

Research paper

Floodplain forest succession reveals fluvial processes: A hydrogeomorphic model for temperate riparian woodlands



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ABSTRACT

River valley floodplains are physically-dynamic environments where fluvial processes determine habitat gradients for riparian vegetation. These zones support trees and shrubs whose life stages are adapted to specific habitat types and consequently forest composition and successional stage reflect the underlying hydrogeomorphic processes and history. In this study we investigated woodland vegetation composition, successional stage and habitat properties, and compared these with physically-based indicators of hydraulic processes. We thus sought to develop a hydrogeomorphic model to evaluate riparian woodland condition based on the spatial mosaic of successional phases of the floodplain forest. The study investigated free-flowing and dam-impacted reaches of the Kootenai and Flathead Rivers, in Idaho and Montana, USA and British Columbia, Canada. The analyses revealed strong correspondence between vegetation assessments and metrics of fluvial processes indicating morphodynamics (erosion and shear stress), inundation and depth to groundwater. The results indicated that common successional stages generally occupied similar hydraulic environments along the different river segments. Comparison of the spatial patterns between the free-flowing and regulated reaches revealed greater deviation from the natural condition for the braided channel segment than for the meandering segment. This demonstrates the utility of the hydrogeomorphic approach and suggests that riparian woodlands along braided channels could have lower resilience than those along meandering channels and might be more vulnerable to influences such as from river damming or climate change.

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1. Introduction

A number of recent studies have investigated how fluvial processes influence floodplain forest dynamics (Fierke and Kauffman, 2005; Latterell et al., 2006) and how hydrogeomorphic processes determine riparian vegetation patterns and successional trajectories (Auble et al., 1997; Robertson and Augspurger, 1999; Johnson, 2000). Prior research has often focused on the functioning of individual riparian ecosystem components but interdisciplinary research that combines hydrology, geomorphology and vegetation ecology is needed to understand and manage riparian landscapes

(Richards et al., 2002). Subsequently, Ward and Tockner (2001) and Ward et al. (2002) considered landscape features and hydraulic processes in the study of riparian ecosystems, and Gurnell et al. (2012) and Perona et al. (2009) considered the mutual relationships linking hydraulics, geomorphology and riparian vegetation. The inter-dependencies among these components produce different spatio-temporal patterns of fluvial forms and riparian vegetation, in response to climatic and hydrodynamic influences (Dykaar and Wigington, 2000; Willms et al., 2006; Corenblit et al., 2009).

Hydrodynamic and morphodynamic processes account for riparian vegetation establishment and removal (Mahoney and Rood, 1998; Bendix, 1999; Bendix and Hupp, 2000; Dixon and Turner, 2006; Asaeda and Rashid, 2012). Sediment deposition from floods creates nursery sites for riparian recruitment and successful

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establishment depends upon the subsequent moisture pattern. Conversely, flood events remove vegetation through erosive scour (Bendix, 1999; Bendix and Hupp, 2000; Asaeda and Rashid, 2012). River flows recharge alluvial groundwater, especially in semi-arid climates, thus avoiding drought-induced mortality (García-Arias et al., 2013a). However, extended inundation produces root anoxia and mortality (Glenz et al., 2006). Ultimately, vegetation colonization, succession and mortality are the result of interrelated and somewhat antagonistic disturbance and resistance gradients (Egger et al., 2013). The interplay between these opposing drivers and their co-evolutionary development was defined by Corenblit et al. (2007) as the ‘fluvial biogeomorphic succession’ concept of riparian landforms and vegetation. This concept explains riparian succession as a bidirectional path with sequential phases dependent upon the hydrogeomorphic and ecological processes. A similar concept was formulated by Hauer and Smith (1998) who developed a “hydrogeomorphologic (HGM) approach” to classify riparian wetlands according to the fluvial processes influencing their formation.

Extending from these concepts, we hypothesized that vegetation characteristics including woodland age and developmental stage would provide observable indicators of fluvial processes and history. To test this, we collected field data to characterize vegetation occurrence and successional stage, and the associated fluvial processes, and to compare these with hydraulic model-based indicators of the underlying physical influences.

To provide the essential experimental variation, we investigated two different river channel forms and reaches along regulated versus free-flowing rivers.

2. Methods

2.1. Study sites

Our study included six river reaches in Montana and Idaho, USA and British Columbia, Canada (Fig. 1; Table 1). Downstream of the large Libby Dam and Kootenai Reservoir, the lower Kootenai River

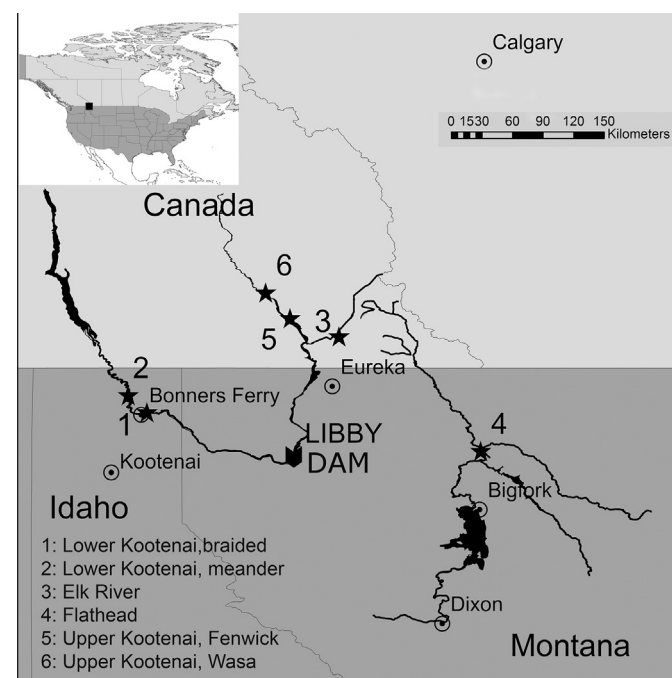


Fig. 1. Study sites situated in Idaho, Montana and British Columbia.

provided a braided reach upstream of Bonners Ferry (R1) and a meandering reach downstream (R2). Site R3 was located along the Elk River that flows into Kootenai Reservoir and upstream of that reservoir, two sites were investigated along the upper Kootenai River, near Fenwick (R5) and further upstream near Wasa (R6). To provide an additional braided reach, a site was investigated along the North Fork of the Flathead River (R4). Study sites R1 and R2 were downstream of the Libby Dam while the other four study sites are along unregulated reaches. This study design allowed us to apply the hydrogeomorphic model to the six reaches while assessing two important factors, with braided versus meandering channel types, and regulated versus free-flowing reaches (Table 1).

