



Compound Influences of River Damming and Beavers on Riparian Cottonwoods: A Comparative Study Along the Lardeau and Duncan Rivers, British Columbia, Canada

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Abstract We investigated interactions between river regulation, riparian black cottonwoods (*Populus trichocarpa*) and beavers (*Castor canadensis*) with a paired comparison between the free-flowing Lardeau River and regulated lower Duncan River in western Canada. Cottonwood saplings occurred more broadly along Lardeau River transects (63 % vs. 38 %) and with increased density. Beavers preferred cottonwoods over other shrubs and cutting was more intense (36 % vs. 7 % of stems cut) along the regulated Duncan River. Beaver cutting occurred in wider bands (25 m vs. 11 m from river) along the Duncan, and there was also evidence for increased cutting of a less-favored alternate, alder (*Alnus incana*), while willows (*Salix* spp.) were substantially cut along both rivers. River regulation has apparently reduced cottonwood recruitment along the Duncan River and regulation may also increase beaver accessibility to saplings since higher river levels in late summer and autumn may promote inland access. These ecosystem alterations may thus create an imbalance between bottom-up cottonwood recruitment versus top-down mortality. We overview some of the ecological interactions in riparian woodlands in a schematic model recognizing river flow regime, sediment patterns and bank forms, and other riparian vegetation as key factors influencing cottonwoods and beavers.

Keywords *Castor canadensis* · Floodplain · Herbivory · Poplars · *Populus trichocarpa* · Willows

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Introduction

Riparian woodlands provide rich habitats for a wide variety of plants and animals (Naiman et al. 2005). Being wetter and ecologically more diverse than surrounding landscapes, these provide essential resources for wildlife such as through travel connectivity or microclimate refuge. These functions may become increasingly vital due to continuing river valley developments and climate change (Naiman and Rogers 1997; Rood et al. 2008; Seavey et al. 2009).

Throughout North America, cottonwoods (riparian *Populus* trees) are a keystone component of riparian woodlands and provide multiple functions, extending from the pioneer stage where they colonize barren sediments, through to characteristics of structurally diverse old-growth forest (Polzin and Rood 2000; Braatne et al. 2007). Cottonwood abundances are determined by a dynamic balance between bottom-up factors that influence recruitment versus top-down influences on mortality. The phrase bottom-up is literally appropriate since seedling and clonal reproduction depend on the substrate conditions created by river flows and sediment redistributions on river banks and floodplains (Scott et al. 1997; Kalischuk et al. 2001; Rood et al. 2003). River damming alters these conditions by changing the flow regime and by altering sediment flux and channel form, and these hydrogeomorphic changes alter cottonwood reproduction (Merritt and Cooper 2000; Polzin and Rood 2000).

For cottonwood populations, top-down processes include aging, drought stress and herbivory (Andersen and Cooper 2000; Breck et al. 2003a; Ripple and Beschta 2003; Bailey and Whitham 2006). This phrase is also literally appropriate for our investigation since beaver (*Castor canadensis* Kuhl) cutting provides decapitation. For other riparian systems, top-down impacts from herbivory can be important determinants of population structure and ecosystem composition (Pastor

and Naiman 1992; Breck et al. 2003b; Ripple and Beschta 2003).

In riparian zones, the beaver is one of the most influential herbivores, and uniquely capable as an ‘ecosystem engineer’ (Wright et al. 2002; Rosell et al. 2005). These large rodents alter riparian hydrology and channel and bank forms through damming, canal dredging and other works (Naiman et al. 1988; Gurnell 1998; Cunningham et al. 2006). These diversify channel habitats, filter and enrich water, and create ponds and wetlands upon which invertebrates, amphibians, aquatic mammals and waterfowl depend (Naiman et al. 1988; Rosell et al. 2005; Green and Westbrook 2009; Hood and Larson 2015).

Beavers cut and remove trees and shrubs along stream banks, and cottonwoods and aspen (*Populus tremuloides* Michx.) are commonly preferred (Northcott 1971; Gallant et al. 2004). Where beavers rely on other plants such as willow (*Salix*) or alder (*Alnus*), body and colony sizes may be reduced (Northcott 1971; Breck et al. 2001). The heaviest cutting occurs from late summer through autumn, in preparation for winter (Northcott 1971; Svendsen 1980; Breck et al. 2003a). In spring and summer, beavers may feed extensively on herbaceous plants (Northcott 1971; Parker et al. 2007), reducing the foraging pressure on trees and shrubs.

Beavers are slow-moving and vulnerable on land and consequently a primary influence on foraging is the distance from water (Naiman et al. 1988). Foraging decisions probably reflect a dynamic weighting between energy output, driven by the need for food or building materials, versus energy conservation and security, producing a ‘central place’ foraging strategy (Raffel et al. 2009). Factors that affect energy output, such as swift currents, or security, including predator abundance, would influence foraging patterns. The availability of alternative foods would also influence foraging.

