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A TWOFOLD STRATEGY FOR RIPARIAN RESTORATION: COMBINING A FUNCTIONAL FLOW REGIME AND DIRECT SEEDING TO RE-ESTABLISH COTTONWOODS

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ABSTRACT

The transboundary St Mary River drains Glacier National Park, USA, and was progressively dammed and diverted over the 20th century to support agricultural irrigation in northern Montana and southern Alberta, Canada. Following reduced instream flows, the riparian cottonwoods collapsed, and by 2000, few parental trees remained to provide seeds for cottonwood replenishment. As a novel twofold restoration strategy we: (1) worked with the dam operators to deliver a functional flow regime, a regulated instream flow pattern intended to recover some ecological function and specifically seedling recruitment, and (2) delivered cottonwood seeds by direct spreading and by sticking cuttings with seed catkins to allow gradual seed dispersal. The combination of river regulation and seeding enabled cottonwood colonization, and around 1.5% of the applied seeds produced seedlings after the first summer, at sites without livestock or heavy recreational use. Around 15% of those seedlings survived through the fourth summer, with mortality due to drought stress and flood scour, and establishment and survival were higher for the prairie cottonwood, *Populus deltoides*, than the narrowleaf cottonwood, *Populus angustifolia*. This study confirmed that the lack of seed source trees limited cottonwood colonization and demonstrated that the twofold restoration strategy provides promise for severe situations where parental trees have been lost. However, this would require substantial effort, and it would be more efficient to provide survivable instream flow patterns that avoid cottonwood collapse. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS: environmental flows; floodplains; instream flow needs; *Populus*; trees

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INTRODUCTION

Originating in northern Montana, USA, the transboundary St Mary River is similar to many other rivers that drain the eastern slopes of the central Rocky Mountains. It was progressively dammed and diverted over the 20th century, primarily for agricultural irrigation in Montana and especially southern Alberta, Canada. Following reduced instream flows, the riparian cottonwood population collapsed, with more than three quarters of the trees along the lower St Mary River lost between 1951 and 1995 (Rood *et al*., 1995), and further decline to 2000. Following this severe loss of mature trees, cottonwood seed-production plummeted, and in contrast to extensive cottonwood seedling colonization along other regional rivers (Kalischuk *et al*., 2001), our attempt to promote cottonwood recruitment through instream flow regulation after a major flood in 1995 was unsuccessful along the canyon segment of the lower St Mary River (Rood and Mahoney, 2000). We consequently concluded that because of the sparse seed source, the restoration of riparian cottonwoods along this river reach would be impossible solely through instream flow regulation and that supplemental seeding or planting would be required. To test this hypothesis and to investigate an innovative restoration strategy, this study combined deliberate instream flow regulation with direct seeding in an attempt to re-establish cottonwood seedlings along the St Mary River.

This twofold restoration strategy extended beyond that of prior applications. It follows from the studies of Johnson (1965), Friedman *et al*. (1995) and Tiedemann and Rood (2015), who cleared riparian surfaces to promote cottonwood colonization from natural seedfall. However, because of the limited seed source along the lower St Mary River, we undertook direct seeding, somewhat similar to that undertaken by Bhattacharjee *et al*. (2006) and Grabau *et al*. (2011). In some prior restoration studies, artificial irrigation water was applied for seed germination and seedling survival (Friedman *et al*., 1995; Grabau *et al*., 2011; Bunting *et al*., 2013), and another approach was to manage surface water and groundwater through canal inflows (Sprenger *et al*., 2002; Bhattacharjee *et al*., 2006; 2008). Our strategy was to manage the river flow and associated alluvial groundwater with an environmental flow regime, thus providing a

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systemic approach that should benefit the full river reach (Rood *et al*., 1998; 2003; Shafroth *et al*., 1998).

To deliver the cottonwood seeds, we compared direct seed spreading with the placement of excised branches with near-mature seed catkins. This latter approach extended from the nursery procedure of Wycoff (1960) and subsequently Bhattacharjee *et al*. (2006), who provided branches with multiple catkins to broaden the seed release timing and dispersal. As a further comparison, we included the two native cottonwood species along the study reach, with the narrowleaf cottonwood, *Populus angustifolia* James, which has substantial capacity for clonal expansion, versus the broad-leaved prairie cottonwood, *Populus deltoides* W. Bartram ex Marshall, which is more dependent on sexual reproduction through seedlings (Gom and Rood, 2000).