2.2. Field data: physical habitat scales and vegetation

Study sites were cover-type mapped based on aerial photographs (1:5000; August 2006) and field visits, and divided into apparently homogeneous polygons related to species composition, plant community and vegetation structure. In August 2007, 76 plots were sampled across the study sites with selection as described in Mueller-Dombois and Ellenberg (1974), to include the full range of environmental and successional conditions. The following variables were recorded: plant species and community type, habitat type, succession phase, percent cover of tree species, and diameter at breast height (DBH) of the largest individuals of target trees. For selected trees, increment cores were removed for ring counts to estimate age, and heights were determined (Nikon Laser 550 AS). Target tree species included the deciduous black cottonwood (*Populus trichocarpa*), plains cottonwood (*Populus deltoides*), and quaking aspen (*Populus tremuloides*) and the coniferous white spruce (*Picea glauca*) and western red cedar (*Thuja plicata*). Local field data were compared to vegetation surveys along these rivers by Hansen et al. (1995), Jamieson and Braatne (2001) and Polzin and Rood (2000).

Three physical habitat scales assessed morphodynamics (MDs), inundation duration (IDs), and depth to groundwater (DGWs) with categories of 1–5, following pre-determined criteria (Table 2). Scores of 1 indicate low morphodynamic activity, short inundation duration, and deep groundwater, while 5 indicates high morphodynamics, frequent inundation and shallow groundwater.

Field plot data were coordinated with the polygons from aerial photos. Vegetation types within each polygon were assigned to succession phases and grouped into succession stages. Succession phases include alternate vegetative states dependent on site-specific trajectories. For example, pioneer vegetation may transition into a community dominated by herbaceous weedy species (herb phase), or one dominated by shrubs (shrub phase). Both of these communities were grouped into the same successional stage (i.e. Transition stage I). The classification of succession types was derived from Naiman et al. (2005) and especially Egger et al. (2013), and included natural primary (^{PS}) and secondary successional (^{SS}) pathways. Successional phases included: initial phase (IP), pioneer (PP), herb (HP), shrub (SP^{PS}, SP^{SS}), early successional woodland (ESW^{PS}, ESW^{SS}), established forest (EFP^{PS}, EFP^{SS}), and mature (MS) phases. Non-natural vegetation types include grassland, farmland, and infrastructure.

2.3. Age analyses of successional phases

Increment cores of predominant tree species were used to determine the relationships between DBH and tree ages (Table 3). This allowed estimation of the oldest tree in each polygon and box plots were then used to compare maximum ages across different successional phases, and determine durations for each phase.

Table 1
Characteristics of the six riparian study sites.

Designation	R1	R2	R3	R4	R5	R6
River	Lower Kootenai R., Braided	Lower Kootenai R., Meander	Elk River	North Fork Flathead River	Upper Kootenay R., Fenwick	Upper Kootenay R., Wasa
Channel Form	Braided	Meandering	Braided	Braided	Meandering	Meandering
Flow Condition	Regulated	Regulated	Unregulated	Unregulated	Unregulated	Unregulated
Jurisdiction	Idaho	Idaho	BC	Montana	BC	BC
Latitude	48°42'0"N	48°50'33"N	49°21'46"N	48°41'5"N	49°28'27"N	49°46'50"N
Longitude	116°15'38"W	116°24'2"W	115°0'33"W	114°11'25"W	115°30'5"W	115°45'36"W
Altitude (m asl)	541	536	946	1040	751	776
Study site area (ha)	480.6	544.4	58.4	134.2	69.6	169.4
Study site length (m)	3000	2500	800	1400	1200	2000
Surface sediments	Gravel	Sand	Cobble, Gravel	Cobble, Gravel	Sand	Sand
Mean discharge (Q, m ³ /s)	370	370	47.0	84.7	205	173
Mean maximum discharge (Q ₁ , m ³ /s)	495	495	279	580	1193	1006
10-year peak discharge (Q ₁₀ , m ³ /s)	1370	1370	451	906	1607	1379
Other	Near KTOI ^a river mitigation projects	Near Nature Conservancy Ball Creek Ranch Preserve	Site E3, Polzin and Rood (2000, 2006)	Boundary of Glacier National Park, Montana	Site K3, Polzin and Rood (2000, 2006)	

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Table 2
Field recorded, expert-based physical habitat scales.

Scales	Morphodynamic (MDs; shear stress)	Flood inundation duration (IDs)	Depth to ground-water (DGWs)
5	Very high: swift flows several times yearly, extensive erosion and sedimentation, sand or gravel with no organic horizon or litter layer; non-vegetated surfaces, may be pioneer vegetation	Very high: repeatedly flooded annually; frequently with flooding indicators of woody debris, sparse vegetation or sporadic flood-tolerant plants	Very shallow: ± 0.1 m
4	High: annual moderate erosion and sedimentation, sand or gravel with no organic horizon and a thin litter layer, pioneer vegetation with reeds and flow-resistant woody plants, often with damage including sheared branches and a braided trunks	High: flooded once or a few times annually by discharges from Q ₁ to bank-full flow, some flooding indicators and flood-tolerant plant species	Shallow 0.1–0.5 m
3	Moderate: morphodynamic processes generally limited to slight sedimentation of sand and local erosion; weak organic layer and distinct litter layer; dense reed or intermediate flow-resistant woody plants	Moderate: stage range from bank-full to medium floods, flooding indicators only after major floods; some moderately flood-sensitive species, mostly perennials, trees and shrubs	Intermediate 0.5–1.5 m
2	Low: low level morphodynamic processes with weak intensity, limited local erosion and sedimentation of fine sand and silt; distinct organic and litter layer; young or intermediate deciduous forest	Low: only inundated with moderate to major floods, flooding plays a minor role, low effect on tree layer, understory with maturity indicator species	Deep 1.5–3 m
1	Very low: morphodynamic processes are confined to rare major floods; only local sedimentation of fine material; distinct organic and litter layer; mature hardwood forest or mixed deciduous-coniferous forest	Very low: achieved only by rare floods, flooding plays minimal role; vegetation approaches the surrounding upland vegetation	Very deep > 3 m

2.4. Hydraulic modeling

Hydraulic modeling has been used in ecological studies to evaluate impact of hydrological alterations (e.g., Brown and Pasternack, 2009; Friedman and Auble, 1999). We used MIKE-FLOOD software to simulate physical processes using the contemporary floodplain topography for R1 (braided) and R2 (meander)

Table 3
Growth functions of dominant tree species (y – diameter at breast height (DBH, cm) and x – age in years).