Browsing by ungulates such as elk (*Cervus canadensis* Erxl.) or deer (*Odocoileus hemionus* Zimm.) can also influence beaver utilization. Beavers avoid heavily browsed plants due to the production of unpalatable phenolics (Basey et al. 1998), and heavy browsing by ungulates can also reduce availability for beavers (Baker 2003; Hood and Bayley 2008b).

In healthy riparian woodlands, beaver cutting is tolerated and even provides a form of rejuvenation since there is often vigorous coppice resprouting and clonal suckering of cottonwoods and willows. Conversely, excessive beaver cutting can thin riparian woodlands and provide another stress on declining populations (Andersen and Cooper 2000; Lesica and Miles 2004). Additionally, river damming and water withdrawal can restrict cottonwood populations (Polzin and Rood 2000; Braatne et al. 2007) and we might anticipate that beaver cutting could become problematic along some regulated rivers.

There have been numerous studies of beavers along small stream systems but few along large rivers, with fewer still along regulated rivers. Along Montana’s Milk River, Bradley and Smith (1986) did not detect differing impacts of beaver cutting on prairie cottonwoods (*P. deltoides* Marsh) upstream versus downstream of the Fresno Dam. In Alberta, beaver cutting of the decrepit narrowleaf cottonwood (*P. angustifolia* James) population downstream from the St. Mary Dam, hindered attempts at cottonwood restoration (Rood and Mahoney 2000). Extensive investigation by Breck et al. (2001, 2003a, 2003b) along the free-flowing Yampa River versus the regulated Green River indicated that river regulation limited downstream cottonwood reproduction and increased willow abundance, and that this and regulated flow patterns altered patterns of beaver foraging on Fremont cottonwoods (*P. fremontii* Watson).

Building upon these prior studies, we investigated effects and interactions between river regulation, beavers and black cottonwoods (*P. trichocarpa* Torr. & Gray) along a mountain river in British Columbia. We used a paired comparison between two adjacent river reaches (Braatne et al. 2008), the large, regulated lower Duncan River and its free-flowing tributary, the Lardeau River (Fig. 1). Our primary hypothesis was that there would be reduced cottonwood sapling recruitment along the regulated Duncan River due to changes in seasonal hydrology, sediment regime and channel form. Our secondary hypothesis was that there would be increased beaver cutting along the regulated Duncan River due to the sparser cottonwood occurrence and possibly due to altered seasonal river stages that could increase beaver access.

Methods

Study Rivers and Flow Patterns

The study compared two sequential river reaches flowing into the north end of Kootenay Lake (Fig. 1). The free-flowing Lardeau River drains Trout Lake and its watershed, and is characterized by a dynamic channel meandering in tight bends through a 600 to 700 m wide floodplain bordered by steep valley sides. The banks are dominated by cobbles and coarse gravels with finer sediments along meander lobes and some channel bars. The Lardeau joins the Duncan River just below the outflow channel from the Duncan Dam, which was completed in 1967 following the North American Columbia River Treaty. That Dam impounded a prior lake and wetlands complex (Fig. 1) that would have trapped sediments and woody debris, as the reservoir continues to do. The Duncan Dam has no hydroelectric power facility but the released flows pass through a sequence of hydroelectric dams downstream and regulation also contributes to downstream flood attenuation.

