.

Cottonwood forest population structure and hydrograph correspondence

Consistent with the population structure of black cottonwoods along Drywood and Yarrow creeks in southwestern Alberta (Samuelson and Rood, 2004), the age distribution for mature cottonwoods along the Yakima River demonstrated apparent pulses of cottonwood colonization (Figure 5). As with other plants, there is expected to be a 'lazy J' distribution across ages with many more young than old trees, and this was observed for the mature trees (>20 years old) with many established between 1960 and 1980 and fewer established in prior decades (Figure 5). In the early decades of the 1900s there were apparently two recruitment pulses, with the first in the late 1910s and the second in the mid-1930s (Figure 5). These were approximately coincidental with, or shortly after the second and third highest flood flows on record. Thus, through the early decades of the twentieth century and prior to about 1980, the black cottonwood population along the Yakima River did demonstrate a 'punctuated progressive population' structure that would reflect some progressive seedling establishment and clonal expansion through root suckering, superimposed on major episodes of recruitment, consistent with the 'flood pulse' concept (Bovee and Scott, 2002; Samuelson and Rood, 2004).

Quantitative analysis of hydrograph requirements for seedling recruitment

The quantitative analysis of the hydrograph requirements for cottonwood seedling recruitment incorporated five hydrograph characteristics and an overall recruitment score was summed to determine the likelihood of recruitment in a particular year (Figure 10, Tables IV and V). (1) First, moderate to major flood events were considered as

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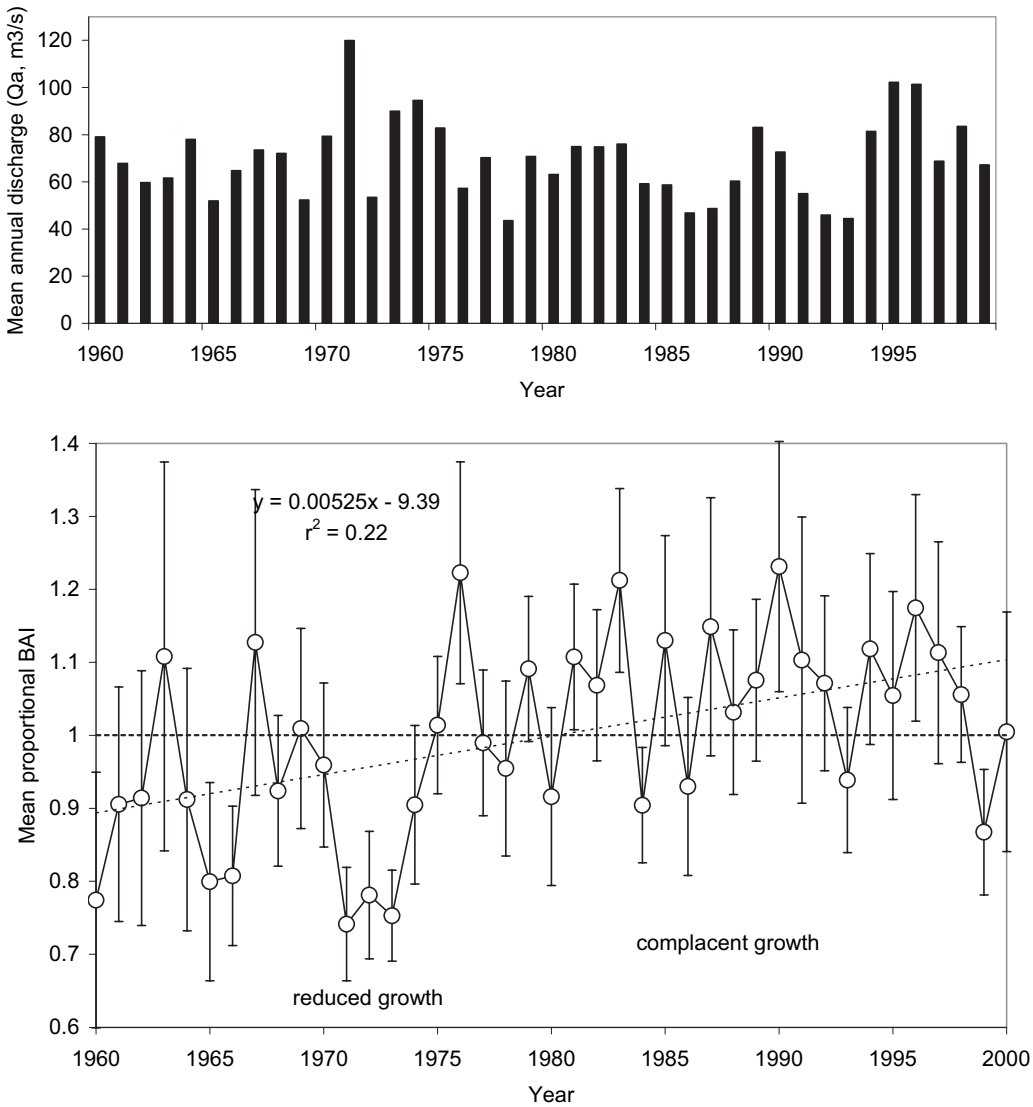