Species	Site(s)	Growth function	N	r ²
<i>Populus trichocarpa</i>				
R1, R2		$y = 0.795x + 10.00$	58	0.82
R3		$y = 0.0064x^2 + 0.280x + 13.98$	33	0.91
R4		$y = 1.01x + 8.42$	12	0.80
R5, R6		$y = 1.47x + 11.11$	44	0.75
<i>Populus deltoides</i> (all sites)		$y = 0.703x + 6.13$	6	0.89
<i>Populus tremuloides</i> (all sites)		$y = 1.98x + 9.14$	32	0.85
<i>Picea glauca</i> (all sites)		$y = 1.33x + 20.19$	40	0.85
<i>Thuja plicata</i> (all sites)		$y = 15.09x^{0.574}$	13	0.89

reaches of the lower Kootenai River (see, Benjankar et al., 2011). One of the key features of MIKEFLOOD is, it integrates the one-dimensional (1D) MIKE11 for the river, and the two-dimensional (2D) MIKE21 for the floodplain into a single, dynamically coupled modeling system by lateral links, which allows reciprocal linkage through which flood waters can move onto the floodplain and then back into the river (DHI, 2004).

The indicator of morphodynamics was chosen as the maximum shear stress (N/m²) of the year (Friedman and Auble, 1999; Benjankar et al., 2011; Egger et al., 2012). For inundation duration (days of submersion, April through September) the flood duration was calculated (Glenz et al., 2008), and groundwater depth was the position above the mean water elevation (García-Arias et al., 2013b; Politti et al., 2014). Frequency analysis was performed for long-term (1973–2003) measured discharges at the USGS Leonia gage. Each year was classified according to the recurrence interval: Q₁, Q₂, Q₅, Q₁₀, Q₂₅ or Q₅₀₊.

2.5. Hydraulic model-based habitat indices

Based on the maximum annual flow for the post-Libby Dam

interval from 1977 to 2006, we assigned the corresponding return intervals. Discharge data were linked to the spatial positions for sites R1 and R2 using shear stress and flood duration from the hydraulic model of the discharges of all return intervals. Based on this, we calculated the Time and Intensity Weighted Index (TIWI) of Morphodynamic Disturbance (MDi) and flood Inundation Duration (IDi).

The TIWI reflects the magnitude and frequency in a single metric. It is calculated on a pixel-by-pixel basis, providing a value for each cell of each study site. The method calculates MDi as the sum of the ratios between shear stress τ (N/m^2) and year ordinal number. The ratios-sum is then divided by the sum of the year ordinals reciprocal (Equation (1)).

$$\text{MDi} = \frac{\sum \left\{ \frac{\tau_1}{1} + \frac{\tau_2}{2} + \frac{\tau_3}{3} + \dots + \frac{\tau_{(T-1)}}{(T-1)} + \frac{\tau_T}{T} \right\}}{\sum \left\{ \frac{1}{1} + \frac{1}{2} + \frac{1}{3} + \dots + \frac{1}{(T-1)} + \frac{1}{T} \right\}} \quad (1)$$

IDi is computed (Equation (2)) similarly to MDi but the numerator is yield by the inundation days (y), instead of τ . The number of inundation days is counted within the April–September interval, which corresponds to the typical growth period.

$$\text{IDi} = \frac{\sum \left\{ \frac{y_1}{1} + \frac{y_2}{2} + \frac{y_3}{3} + \dots + \frac{y_{(T-1)}}{(T-1)} + \frac{y_T}{T} \right\}}{\sum \left\{ \frac{1}{1} + \frac{1}{2} + \frac{1}{3} + \dots + \frac{1}{(T-1)} + \frac{1}{T} \right\}} \quad (2)$$

MDi and IDi were calculated for the interval prior to the field studies, beginning with the recent year 2006 (year 1) and extending back to 1977 (year 31).

An additional link to the hydraulic condition was provided by the Ground Water Depth Index (GWDi). This was calculated as the distance between the surface elevation and the mean water level simulated for 2006. Water surface level was considered an indicator of groundwater level, as previously applied (Benjankar et al., 2011; Politti et al., 2014).

2.6. GIS analysis

The field data were digitized in vector format using ArcGIS 9.2™ (one shape-file for each site), and the hydrodynamic model results were stored in raster format with cell sizes of $10 \text{ m} \times 10 \text{ m}$. To combine the different data sets (vector and raster), an artificial point sampling was performed with a regular network with one point element for each 10 m. The network points were intersected with the shape-file and the rasters by applying Geospatial Modeling Environment (Beyer 2012). The resulting data set for each point location included the sampled field data, shear stress, inundation duration and depth to groundwater for different flood recurrence intervals. Both the field data in the vector format and the artificially sampled points were exported to Excel to calculate the areal proportions of the phases and habitat classes for further statistical analysis.

2.7. Statistical analysis

Statistical analyses were performed in IBM SPSS Statistics v.20 considering only those polygons with natural successional phases. Artificial cover types including grassland pasture, farmland and infrastructure were excluded. The aims of the analyses were: (1) to assess the consistency of the field habitat classes and physical hydraulic modeling measures, and (2) to investigate correspondence between the habitat classes and the succession phases, thus

allowing characterization of the vegetation succession based on the underlying hydro-morphological processes. These analyses extend from an analysis where we investigated relationships between the succession phases at sites R1 and R2 and the hydraulic model-based habitat indices MDi and IDi. Correlations between the field-determined physical habitat scales and the hydraulic model-based habitat indices were tested with Spearman correlation for the two lower Kootenai reaches, where the hydraulic models were developed.