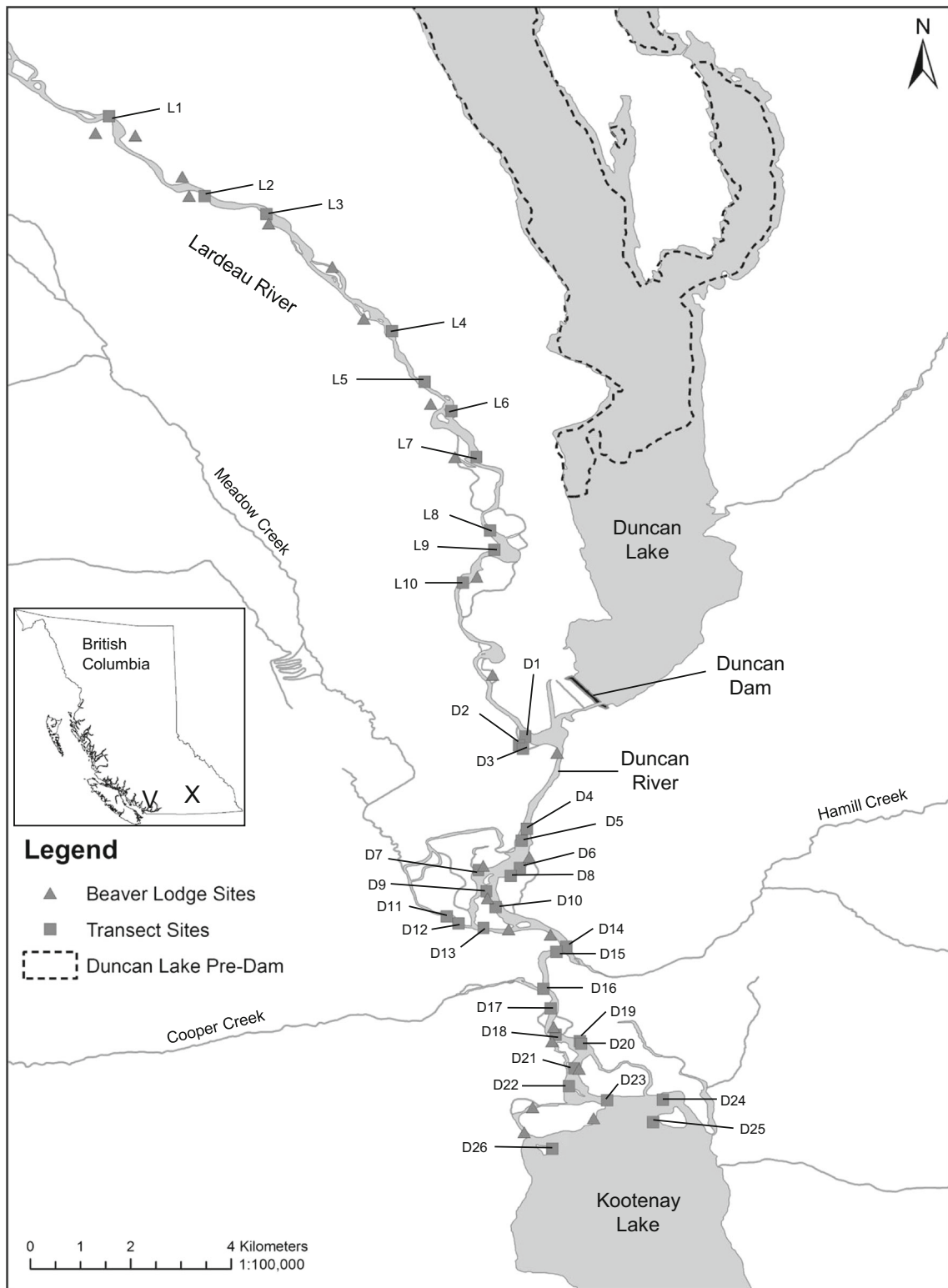


Fig. 1 Map of the study area showing the Lardeau (L) and Duncan (D) Rivers, Kootenay Lake, the Duncan Dam and Duncan Lake (reservoir), with the shoreline of the prior natural Duncan Lake indicated with a

dashed line. Study transect locations are indicated as well as the positions of beaver lodges. The inset displays British Columbia with X indicating the study area and V indicating Vancouver

Below the Lardeau, the lower Duncan River provided the regulated study reach. This floodplain is about 1800 m wide, and the channel bed and banks are characterized by finer

sediments than along the Lardeau, with gravels, sands and silts. Following damming, the Duncan River channel narrowed by about one-third, and some side-channels were

abandoned (Miles 2002). The large, free-flowing Meadow, Hamill and Cooper Creeks (Fig. 1) provide additional contributions of water, sediments and woody debris.

To assess historic hydrology, we obtained mean daily discharges (Q) from the Water Survey of Canada's HYDAT database for the Lardeau River At Marblehead (08NH0070, from 1929) and for the Duncan River Below Lardeau River (08NH118, from 1963). We averaged daily values across years for the pre-dam interval from 1963 to 1967 and for subsequent decade intervals after damming. The post-dam flows were fairly similar across those decades (Polzin et al. 2010) and we present the mean hydrograph for the interval 1998–2008 (Fig. 2), which preceded the field study.