To promote the cottonwood colonization, we collaborated with the dam operators to deliver a flow regime in accordance with our Recruitment Box Model (Mahoney and Rood, 1998; Amlin and Rood, 2002; Benjankar *et al*., 2014), and followed the seedling responses over 4 years. We hypothesized that:

(1) the direct seeding should enable cottonwood seedling establishment,
(2) this seeding in combination with the flow regulation would permit seedling survival, and
(3) the prairie cottonwoods seedlings would be more successful than the narrowleaf cottonwoods because of increased seedling vigour (Kalischuk *et al*., 2001).

METHODS

Hydrology

We have previously described aspects of river management and historic hydrology of the lower St Mary River (Rood and Heinze-Milne, 1989; Rood *et al*., 1995; Rood and Mahoney, 2000). In this study, the peak flow record was extended to 2014, with comparison of the upper St Mary River near the international border (Water Survey of Canada no. 05AE027, Figure 1) versus the lower river below the St Mary Dam (no. 05AE006). Daily discharges along the lower river for the study interval from 2010 through 2014 considered provisional data from Alberta Environment and Sustainable Resource Development (AESRD).

The functional flow regime

We use ‘functional flow’ to describe a deliberately regulated, artificial flow pattern that is intended to support one of more ecological components or processes. In this case, the functional flow was developed to promote cottonwood seedling colonization based on the Recruitment Box Model (Mahoney and Rood, 1998; Amlin and Rood, 2002). For this, the key interval commences with cottonwood seed release and requires an establishment flow through the elevational band that extends from 0.6 to 2.0 m above the base stage, that of the typical late summer low-flow (Figure 2). Below this band, there would be the loss of seedlings because of scour, and the upper limit reflects the root elongation capacity, with higher seedlings suffering from drought-induced mortality (Segelquist *et al*., 1993). After establishment, gradual ramping of stage decline to 4 cm per day or less (Mahoney and Rood, 1998; Bhattacharjee *et al*., 2006) enables the seedling root elongation to track the receding moisture zone provided by the capillary fringe above the alluvial groundwater table (Rood *et al*., 2013).

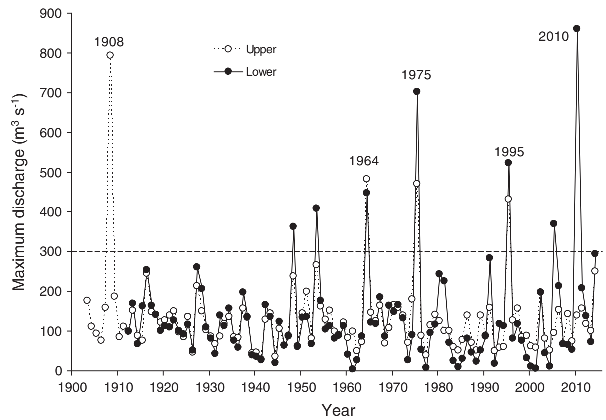

Figure 1. Historical maximum daily peak flows for the upper St Mary River near the international border and for the lower St Mary River near Lethbridge. Major flood years are identified and the dashed line at 300 m^3/s approximates the 1-in-10-year recurrence

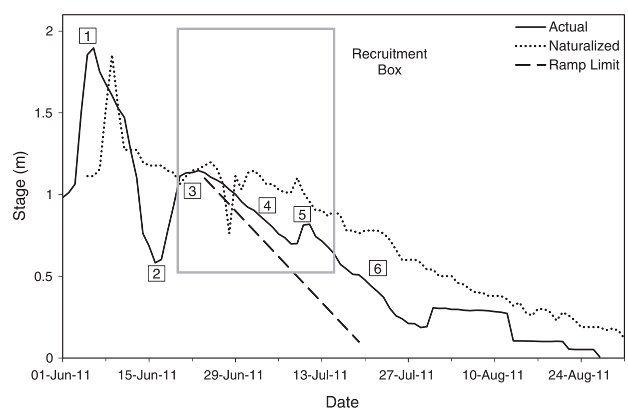

Figure 2. The cottonwood Recruitment Box and the river stage hydrograph for the lower St Mary River for the functional flow interval for cottonwood colonization, from June through August 2011. The naturalized hydrograph approximates the pattern that would have occurred without regulation. Numbers indicate aspects of the regulated regime as described in the section on Results, and the dashed line represents the steepest survivable stage recession