Succession phases at each study site were investigated by testing their relationships with the field-based physical habitat scales by means of χ^2 -test, Cramer-V contingency coefficients, and corrected standardized residual analysis (prediction configural frequency analysis). In addition, differences in MDs, IDs, and DGWs among succession phases and study sites were tested with analyses of variance (ANOVAs). Measures of effect size (R^2/ETA^2) were examined to determine the relative influence of the two factors and their interaction term.

3. Results

3.1. Spatial distribution of plant communities and succession phases

The spatial mosaic maps revealed differences in the distribution of succession phases and vegetation communities between the braided and meandering channel types (Fig. 2). Differences were also observed between the dam-regulated, agriculturally-impacted reaches of the lower Kootenai River and the free-flowing, relatively pristine sites along the other rivers (Supplemental Table S1). Along the lower Kootenai braided reach (R1), the natural vegetation was present only along the active channel, while the floodplain was largely subjected to artificial land use. Despite flow regulation, there were still some areas demonstrating colonization stages (initial and pioneer phases) but with much lower extent than along the free-flowing braided reaches R3 and R4. Those free-flowing reaches exhibited more diverse river channel structure with side and back-channels and islands, and a more diverse arrangement of successional stages.

Land use intensity was also high along the lower Kootenai meander reach (R2) but there were remnants of natural vegetation patterns. In particular, arcuate bands of woodland and saplings followed the line of floodplain accretion on the convex meander lobe, paralleling the river axis (Fig. 2; Everitt, 1968). This pattern was also recognizable on the upper Kootenai sites R5 and R6, although these sites were generally covered by secondary succession phases.

3.2. Age analysis of succession phases

As communities transition from earlier to later stages of primary succession (PP, SP^{PS}, EF^{PS}, MP), the ages of *Populus trichocarpa* increased (Fig. 3). *Picea glauca* was found in fewer successional phases, and the median age showed an increase from the early successional woodland (ESW^{PS}) to the established forest phase (EFP^{PS}). Secondary succession stages displayed less consistency in the progression of tree ages.

Ages of the largest trees in each plot based on growth functions (Table 3) allowed for the estimation of polygon surface ages and determination of the temporal changes in forest types. For the first two decades, sites were dominated by *Populus* (Fig. 4). Spruce (*Picea*) was established after about 25 years and cedar (*Thuja*) was detected after around 50 years. After about a century, tree cover decreased, with *Picea* abruptly diminishing, *Populus* gradually decreasing, and *Thuja* persisting.

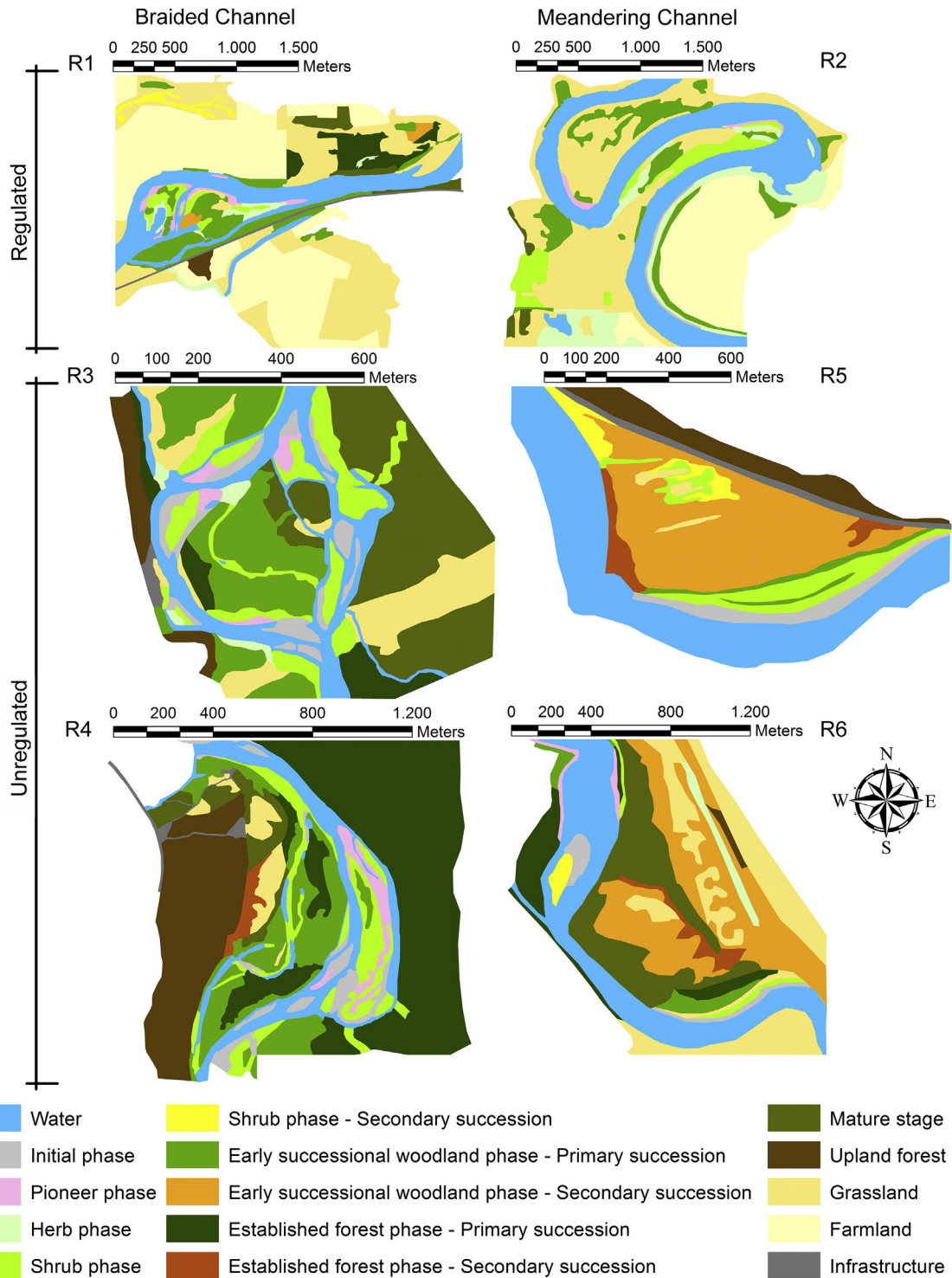


Fig. 2. Mosaic maps of the primary and secondary succession phases (PS, SS) along the six study reaches: R1, R3, and R4 show braided sections along the lower Kootenai, Elk, and Flathead rivers respectively, and R2, R5, and R6 show meandering sections along the lower Kootenai River (R2), and upper Kootenai River (R5 and R6).