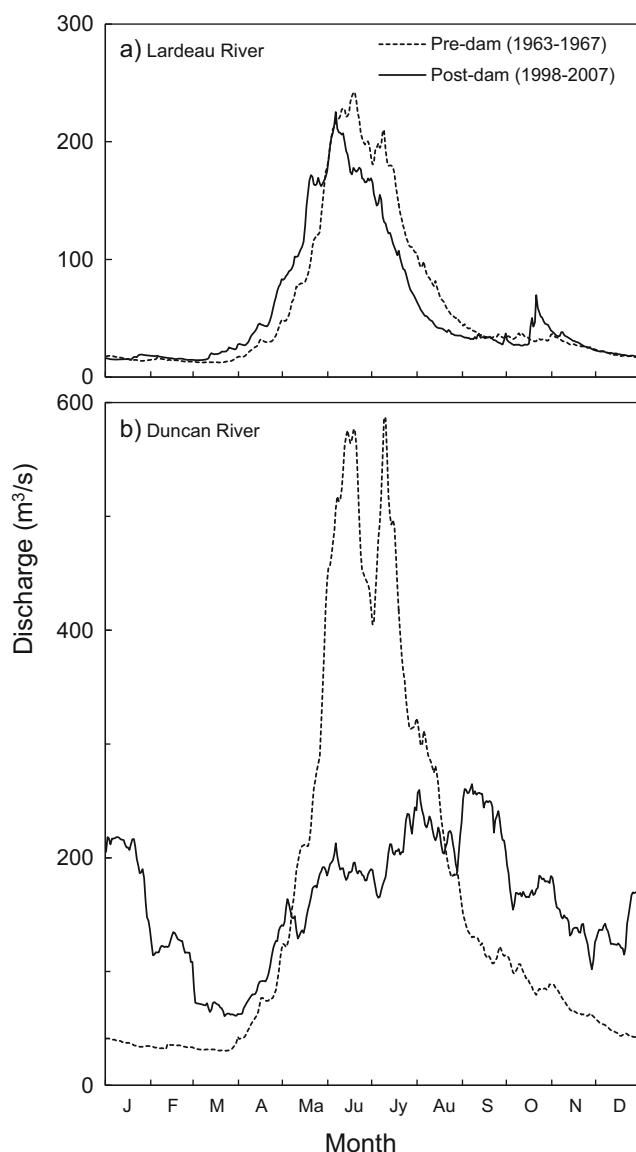


Fig. 2 Average daily discharges (Q) of the Lardeau River (top) and lower Duncan River (bottom) for a decade prior to the Duncan Dam and the decade prior to the field study

Study Design

To assess vegetation we utilized cross-sectional belt transects that extended perpendicular from the river up through the barren and sapling zones to tagged trees in the mature cottonwood (*Populus trichocarpa*) forest. For transect positioning, we divided the river reaches into numbered segments but excluded higher terraces, older forest, building developments or agricultural lands. From the remaining locations, the transect positions were randomly selected, and assessed in 2009 and 2010. There were 10 transects along the Lardeau River and 26 along the Duncan River (Fig. 1), with the increased Duncan sampling reflecting the emphasis of an overlapping study (Polzin et al. 2010).

Along each transect we established successive 5 m (along transect) \times 10 m quadrats on the downstream side of a tape line. In each quadrat, we counted the intact and beaver cut stems of all trees and shrubs by species, within five basal diameter classes: 0–2, 2–4, 4–7, 7–15 and >15 cm. For each quadrat we rated ungulate browse intensity with a scale of 0 to 5 (none to complete browsing, Luttmerding et al. 1998).

To determine the width of the beaver cutting zone, we averaged two values for each transect. One value was the distance along the transect line to the furthest inland beaver cutting. The other was the distance of beaver cutting along a line running at 45° toward the river from the tag tree or furthest inland cutting position. Where cutting continued inland past the tag trees along two transects, we extended the lines. Four transects were positioned across narrow islands with beavers browsing right across the islands and we used the mid-island widths as the cutting width. We also assessed substrate texture, woody debris accumulation and adjacent water depth at each transect. As another approach to assess beaver cutting along the Duncan River, we reassessed twenty-seven 11 m circular plots that had been established in 2002, recording juvenile cottonwood numbers and sizes and beaver cuts.

Beaver Colonies and Developments

We recorded and mapped the beaver developments along both rivers, including dams, canals, dens, food caches, dragging trails and scent mounds (Naiman et al. 1988; Green and Westbrook 2009). We inventoried beaver colonies through a count of winter food cache and den complexes in late fall and early spring (2010–2011) as described by Hay (1958), and as supported by findings that northern beaver colonies cluster together in winter (Novak 1977; McTaggart and Nelson 2003). Caches were identified as large piles of freshly cut sticks, anchored in mud or logs, with den entrances within about 10 m. The survey scanned all channels over 50 cm deep but small portions of the Lardeau River floodplain were inaccessible. We noted scent mounds, 10 to 100 cm tall piles of mud and vegetation, which indicate colony territory boundaries (Svendsen 1978; Sun and Muller-Schwarze 1998).

Data Analyses

Sapling values for cottonwoods, alders (*Alnus incana*) and willows (*Salix* spp.) were recorded by quadrat and these were aggregated to provide single values for each transect. For each transect, we assessed the sapling interval as extending from the first to last quadrat with any intact or cut sapling. We assessed the sequential quadrats within this interval and for Occurrence we calculated the percentage of those quadrats that contained at least one cottonwood, alder or willow sapling. We summed the numbers of intact or cut saplings from the quadrats within the sapling interval and this provided the basis for the density values for each of the three plants for that transect. The intact and cut densities were combined to provide the total density, and the extent of beaver cutting was calculated as the number of cut stems/total stems (cut + intact) for each plant. For ungulate browsing we chose the maximum intensity value along each transect and this provided a similar outcome as comparison with the mean intensities per transect.