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Seeds, seeding and seedlings

Regional cottonwood seed release commenced around 20 June 2011, about a week later than normal because of cool spring weather. Branches with near-mature seed catkins were collected on 27 June 2011 from native cottonwood trees along the Oldman River in Lethbridge (Rood *et al*., 2013), placed in large black plastic bags and stored at room temperature. Collections were from a reference tree for each of two species, with the narrowleaf cottonwood, *P. angustifolia* tree number 6 (Evans *et al*., 2015) and the prairie cottonwood, *P. deltoides* tree number 31 (Rood *et al*., 2013) and from six additional trees of each species.

Estimates of seed numbers were based on sampling representative catkins and seed counts within capsules (Table I). This provided estimates for each branch cutting that was stuck. Seeds were also separated from the capsules, and samples were counted and weighed to estimate the numbers spread along each study transect section. To assess viability, three 50-seed samples from each tree or mixture were placed on filter paper discs in Petri plates, moistened with 2 ml water, and germination was observed over 4 days at room temperature with windows providing natural light.

Similar seeding treatments were provided at each of the six sites, with upstream and downstream sites along three meander lobes. Each site was chosen to provide a fairly typical and apparently favourable colonization band, with a gradually sloped surface of gravels and sands, and little established vegetation. A measuring tape was positioned about 0.3 m inland from the water edge to provide each 48-m longitudinal transect. Rebar stakes with rock piles enabled relocation of transects and their eight 6-m segments.

Seeding included two treatments, the sticking of branches with near-mature catkins, and the direct spreading of separated seeds. Starting at the upstream end, each transect commenced with a 6-m segment of non-seeded reference (control). The number 31 *P. deltoides* branch cutting was stuck in the middle of the next segment, followed by the second *P. deltoides* branch in the following segment. Next, *P. deltoides* seeds were spread along a 20-cm wide band that extended along the middle 4 m. The next four 6-m segments provided the same sequence for the two *P. angustifolia* branches and then *P. angustifolia* seeds and the final non-seeded downstream reference.

Table I. Cottonwood seed characteristics; different letters indicate differences ($p < 0.05$)

Trait	Narrowleaf cottonwood *Populus angustifolia*	Prairie cottonwood *Populus deltoides*
Capsules per catkin	33.0 ± 3.3a	32.6 ± 2.9a
Seeds per capsule	4.9 ± 0.8b	15.8 ± 4.7a
Seeds per catkin	157 ± 22b	523 ± 176a

For sticking cuttings, a rebar stake was pounded into the substrate, rotated and removed. The cutting stem was placed in the hole, and the substrate was repacked. For direct seed spreading, river water was poured over the surface to increase the seed catch; seeds were dispersed to provide uniform application over the 20 cm × 4 m band, and water was sprinkled over the seeded zone.

Seeding occurred on 28 and 29 June 2011 and sites were observed at 2-week intervals through the first summer. Seedlings were counted within sequential 20 (parallel to river) × 50-cm quadrats on 3 and 13 October 2011. Site visits continued through to 2014 (Year 4) and seedling counts were made before the spring peak and in middle to late summer, 15 May 2012 and 18 July 2012; and 16 May 2013 and 27 August 2013. For the 2013 counts, the quadrat size was expanded to 1 × 1 m because we observed some establishment outside of the original quadrats, probably primarily because of wind dispersal, and rarely from natural seeding. With the older seedlings, species assignments were made in 2013, and the heights of the tallest 10 seedlings per quadrat were recorded for the late 2013 measurement. The final seedling counts and heights by species were made on 7 August 2014, and leaves were sampled for morphological measurements.

Seedling distributions along transects were assessed over the 4 study years to analyse establishment and survival. Over-winter mortality was slight, and only plots for the late summer sampling are presented. Additionally, *t*-tests compared characteristics between the two species.