Populus and *Picea* increased in height with age, but the height-age relationships differed (Fig. 5). The heights of *Populus* increased rapidly to maxima after 40–60 years. Some of the shorter *Picea* juveniles sampled at around one meter tall were already 15–20 years old, thus displaying slower initial growth. After about 40 years, when *Populus* heights had peaked, *Picea* growth accelerated until the final heights of the two trees were similar.

3.3. Area proportion and consistency of physical habitat scales

There were fairly consistent patterns between the physical habitat scales MDs and IDs, and these varied with river regulation. The free-flowing sites (R3 – R6) had greater proportions of site area with very high (class 5) and high (class 4) morphodynamics and inundation duration, with proportions mostly around 10–20% (Fig. 6).

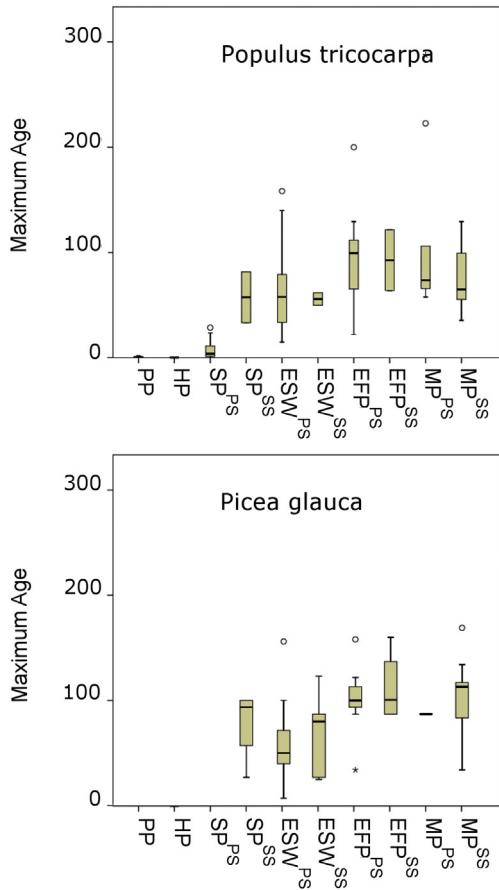


Fig. 3. Box-plots relating succession phases and ages of *Populus trichocarpa* and *Picea glauca*. Hollow points represent outliers and asterisks represent extremes. Abbreviations are in accordance with Fig. 2.

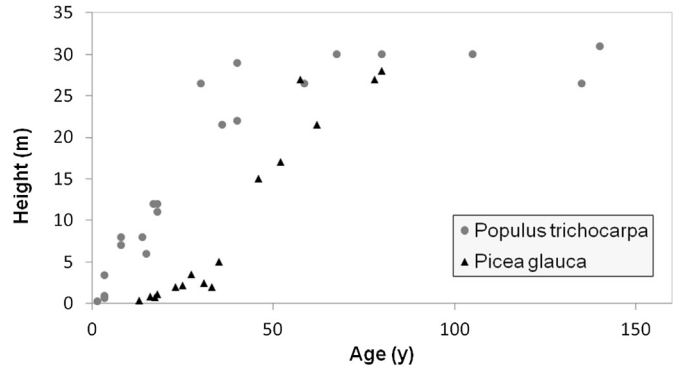


Fig. 5. Height versus age of riparian *Populus trichocarpa* and *Picea glauca*.

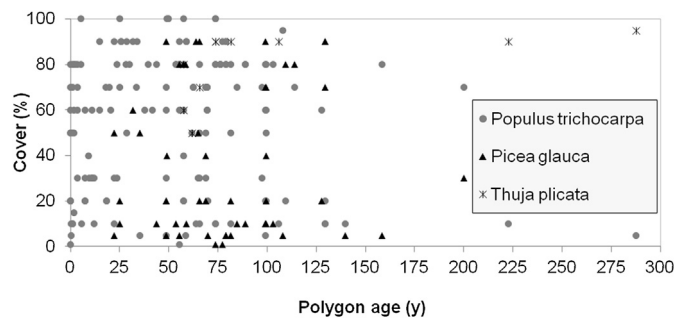


Fig. 4. Relationship between tree species cover and polygon age.

Along the flow regulated reaches, only 1% (R1, braided) and 2–5% (R2, meander) of the sites were in MD class 4 and 5. IDs also showed differences between regulated and free-flowing reaches with about 90% or more of each site R1 and R2 having very low inundation duration (class 1), whereas no site area was in class 1 along the free-flowing reaches. Differences between free-flowing and regulated reaches were less clear for the depth to groundwater scale (DGWs). There appeared to be an interaction between flow regulation and channel type and for the braided reaches, R1 generally had lower DGWs classifications than R3 and R4, but for the meander reaches, R2 was more similar to R5 and R6 (Fig. 6).

The model-based indices (TIWI) showed high levels of correlation with the habitat scales at both study sites (Table 4), thus

confirming the consistency of the habitat classes.

3.4. Characterization of succession phases by fluvial processes

According to cross tabulation analysis and Cramer-V correlation coefficients, MDs, IDs, and DGWs strongly corresponded with the succession phases at each study site (Table 5). The early colonization stage (initial and pioneer phases) corresponded with very high and high categories of the morphodynamic (MDs) and flood inundation scales (IDs). In general, values for the young transition stage (herb and shrub phases) were scattered around the moderate category, and the older transition stage (early successional woodland and established forest phases) corresponded with low and very low categories (Table 6). Regarding depth to groundwater table (DGWs), young succession stages corresponded with shallow groundwater and older stages had increased depths (Table 7).

The ANOVAs showed that differences among classes for each of the physical habitat scales were associated with the succession phases, study sites, and the interaction between these two factors. Succession phases accounted for much more variation than study sites, and consideration of the interaction term increased the model correspondence (Table 8), indicating different successional patterns among the study sites.