We thus determined a value for each characteristic for each transect, and then considered the values from the 10 Lardeau transects versus the 26 Duncan transects, with statistical analysis with SPSS (PASW 18, IBM Corp., NY). We undertook t-tests, following Levene's Test for Equality of Variances to determine if equal variances would be assumed or not, and undertook log transformations for density data. With the 10 and 26 values, the degrees of freedom was consistently 34 and we assessed outcomes as: trend (t) $p < 0.1$, significant (*) $p < 0.05$ or highly significant (**) $p < 0.01$. We also undertook Mann–Whitney U non-parametric paired comparisons and these provided very consistent outcomes, and only the t-test results are presented (Table 1).

Results

River Flow Patterns

Prior to damming, the natural flow regimes of both rivers displayed nival, snow-melt dominated patterns (Fig. 2). Winter flows were low and discharge rose in spring to maximal flows commonly in June. Flows declined through the summer and autumn to return to low flows in the winter. This is illustrated with the averaged Lardeau River hydrographs in the pre- and post-dam intervals and the averaged Duncan hydrograph prior to damming (Fig. 2).

Following damming in 1967, the seasonal patterns changed considerably along the lower Duncan River (Fig. 2). High flows were attenuated, with 2-year and 10-year maximum daily discharges reduced to about one-half of the pre-dam values (pre-dam: 530, 800 m³/s; post-dam: 310, 430 m³/s), and late summer to winter discharges substantially increased (Fig. 2). The regulated patterns for the three decades from

1968 through 1997 were generally similar (not shown) and then the flow regime was further altered during the decade from 1998 to 2007 (Fig. 2).

Cottonwoods

Black cottonwoods were the predominant riparian trees along both rivers. At higher elevations on older surfaces there were large mature cottonwoods, commonly with western red cedar (*Thuja plicata* Donn), white spruce (*Picea glauca* (Moench) Voss), paper birch (*Betula papyrifera* Marsh.) and mountain alder (*Alnus incana* (L.) Moench ssp. *Tenuifolia*). At lower-positions on younger surfaces, patches of black cottonwood saplings occurred on gravel bars, young islands, accreting edges of meander lobes and older islands, flood channels and some side channels. Young patches of cottonwood were mixed with willow while older patches were mixed with alder, red osier dogwood (*Cornus stolonifera* Michx.), river birch (*Betula occidentalis* Hook.) and other plants.

Testing our primary hypothesis, we found that cottonwood saplings occurred in a significantly higher percentage of the quadrats along transects by the Lardeau than the Duncan River (Fig. 3, Table 1). Cottonwood sapling densities were variable and averaged about five times higher along the Lardeau, another significant difference (Fig. 3, Table 1). Beaver cutting was apparently slight along the Lardeau and about five times higher along the Duncan River (Fig. 4, Table 1). Cutting heights ranged from 5 cm to 120 cm, with 30 to 40 cm being common.

Widths of Beaver Foraging Zones

Testing our second hypothesis, the beaver cutting bands were significantly wider along the Duncan than Lardeau River transects (Table 1). The circular plot reassessment supported the widths along the Duncan River (Fig. 5). Within plots 20 m or closer to the channel, 80 to 100 % of the cottonwoods were generally cut over the interval from 2002 to 2010. The extent of cutting dropped abruptly around 25 m from the water, with minimal beaver cutting beyond 35 m.

Alder and Willow

Mountain alder was a frequent riparian shrub that tended to be more common along the Lardeau than Duncan River (Fig. 3; Table 1). Beavers rarely cut alders along the Lardeau River but sometimes cut alders along the Duncan River, with results suggesting a difference (Table 1). There were several sites where beavers left alder standing after cottonwood and willow were cut, indicating a lower preference, consistent with Northcott (1971).

Willows were abundant in the lower position riparian zones with the most common being Bebb willow (*Salix bebbiana*

Table 1 Characteristics and t-test comparisons for saplings and beaver influences in transects along the Lardeau and lower Duncan Rivers. Significant ($p \leq 0.05$) values are in bold and a trend ($p < 0.1$) is italicized. With 36 transects the df was generally 34, but slight reductions occurred for beaver cutting when a plant species was absent

Characteristic	Lardeau R.	Duncan R.	t	probability
Transects	10	26		
Occurrence (% of quadrats)				
Cottonwood	63.0 ± 11.5	38.2 ± 6.1	2.04	0.050
Alder	56.0 ± 9.3	40.6 ± 5.3	1.45	0.143
Willows	64.9 ± 9.5	75.0 ± 4.8	1.05	0.304
Density (#/ha)				
Cottonwood	6914 ± 3127	1398 ± 538	2.65	0.012
Alder	1716 ± 118	2126 ± 636	0.39	0.695
Willows	16,396 ± 6120	39,983 ± 11,300	1.26	<i>0.075</i>
Beaver Cutting (% of saplings)				
Cottonwood ($n = 9,21$)	7.34 ± 2.99	35.94 ± 8.75	2.10	0.045
Alder ($n = 10,25$)	0.244 ± 0.244	6.69 ± 4.04	0.99	0.125
Willows ($n = 9,26$)	14.8 ± 8.37	19.3 ± 3.97	0.55	0.588
Width of Cutting (m)	10.95 ± 2.99	25.22 ± 2.17	3.60	0.001
Beaver lodges & food-caches	10	13		
Ungulate browsing index	1.80 ± 0.36	2.46 ± 0.15	2.03	0.050