Figure 9. Comparative analyses of growth rates in basal diameter for black cottonwood in relation to mean annual discharge (1960–2000) along the Yakima River

essential triggering flows to provide physical disturbance that produced barren nursery sites suitable for cottonwood seedling colonization. Along the Yakima River these often occurred as abrupt floods associated with winter rains, and these would produce sediment scour and deposition but its timing would not be directly associated with seedling establishment. Colonization would follow if sufficient flow patterns occurred soon enough after the winter flood to avoid revegetation of the barren sites by other plants, including invasive species, an interval that extended for 2–3 years.

Within the opportunity interval following the disturbance flood, the next two essential hydrograph characteristics enable seedling establishment (Figure 10, Tables IV and V). Successful seedling establishment would subsequently require the second hydrograph parameter, (2) sufficient moderate flow during the period of seed dispersal to enable germination in the appropriate elevation of the establishment band (Mahoney and Rood, 1998). Subsequently, this should be followed by (3) appropriate stage recession to expose the appropriate, saturated barren sites and subsequent gradual recession to permit the small and vulnerable seedlings to maintain root contact with the

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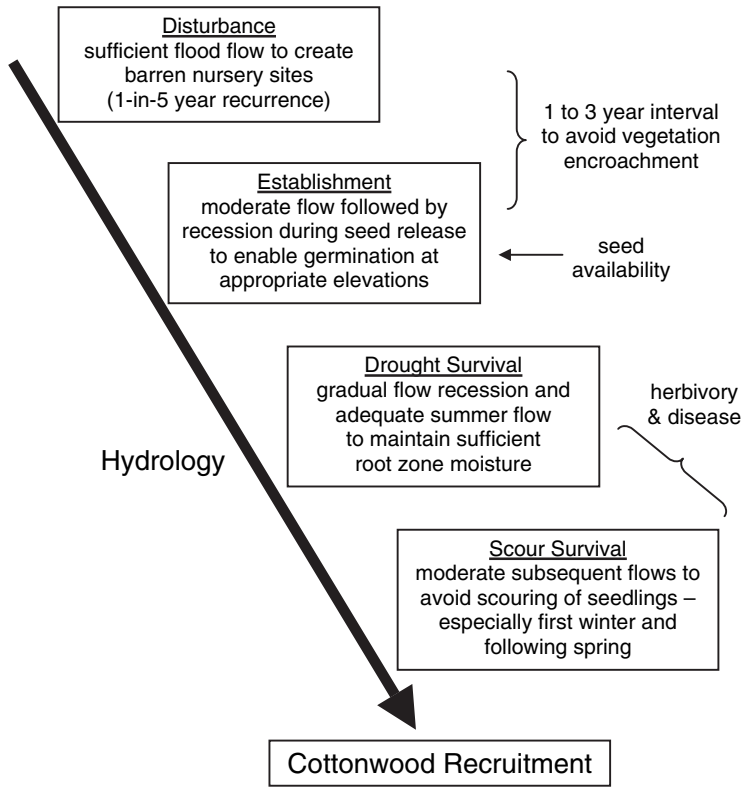

Figure 10. Criteria for the analysis of fluvial geomorphology and cottonwood recruitment

receding moist zone. Thus, 'establishment' considered the timing of a late spring high flow and the pattern of subsequent hydrograph recession.