4. Discussion

4.1. Phytosociological progression

Riparian vegetation succession starts with the colonization stage on barren alluvial bars with sands at meander sites (R2, R5, R6), or gravels and cobble at braided channel sites (R1, R3, R4). Subsequently, the distribution of tree ages indicates early to late succession phases and the duration of the succession phases. At the initial phase, plants are sparse although seedlings or ruderal annuals may establish temporarily. The groundwater table is shallow and the area is characterized by frequent disturbance (Table 7). Primary succession commences when seedlings especially of the black cottonwood (*Populus trichocarpa*) colonize the barren gravel and sand bars, or occasionally expand through clonal suckering. The physical habitat of the pioneer phase plays a key ecological role for the long-term development of these temperate riparian woodlands. The dominant native trees and shrubs, including willows and cottonwoods, depend on the specific establishment conditions characterized by open locations due to frequent and high disturbance and a moist seed bed. These pioneer species do not establish at shaded locations within the floodplain forest (Polzin and Rood, 2006; Mahoney and Rood, 1998).

During the following years the vegetation cover increases due to

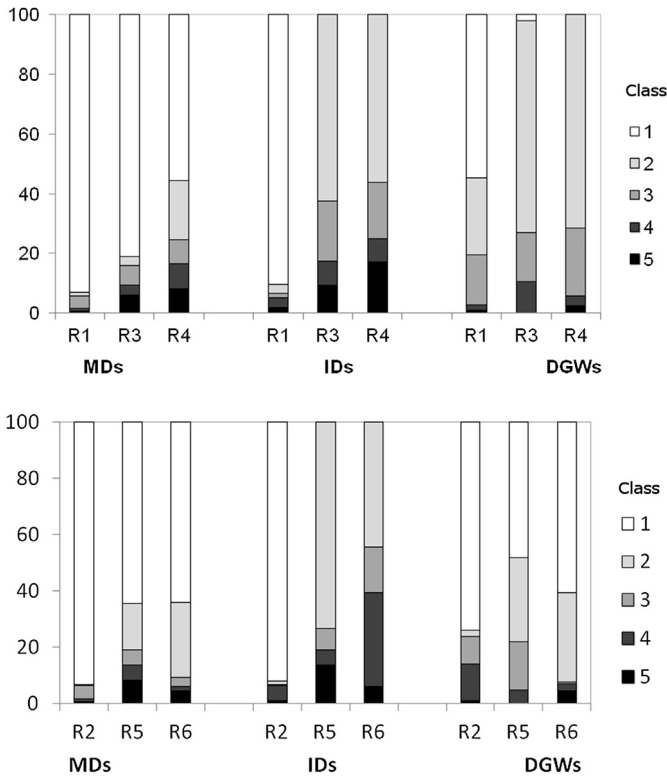


Fig. 6. Proportional area in each class of the morphodynamic (MDs), inundation duration (IDs), and depth to groundwater (DGWs) scales at braided sites (R1, R3, R4; top) compared to meander sites (R2, R5, R6; bottom).

Table 4
Results of Spearman correlation of the expert-based habitat scales MDs, IDs, DGWs and the hydraulic model-based habitat indices MDi, IDi, GWDi for study sites R1 and R2 along the lower Kootenai River.

	R1	R2
	Spearman correlation	
MDi & MDs	0.789	0.705
IDi & IDs	0.732	0.670
DGWi & DGWs	-0.704	-0.641

All correlation are significant ($p < 0.01$).

Table 5
Strength of contingency (Cramer-V) between the succession phases and the expert based habitat scales MDs, IDs, DGWs of the study sites R1 to R6.

	R1	R2	R3	R4	R5	R6
MDs	0.711	0.765	0.713	0.761	0.765	0.866
IDs	0.594	0.642	0.737	0.703	0.575	0.917
DGWs	0.579	0.684	0.690	0.653	0.855	0.768

Note: all crosstabs (MDsc * succession phase, IDsc * succession phase, DGWsc * succession phase) are statistically significant for all study sites ($p < 0.01$).

vigorous growth of the transition or consolidation stage (Naiman et al., 2005). In the first transition phase, short-lived herbaceous species with a ruderal or competitive strategy like the sedges and reeds can be dominant, covering more than 30% of the patch and producing the herb phase. On some study sites the invasive or naturalized reed canary grass (*Phalaris arundinacea*) formed dense, monotypic mats which impede further succession to the forest woodland. This reed has proliferated along the flow-stabilized lower Kootenai River and especially at silted backwaters, former side channels and wetlands (Egger et al., 2013). Under certain

conditions, the shrub phase can directly follow the pioneer phase to provide the woodland series (Egger et al., 2013). Succession to the cottonwood shrub community can take 5–15 years after a pioneer phase, depending on the disturbance intensity. Replacing shrubs as the dominant life form, fast-growing cottonwood trees are typically dominant for early successional woodlands (also called the stem exclusion phase, Naiman et al., 2005). Within the first 20–30 years, they build monodominant woodlands (Fig. 4) and at about 30–50 years they reach their maximum height of about 30 m (Fig. 5).

Under the cottonwood canopies, white spruce (*Picea glauca*) seedlings arise and these grow up to reach the cottonwood crown by 60–80 years Fig. 7. Due to shading, the spruce grow only a few meters in the first decades (Fig. 5), as they are repressed in the understory. After 40–60 years, the aging cottonwoods display branch and crown die-back, and within these gaps the spruce receive more light and grow more rapidly (Fig. 5). This transition phase from dominant cottonwood forest to a mixed forest of cottonwoods and conifers (mainly white spruce, Fig. 7) is referred to as the established forest phase and has previously been described as the understory initiation phase (Nanson and Beach, 1977; Naiman et al., 2005).