Sarg.) and Pacific willow (*S. lucida* Muhl. ssp. *Lasiandra*). Extensive and dense thickets of willows occurred in low-lying areas with fine-textured sediments, which were more common along the Duncan River. Smaller patches of willows occurred along the main and side channel banks and around backwater areas and beaver ponds and about two-thirds of quadrats in the sapling intervals along both rivers included willows (Fig. 3; Table 1). Sandbar willow (*S. exigua* Nutt.) was abundant along the downstream end of the Duncan River especially on the delta. Willow densities were apparently lower along the Lardeau River (Table 1) and this may have included a longitudinal pattern since willows were sparse along the upstream transects of the Lardeau (Fig. 3).

Beavers substantially utilized willow along both rivers (Table 1). Along the Duncan River this cutting was about one-half of that for cottonwoods and around three times that for alder (Table 1), indicating a preference of cottonwood, willow and then alder. Willows in extensive patches such as on the delta near Kootenay Lake were generally lightly cut while small patches near channel edges were sometimes heavily cut, and apparently cut over successive years to produce coppice forms resembling managed hedges.

Ungulate Browsing

There was increased intensity of ungulate browsing along transects of the Duncan River (Table 1). Beavers may have avoided ungulate-browsed plants since we did not observe ungulate browsed stems in beaver cut piles or caches. Conversely, ungulate browsing was common on coppice shoots sprouting from beaver cut stems.

Beaver Developments

Most winter lodges (Fig. 1, Table 1) were a combination of bank dens and stick lodges and were located along small side channels, back channels and distributaries that had been beaver dammed or deepened by beaver dredging. Two lodges were located along the Duncan River main stem. Several were located under log jams and two were free-standing stick lodges in ponds on old side channels. There were ~0.4 colonies per km of Duncan River channel, and ~0.3 colonies per km of channel along the Lardeau River. Winter food caches were typically observed within a few m of lodge entrances.

Beaver dams were built across small channels and ranged from small seasonal stick dams to more permanent large mud and log structures. The major dams and pond complexes were associated with fine-textured alluvial sediments, sands and silts. All dams created some ponding that was associated with wetland habitat development.

We also observed beaver canals, which were apparently excavated to bring supplemental water to smaller channels or ponds or to dry low-lying areas, or alternately as waterways to access food. Some canals appeared to improve access for beavers to inland cottonwood saplings. Most canals were also located in fine textured sediments and the most extensive canal systems were associated with low-lying willow communities.

Discussion

At the study outset we anticipated that cottonwoods, beavers and their interactions would be influenced by river regulation. Our field observations demonstrated these influences,