After establishment, seedling survival was considered to require two independent aspects. In the establishment year, the small seedlings remain especially vulnerable to drought-induced mortality and thus, (4) sufficient late summer flow was regarded as essential (Figure 10 and Table IV). The other major cause of seedling mortality would be through (5) scour from high flows in the late summer or through the winter (Figure 10 and Table IV). This aspect had generally received minimal emphasis in prior hydrogemorphic analyses of cottonwood seedling recruitment but is probably very important along the Yakima River due to the prevalence of winter floods.

Following from the individual hydrograph components, an overall recruitment score was determined as the sum of the components with variable numerical ranges for those components providing the option for differential weighting (Tables IV and V). A challenge in our hydrograph analysis related to the prospect of lethal thresholds. A single lethal aspect would eliminate recruitment and thus despite the possibility that all other aspects were favourable, this would provide the critical aspect in that year. To accommodate this prospect we followed our integrative summation with a prediction of whether recruitment would occur.

With these hydrograph criteria and weightings, we considered the period of hydrologic record and present data relevant to the apparent pulses of cottonwood recruitment (Figure 5). The hydrograph analyses revealed a few years in the 1910s with some prospective colonization and 1919 was recognized as providing very favourable conditions in accordance with the hydrogeomophic model (Table V).

The second apparent recruitment pulse in the age structure record occurred in the mid 1930s and this outcome is somewhat consistent with the application of the hydrogeomorphic model (Table V). The hydrograph analysis suggested that 1935 would have enabled some cottonwood colonization.

The hydrograph analysis was less satisfactory for the 1960s and 1970s as the cottonwood age structure revealed considered contribution but the hydrograph analyses suggested generally unfavourable conditions for seedling

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Table IV. Rating Criteria for hydrological analysis of cottonwood recruitment. The criteria, based on a conceptual model (Figure 11) and Mahoney and Rood (1998), quantify the five components of the hydrograph that affect cottonwood recruitment. These criteria can be used to analyse annual sequences of streamflow data to determine the likelihood of recruitment in any particular year (see Table V)

Hydrograph component		Rating criteria	Weight
1. Magnitude of disturbance flow (Q_{max})	+++	>10 yr (822 m^3/s)	1
Return periods determined using Log	++	>5 yr (632 m^3/s)	0.66
Pearson Type III distribution	+	>3 yr (490 m^3/s)	0.33
Recruitment event occurred within two years of disturbance flow	−	<3 yr	0
2. Timing of spring peak flow (Q_{sp})	+	Q_{sp} from early May to mid June	1
Q_{sp} should occur during estimated period of seed release and be in sufficient amounts			
	−	Q_{sp} too early, too late or <0.6 m elevation	0
3. Stage recession rate	++	M ≤20	1
Daily stage declines calculated using 3-day moving averages	+	M = 20–30	0.5
	−	M >30	0
Declines classified as favorable (<5 cm/d), stressful (5–10 cm/d), or lethal (>10 cm/d) Weighted proportions used to calculate mortality coefficient M (M = [prop. of lethal days × 3 + prop. of stressful days]/3)			
4. Late summer flows	++	Q_A ≥8 m^3/s	1
Mean and minimum August flow (Q_A) for 1908–1914 determined upper and lower criteria respectively	+	Q_A = 3–8 m^3/s	0.5
	−	Q_A <3 m^3/s	0
5. Magnitude of post-recruitment scouring flow	++	$Q_{sc} < Q_{sp}$	4
Scouring flow (Q_{sc}) occurred within 2 years of recruitment event	+	$Q_{sc} \approx Q_{sp}$	2
Magnitude of Q_{sc} compared to spring peak flow (Q_{sp}) of recruitment year	−	$Q_{sc} > Q_{sp}$	0
Total score			8

establishment (data not presented). However, this historic interval involved extensive gravel extraction in the floodplain zones near the study sites and it is likely that this artificial, physical disturbance created extensive areas suitable for cottonwood seedling colonization. In addition, the mechanical excavation would have imposed some scarification, physical abrasion of shallow roots that would have promoted root suckering, the emergence of adventitious shoots from roots. While surface contours persisted from the gravel mining there are few records regarding the timing and pattern of excavations and subsequent recontouring, and thus a more detailed analysis is impossible. The observation of extensive colonization following gravel mining supports the importance of physical disturbance to create barren, nursery sites and the patterns of the trees around the former gravel pits also supports the elevational banding of cottonwood colonization and expansion.