RESULTS

Hydrology

The opportunity for the functional flow regime was provided by the exceptionally wet summer of 2010. This resulted in the highest recorded flows along the lower St Mary River (Figure 1), which exceeded the major floods of 1964, 1975 and 1995. In contrast to those prior floods that largely originated with high flows from the mountain headwaters, the upper St Mary displayed only a modest peak in 2010. This revealed an unusual spatial distribution of rain, with more in the prairie region than occurred for the prior floods.

The spring 2011 weather was unusual with the combination of cool but dry conditions (Figure 3). April, May and June were consistently cooler than normal, and the monthly precipitation averaged only 16% of normal. The cool weather slightly delayed cottonwood seed maturation, and the dry spring prompted additional caution relative to the functional flow regime.

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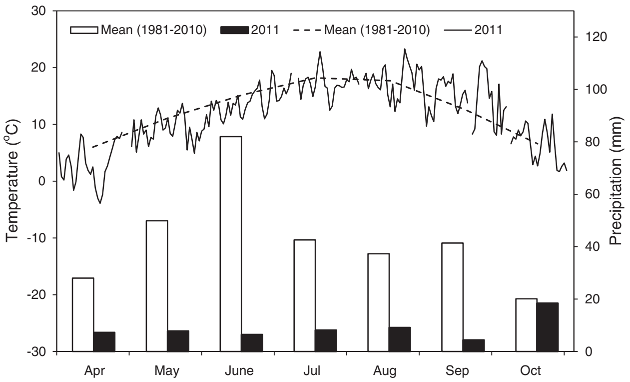

Figure 3. Mean daily temperatures (lines), and monthly precipitation (bars) for the growth interval of May through October 2011, for the seedling establishment year. Climate normals are based on 1981 to 2010.

Despite the dry weather, following from the saturated watershed and substantial winter snow-pack, the June 2011 peak of 207 m^3/s represented about a 1-in-5-year recurrence. That peak was limited in duration, and flows fell over the next 2 weeks (Figure 4), prior to the cottonwood seed release that was the ecological trigger for the functional flow implementation. As a consequence, the flow regime commenced with a river stage towards the lower level of the Recruitment Box (Figure 2).

The functional flow regime

The summer 2011 flows from the St Mary Dam were deliberately managed by AESRD to produce the river stage pattern in Figure 2. Two plots are provided with the implemented functional flow pattern and the naturalized flow that would have occurred without regulation. As indicated, there was a moderate peak in early June that was slightly elevated by release from the St Mary Dam (Figure 2, '1'). After the spring peak interval passed, the flow from the St Mary Dam was reduced to capture additional storage for the irrigation season (2). Subsequently, flows were increased towards the natural discharge around 20 June. With the commencement of seed release, the flow was held constant for a few days (3) and the deliberate flow ramping followed (4). However, by mid-July, the water budget required further spilling, and there was a slight increase in flow (5), followed by renewal of gradual ramping (6). The ramping rate approximated 2.5 cm/d and was more gradual than the 4 cm/d maximum.

Seeds, seeding and seedlings

Cottonwood seed viabilities were almost complete. For *P. deltoides*, there was 98.7 ± 0.7% germination in seeds from tree number 31 and 96.7 ± 1.0% in the seed mixture from the other trees. For *P. angustifolia*, there was 99.3 ± 0.7%