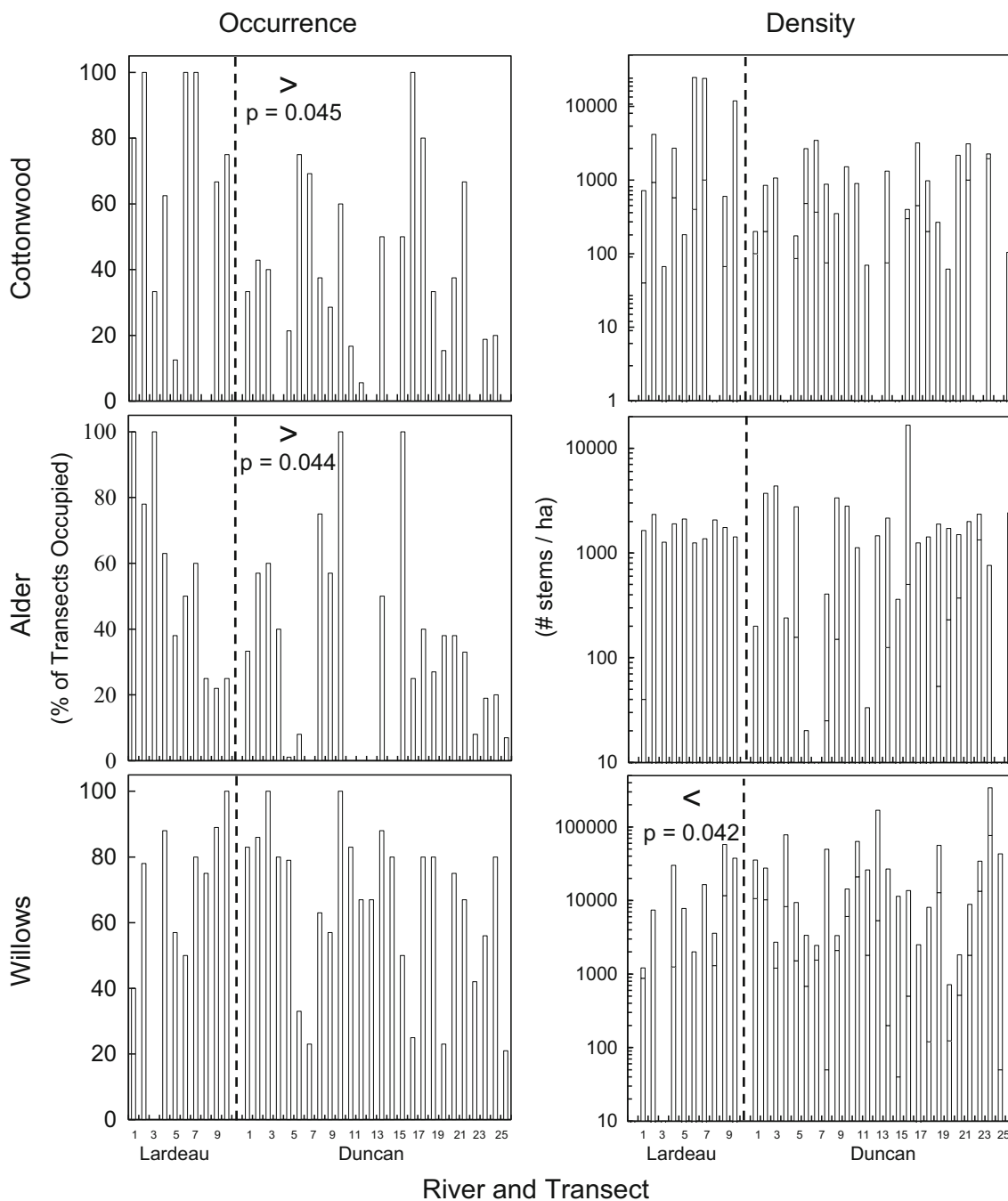


Fig. 3 Occurrences (left) and densities (right) of saplings of the three primary woody plants in transects along the Lardeau and lower Duncan Rivers. The vertical dashed line designates the position where the Lardeau River joins the Duncan River below Duncan Dam. Note the

different y-axis log scales for densities. The > or < indicate differences across the two rivers, with statistical results in Table 1 ($t = \text{trend}, p < 0.1$; * $p < 0.05$)

suggesting that flow regulation of the Duncan River has impacted the cottonwood population through bottom-up impediments to cottonwood reproduction, and by increasing the top-down pressure from beaver cutting. The results support our primary hypothesis, as cottonwood saplings along the lower Duncan River were more limited in occurrence and less dense than along the free-flowing Lardeau River. The results also support our second hypothesis, as beaver cutting was more

intense and influenced a broader zone inland from the river edge along the Duncan River.

The reduction in juvenile cottonwoods is probably partly due to the altered flow regime following operation of Duncan Dam. With regulation, there were high and even increasing flows through July and August (Fig. 2), about a month after the primary interval of seedling establishment (Polzin and Rood 2006; Herbison et al. 2015). The augmented flows

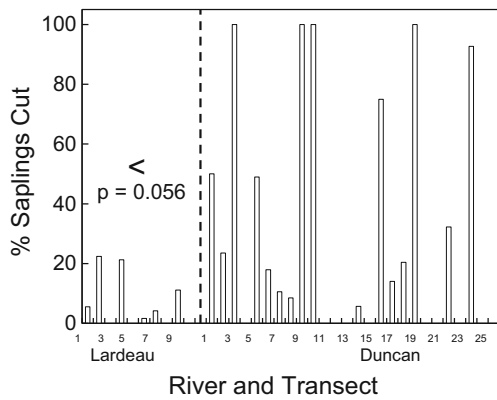


Fig. 4 Percentages of beaver cut cottonwood saplings in transects along the Lardeau and Duncan Rivers (<math>< </math> indicates lower value for Lardeau, *

would submerge and erode new germinants that had established during the receding limb of the spring freshet. High winter flows would also scour recruitment zones, removing more seedlings (Benjankar et al. 2014). The attenuation of spring peaks reduces geomorphic disturbance and the creation of cottonwood colonization zones (Polzin and Rood 2006; Tiedemann and Rood 2015), and along the lower Duncan River flood attenuation has also resulted in simplification and narrowing of the river channel (Miles 2002), further reducing cottonwood colonization sites.