Within the next half-century, spruce replaces cottonwood providing the transition from mixed to coniferous riparian forest. Subsequently a second conifer, western red cedar (*Thuja plicata*), progressively replaces spruce after 150–200 years (Fig. 4). Occasionally, very old cottonwoods survive up to 300 years (R3, Fig. 4) and longer (Rood and Polzin, 2003). However, succession to the climax cedar stand is naturally rare since either progressive bank erosion with river channel migration, or more abrupt channel change with major flooding, resets the sequence and reestablishes barren alluvial bars. A simplified schematic outlining floodplain forest succession along these rivers in central Rocky Mountains is provided in Fig. 8. Observation of the morphological traits of the individual patches, together with the increment core analyses, led to the approximate time ranges (years) spanned by each succession phase (Fig. 8, Table 8).

If the primary succession path is interrupted by disturbances such fire or tree harvesting that do not completely remove vegetation and organic soil but do reset vegetation to the herb phase, then succession switches to a secondary successional path. At the Upper Kootenai sites (R5, R6) forest fires that occurred in the 1930s (Jamieson and Braatne, 2001) destroyed nearly all trees older than 75 years and the secondary early successional woodlands (ESW^{SS}) following fire were dominated by quaking aspen (*P. tremuloides*) (Fig. 2, Table S1). In the case of the lower Kootenai sites (R1, R2), stands older than 100 years have generally been harvested and the zones converted into agricultural pastures and farmland.

4.2. Different river channel types

The hydraulic-based habitat indices showed substantial differences between the two river channel types (braided and meander) for the succession phases (Fig. 6). With successional progression at the two lower Kootenai sites, MDi (shear stress) and IDi (inundation duration) decreased and GWDi (depth to the groundwater table) increased. However, mean values for the indices differed across the succession phases between the reaches. Shear stress was approximately five times higher and flood inundation durations were double at the braided site R1 compared to the meander site R2. Further, depth to groundwater table was considerably lower at R1 than R2 for common phases. The shear stress (MDi) values for both river types were more consistent (ETA^2 0.484/0.541), while flood inundation (IDi) (ETA^2 0.436/0.351), and depth to the groundwater table (GWDi) were more variable (ETA^2 0.385/0.447). This suggests that succession phases might be better correlated with the

Table 6
Frequency (%) and significance level of the expert based habitat scales MDs, IDs, DGWs versus succession phases of all study sites R1 to R6.

	MDs						IDs						DGWs					
	VL	L	M	H	VH	total	VL	L	M	H	VH	total	VD	D	I	S	VS	total
R1																		
IP						0						0		SC				0
PP				30	70	100			6	94	100			5	35	60	100	
HP			9	91		100			6	94	100			97		3	100	
SP			98	2		100			91	9	100			98	2		100	
ESW	79	10	11			100	76	3	10	11	100	75	4	20	1		100	
EFP	100					100	100				100	100					100	
MP	100					100	100				100	100					100	
R2																		
IP						100						100						100
PP				100		100			68	32	100		32	68			100	
HP	17	7	69	7		100	9	8	7	76	100	7	15	59	19		100	
SP			100			100				100	100			100			100	
ESW	100					100	93	7			100	93	7				100	
EFP						0					0						0	
MP	100					100	100				100	100					100	
R3																		
IP						100						100						100
PP				77	23	100						100		17	46	37		100
HP	20	70		10		100			53	37	10	100		21	79			100
SP	30	14	44	12		100		7	28	53	12	100		8	87	5		100
ESW	99	1				100		55	45			100	1	79	6	14		100
EFP	100					100		100				100	19	81				100
MP	100					100		100				100		100				100
R4																		
IP						100						100		3	25	25	47	100
PP						100						100			100			100
HP						0						0						0
SP		3	17	80		100		2	11	87	100			82	18		100	
ESW	7	58	34	1		100		7	58	34	1	100		46	54			100
EFP	85	15				100		85	15			100		100				100
MP	87	13				100		100				100		100				100
R5																		
IP						100						100			41	59		100
PP				100		100						100			100			100
HP						0						0						0
SP	0	18	37	45		100		18	37	45	100			100			100	
ESW	74		26			100		74	26		100		100				100	
EFP						0						0						0
MP						0						0						0
R6																		
IP						100						100				46	54	100
PP						100						100				80	20	100
HP	100					100				100		100						100
SP				100		100						100		68	32			100
ESW		98	2			100			29	71		100	69	31				100
EFP		96	4			100			96	4		100	22	78				100
MP	100					100		94	6			100	100					100

Note: grey marked cells: frequencies statistical significant minimum $\alpha = 0.01$ (residual analysis)

observable effects of fluvial processes (classes in Table 2) rather than the hydraulic metrics. The differences especially for MDi and IDi probably reflect differences in physical conditions between braided and meandering reaches and this would be worthy of further study.

4.3. Effects of damming and flow regulation

The greatest impact from the implementation and operation of Libby Dam has been the attenuation of morphodynamics and flooding impacts, as revealed by the physical habitat variables (Fig. 6; Polzin and Rood, 2000 Benjankar et al., 2012). At the

Table 7
Statistical influence of the expert based habitat scales MDs, IDs, GWDs results of the variance analysis ANOVA (R^2/η^2).

Model	MDs	IDs	GWDs
Succession phase	0.789	0.647	0.612
Study Site	0.020	0.099	0.113
Succession, Study Site & Interaction	0.893	0.854	0.823

Note: all effects are significant ($p < 0.01$).

regulated sites along the lower Kootenai, over 90% of the zones were categorized as having very low shear stress and inundation duration (scale values of 1). In contrast, at the unregulated sites, higher areal proportions were classified as having moderate to very high MD and ID values. Despite similar river flow changes, the

Table 8
Time spans (average) of succession phases and stages.

Succession phases	Age (years)
Colonization stage (Open bar)	
Initial phase	0–1
Pioneer phase	1–3
Transition stage I – Herb and shrub phases	
Herb phase (Reed)	3–5
Shrub phase (Willow/Cottonwood shrub)	3–15
Transition stage II – Early successional woodland	
Primary succession (Cottonwood forest)	15–60
Secondary succession (Aspen forest)	25–60
Transition stage III – Established forest	
Primary succession (Coniferous-cottonwood forest)	60–150
Secondary succession (Coniferous-aspen forest)	60–150
Mature stage	>150



Fig. 7. (Top) An overview of site R5, the upper Kootenay River, with the successional chronosequence from: A – barren sand, B – sandbar willow, C – *Populus trichocarpa*, D – *P. tremuloides* with some *Picea glauca*, to E – the upland coniferous forest. (Bottom) The transition from *Populus trichocarpa* to *Picea glauca* as revealed in an oblique view along the Elk River near R3 in winter when the cottonwoods were leafless.

effect on the vegetation mosaic differed between the channel types. Along the braided reach (R1), the young stages (colonization and young transitional) were less common than in the free flowing sites R3 and R4 (Table S1 in Supplementary Material). Conversely, in the meandering reach (R2), only the colonization stage was reduced, while the other stages were comparable to the free-flowing meandering reaches R5 and R6.