DISCUSSION

Our study clearly shows that altered flow regimes along the Yakima River have negatively impacted the species composition and structure of riparian cottonwood forests. In particular, seedling recruitment along with sex ratios and the age-structure of riparian cottonwoods were significantly altered.

The Cle Elum, Union Gap and Wapato reaches were selected for study on the basis of their distinctive patterns of flow regulation. High flows along the Cle Elum reach are maintained near bank-full throughout the summer months.

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Table V. Cottonwood recruitment predictions based on hydrograph criteria analysis

Year	Disturbance	Establishment		Drought survival	Scour survival	Overall recruitment score (#/8)	Predicted recruitment
	1. Q_{max} (/+++)	2. Timing (/+)	3. Stage recession (/++)	4. Q_A (/++)	5. Q_{sc} (/++)		
1916	++	−	++	++	−	2.7	No
1917	++	+	+	++	−	3.2	No
1918	+++	+	−	++	−	3.0	No
1919	+++	+	++	+	++	7.5	Yes
1920	+	−	−	++	−	1.3	No
1921	+	+	+	++	−	2.8	No
1922	+++	+	−	++	+	5.0	Yes
1932	−	+	−	+	−	1.5	No
1933	−	+	++	++	−	3	No
1934	+++	−	+	+	−	2	No
1935	+++	+	++	+	−	3.5	Some
1936	+	+	+	+	−	2.3	No
1937	−	−	−	+	+	2.5	No
1958	+	+	+	++	−	2.8	No
1959	+	+	−	++	−	2.3	No
1960	++	+	+	++	−	3.2	No
1961	++	+	−	++	+	4.7	Yes
1962	−	−	−	++	−	1.0	No
1963	−	+	−	++	−	2.0	No
1964	−	+	++	++	−	3	No
1965	+	+	−	++	+	5	Yes
1966	+	+	−	++	−	3	No

In early September, flows are diminished to support spawning by fall Chinook salmon. A different regime occurs in the Union Gap reach where high flow regimes are maintained throughout the irrigation season (May to September). In contrast, flow regimes on the Wapato reach are extremely low throughout the summer and early fall. Collectively, these regulated flow regimes contrast sharply with the historic patterns of seasonal flow that occurred prior to the construction of headwater dams and diversions to irrigate crops and pastures within the Yakima Basin. Prior to dam construction and irrigation withdrawals, seasonal flows along the Yakima River actively supported the recruitment of cottonwood seedlings. High spring flows drove geomorphic processes (such as cut and fill alleviation) that create suitable recruitment sites and gradual stage declines following germination to permit the roots of seedlings to maintain contact with the receding moisture zone. There were also sufficient flows through hot, dry periods to promote seedling survival, and to provide seedlings and adults with a favourable water balance to withstand desiccation during winter months.

Although current flow patterns along selected study reaches did not affect the growth rates of mature trees, they did have a negative effect on the recruitment of cottonwood seedlings. These findings correspond to our understanding of the life history and ecology of cottonwoods (Braatne *et al*., 1996; Mahoney and Rood, 1998; Johnson, 2000; Cooper *et al*., 2003). High flows during the periods of seed dispersal (May–July) along the Cle Elum and Union Gap reaches completely inundate potential sites for seedling recruitment. During the same time period, low flows along the Wapato reach result in the germination of seedlings at low elevations near the base of riverbanks. After the irrigation season is over, higher flows along the Wapato reach scour and remove these young seedlings (a similar pattern is also apparent along the Naches River). As a result, there was no seedling recruitment

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observed in these study reaches. The extent of younger stands (<25–35 years old) was also extremely limited in all three reaches, and largely limited to clonal expansion. Riparian cottonwoods are thus dominated by an older age class that established prior to initiation of current flow regimes. If these altered flow patterns persist, cottonwood populations will become more fragmented and largely composed of decadent individuals with lower levels of genetic diversity.