The higher intensity of cutting and broader foraging zone along the regulated Duncan River might reflect reduced cottonwood abundance, as the remaining saplings would face greater cutting pressure and be sought further inland. These differences might also be explained by improved inland access for beavers along the Duncan. The elevated river stage from late summer through autumn could increase water access to the inland saplings when the heaviest cutting occurs for winter food caches (Svendsen 1980; Gallant et al. 2004). In contrast, in late summer and autumn the Lardeau River is low and dropping, limiting water access to cottonwood saplings.

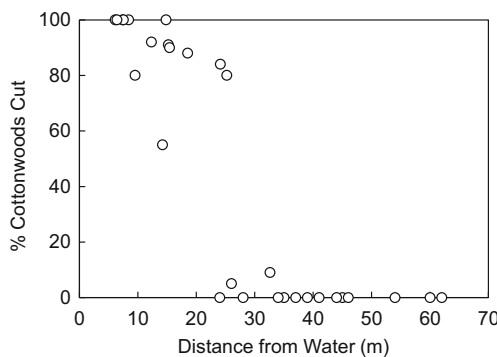


Fig. 5 Percentages of cottonwoods cut by beavers versus distance from water for circular plots along the lower Duncan River that were established in 2002 and reassessed in 2010

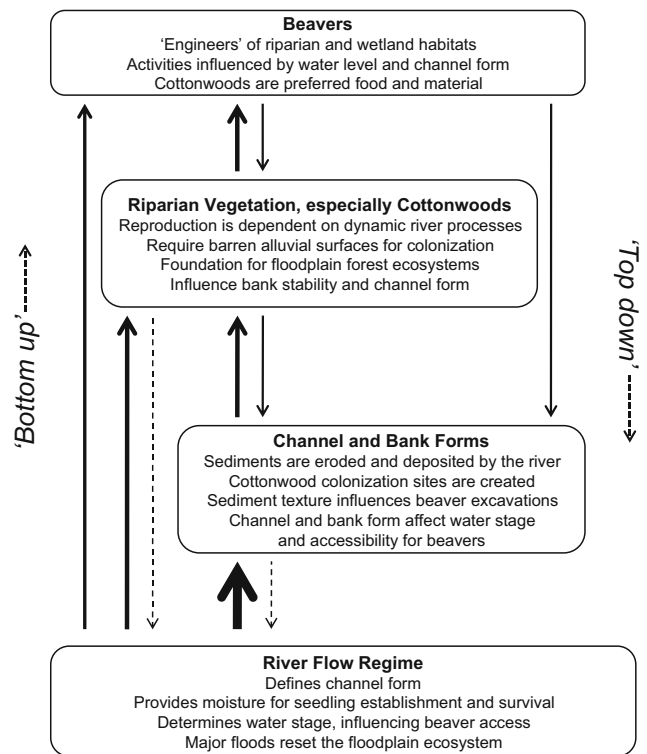


Fig. 6 Apparent ecological interactions related to riparian woodlands along the Lardeau and Duncan Rivers, with ‘top-down’ and ‘bottom-up’ components of the ecosystem

Our study also indicates the importance of geomorphological factors that affect beaver occurrence and their influence on cottonwoods. Bank and channel sediment texture is probably important, with silts to clays apparently preferred for bank dens, canals and other structures. Channel morphology and stability are also likely to be important and probably differ along the Lardeau versus lower Duncan River.

In addition to cottonwoods, our study also indicated that other woody riparian plants are important for beavers and are also probably influenced by river regulation. Willows were abundant along both rivers and were extensively cut by beavers, providing an alternate source of food and building materials. Beaver developments such as canals and ponds were common with low-lying willow thickets, especially along the lower Duncan River. Like cottonwoods, willows are responsive to river damming (Rood et al. 2010, 2011) and Breck et al. (2003b) suggested that willows might thrive with the flow-regulated conditions along the Green River and that this might increase the beaver population, which could then increase impacts on cottonwoods. Conversely, we believe that there may be the potential for willows and the wetland plants around beaver ponds to buffer the impacts of beavers on cottonwoods, especially if combined with complementary beaver-wetland management practices such as described by Pollock et al. (2014).

Floodplain Woodlands–Ecological Interactions

We recognize the factors and interacting processes observed along the Lardeau and Duncan Rives in an integrative model (Fig. 6) that relates river flow regime, sediment fluxes and the channel and bank forms, riparian vegetation and especially cottonwoods and willows, and beavers as an ‘ecosystem engineer’. We would expect generally similar interactions along other North American rivers. This model blends some of the concepts of floodplain biogeomorphology as advanced by Hughes (1997), with concepts from the hydrogeomorphic analysis for river and floodplain processes (Tockner et al. 2010; Rood et al. 2015). This conceptualization could contribute to river flow scheduling and floodplain management for woodland conservation and restoration, and may also provide insight into influences from watershed development or climate change (Hood and Bayley 2008a; Rood et al. 2008).

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