These early successional stages require open and barren plots, which are primarily created during large floods. However, the development of such plots differs between channel types. These are formed by deposition of bank-eroded sediments but there is limited longitudinal transport in braided systems, versus greater downstream transport along meandering systems (Brotherton, 1979). Conversely, the bank and bar sediments tend to be coarser gravels and cobbles in braided reaches than in meandering reaches where more sediments are often finer-grained sands and silt (Church, 2002; Gurnell et al., 2009). Ultimately, our results suggest that the changes in successional phases along the braided reach were more sensitive to flow regulation than along the meandering reach. Thus, the alterations from river damming were apparently within the resilience capacity of the meandering reach system. This

conclusion could have important management implications because it suggests that braided reaches would be more impacted by damming and flow regulation, and would thus require more attention to sustain their ecological functioning.

Relative to channel form and geomorphic context, our model considered hydraulic factors but river damming also dramatically alters sediment fluxes (Kondolf, 1997). Our field site assessments did consider substrate sediments and for future improvement the physical model component could be expanded to incorporate sediment availability and sorting, and the influence on vegetation colonization and successional dynamics (Mahoney and Rood, 1992). Further work could also consider a wider range of rivers and reaches to develop common measures that would allow reasonably confident analyses even when no detailed hydraulic model is available.

5. Conclusions

This study analyzed riparian vegetation successional development and associated fluvial processes along free-flowing and regulated rivers of the central Rocky Mountains. We developed a

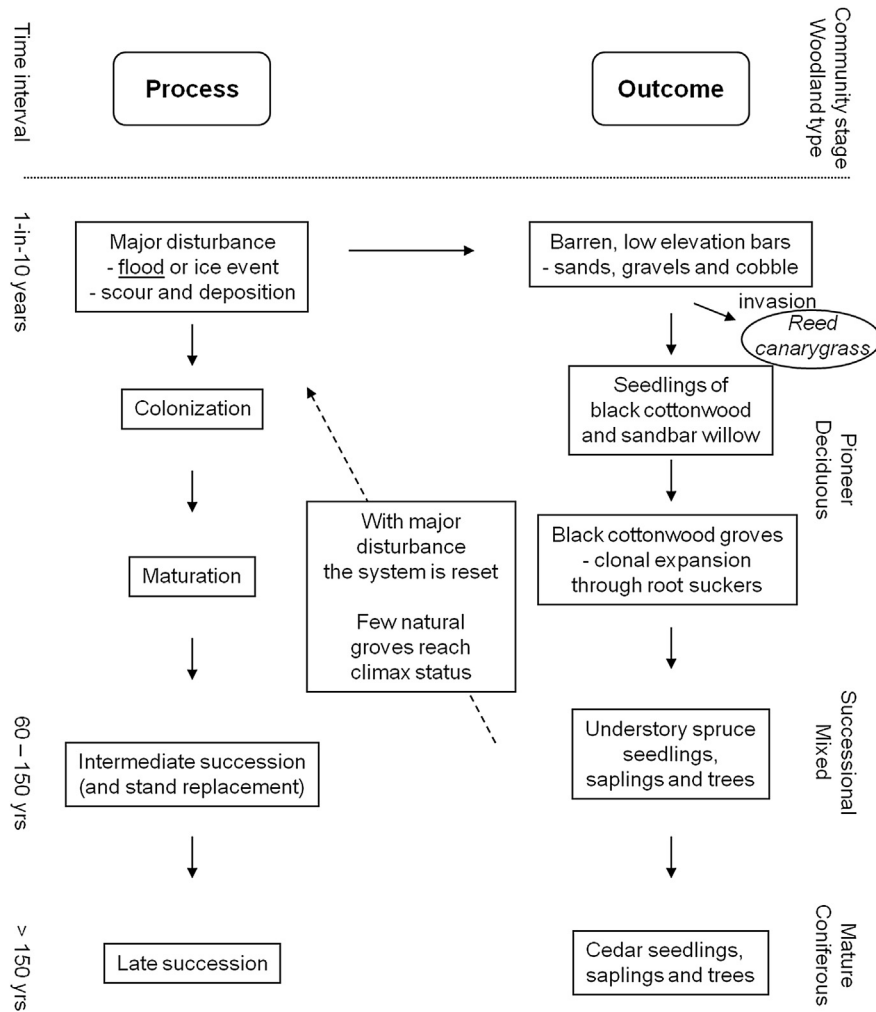


Fig. 8. Floodplain forest primary succession along the study rivers.

hydrogeomorphological (HGM) modeling method based on the correspondence between field-based measures of riparian woodland development and the underpinning physical habitat processes. The associations were confirmed by coordination of key physical processes that were assessed by hydraulic modeling. The method is novel because it describes riparian vegetation succession from different perspectives encompassing both biological and physical aspects, thus providing a more comprehensive characterization of riparian sites. The subsequent descriptors provided clear distinction between different river channel types and also revealed differences between regulated and free-flowing river reaches.

This HGM model is useful to characterize vegetation patterns and it will also be applicable for environmental impact analyses especially related to river damming and flow regulation. River damming was extensive in North America through the mid-twentieth century (Graf, 1999) and many of those dams are requiring relicensing that must include environmental impact analyses that consider riparian ecosystems (Braatne et al., 2008). Our HGM model would assist with this consideration and even the development of environmental flow regimes to conserve and restore riparian woodlands (Rood et al., 2005). Finally, as well as contributing towards analyses of river damming, climate change is altering river flow regimes and aspects such as declining summer flows would stress riparian woodlands (Rood et al., 2008; Capon et al., 2013) and further demand analyses of the hydraulic

processes and subsequent responses relative to riparian woodland colonization and succession, as characterized by this HGM model and study approach.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jenvman.2015.06.018>.

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