Sex ratios of local populations shifted from a balanced ratio of 1:1 (male:female) near the confluence of the Yakima and Teanaway Rivers (Cle Elum Reach) to a highly skewed ratio of 7:1 along the Wapato Reach. This shift in sex ratio and lack of reproductively mature females significantly lowers the reproductive fitness of these cottonwood populations. This finding appears related to the habitat partitioning between sexes as observed for riparian box elder (Dawson and Ehleringer, 1993; Kolb *et al*., 1997) and arctic willows (Dawson and Bliss, 1987). In those studies, females were more common in resource-rich environments and males in resource-poor environments (particularly in relation to soil water deficits). High soil water deficits due to extensive irrigation withdrawals along the Wapato reach may account for the skewing of sex ratios toward males. These observations, combined with the absence of cottonwood seedlings, clearly show that current flow regimes have altered the reproductive potential of cottonwoods in the Wapato reach. This loss of reproductive potential significantly increases the risks for losing locally adapted genotypes.

Our studies further reveal that regulated flows have promoted the invasion of alluvial floodplains by exotic herbaceous and woody species such as St. John's wort, several species of knapweed, pepper-weed and thistle, silver and Norway maple, green ash, American and Chinese elm and European willow. Altered flow regimes also favour the vegetative propagation of reed canary grass, a highly invasive perennial grass. These invasive and exotic species have a life history strategy that allows them to more readily adapt to the regulated flow regimes of the Yakima Basin. These exotic species appear to have a distinct competitive advantage over black cottonwood and other native riparian shrubs. Basic fluvial geomorphic processes, such as cut and fill alluviation, have also been significantly altered by these regulated flows (Lorang *et al*., 2005). These fluvial processes are critical to the long-term viability of cottonwood forests along the Yakima River.

Although the results of our study show that there is a significant risk to the viability of cottonwood forests along the Yakima River, there has been extensive documentation of the recovery of cottonwoods in response to modified flow regimes along several regulated rivers in western North America (Rood *et al*., 1998, 2003b, 2005). Spring flow releases below dams to mimic spring flood events on regulated rivers have been tested and proven effective to promote native willow and cottonwood recruitment within the Saskatchewan River Basin in Alberta and the Truckee River in Nevada (Rood *et al*., 1998; Rood and Mahoney, 2000; Rood *et al*., 2003b, 2005). In these cases, higher water volumes available in 'high snow-pack years' were released from reservoirs in a manner that was compatible with the timing of seed dispersal and germination by willow and cottonwood seedlings. These flow management practices are increasingly accepted by resource managers and integrated with regional programmes to restore native fish populations (Rood *et al*., 2003b, 2005). The Yakima River Basin offers similar opportunities for modifying flows to sustain both riparian cottonwood forests and native salmonids.

ACKNOWLEDGEMENTS

This work was funded under Innovative Projects Program (Project No. 20034) of the Northwest Power Planning Council (NWPPC), Columbia Fish and Wildlife Authority (CBFWA) and Bonneville Power Authority (BPA). The authors thank Greg Allen, Alexis Hall, Cathy Metzler, and Mary Louise Polzin, for their efforts in river navigation, field data collection and laboratory and computer analyses. Bonneville Power Administration, Northwest Power Planning Council, Columbia Basin Fish and Wildlife Authority, University of Idaho and University of Lethbridge.

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OBITUARY

Jeffrey Braatne passed away peacefully in the company of family and friends in his home in Moscow, Idaho on October 14, 2006, following a valiant two-year fight with cancer. A cherished husband and loving father, Jeff was a friend, mentor and colleague to students and river scientists and managers throughout the Pacific Northwest region of the United States and Canada. As a research associate at the University of Washington, an environmental consultant out of Seattle, and an assistant professor of floodplain ecology in the Department of Fish and Wildlife Resources at the University of Idaho, Jeff brought enthusiasm, an expansive breadth of knowledge, and common sense to river research and management projects that often involved the splendid but challenged rivers of the Columbia Basin. Jeff will be greatly missed and as he slipped away we indicated, 'We'll meet you at the take-out'.

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