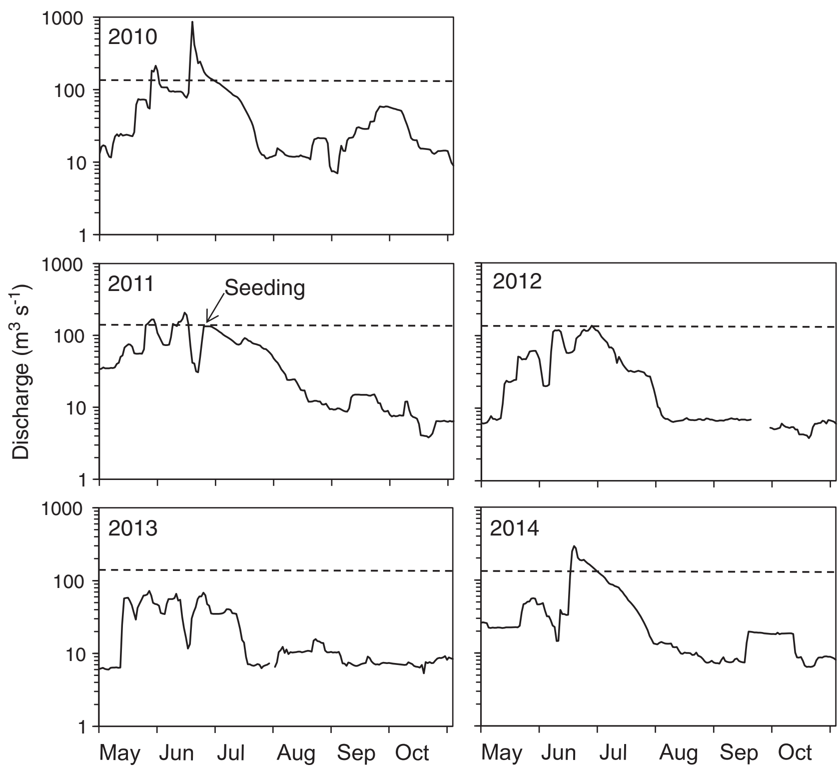

Figure 4. Daily hydrographs for the lower St Mary River for May through October for the pre-project flood year of 2010 and the study years from 2011 to 2014, including provisional data with gaps. The dashed line indicates the discharge during the cottonwood seeding

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germination from multiple trees, and slightly lower viability, 88.7 ± 0.7%, in seeds from tree number 6.

The field seeding advanced smoothly, and each site required four people working for about 1 h. The sticking of branches was quicker than the seed spreading, and combined with the variation provided by the gradual seed release and wind dispersal, this approach could be especially efficient.

The 2011 weather after seeding extended the dry late spring pattern (Figure 3). Precipitation was limited through July, August and September, averaging 18% of normal. July temperatures were quite normal and then warmer than normal in August and especially September and October. The combination of low precipitation and warm late summer weather would probably have increased drought stress on the newly established cottonwood seedlings.

Two weeks after seeding, tiny seedlings were abundant below the stuck branches and along the seed spreading bands. The seedlings were common on sandy surfaces and emerged from the sand-filled interstitial gaps between the larger gravels or cobbles. There were patches below the cut branches with seedling densities in the hundreds per 20 × 50-cm quadrat, and it is likely that the maximum number of seedlings was in late July, when we estimated a few thousand germinants per transect, representing around one-tenth of the seed number.

By early August, there was considerable drying of some of the seeded zones, and many of the seedlings displayed senescence or desiccation. Seedling stresses were more apparent in late August, but there appeared to be little further mortality through to the final Year 1 assessment in October.

Figure 5. Bands primarily of *Populus deltoides* seedlings at Site 3, 1 July 2012 in the second growth year after seeding (15-cm pen) This figure is available in colour online at wileyonlinelibrary.com/journal/rra

By August 2011, other challenges were prominent at some sites (Table II). For Sites 5 and 6, sheep grazing to control leafy spurge resulted in trampling and uprooting of the shoreline seedlings, providing almost complete mortality. At the Bevers sites, portions of the Site 1 transect were lost through bank slumping. At Site 2, there was reasonable initial seedling establishment, but recreational use resulted in some trampling and bank slumping. The most promising sites were Sites 3 (Figure 5) and 4, and these sites required access by walking in or floating downstream, as opposed to the other sites that were vehicle accessible.

Table II. Cottonwood seedling establishment at six study sites along the lower St Mary River

Seeding site	Latitude longitude	Substrate	Vegetation	Outcome	Explanation
1. Bevers	49.372°N 113.029°W	Gravel and sand	Grasses	–	Seedling establishment was limited along a shoreline with a narrow barren band that was repeatedly scoured with higher flows.
2. Bevers launch	49.370°N 113.029°W	Gravel	Sparse grasses	+	Along the downstream zone of a meander lobe some seedlings established, but recreational use produced uprooting, trampling and bank slumping—reducing survival.
3. Fish hole	49.378°N 113.018°W	Cobble, gravel and sand	Barren	+++	A zone with modest expectation due to some exposed bedrock was very successful. Seedlings were thriving although flood flows in 2014 resulted in substantial scour.
4. Kayak launch	49.379°N 113.018°W	Sand	Sparse grasses and horsetail	+++	A sand bar along a meander lobe appeared promising but was extensively colonized by horsetail. The shading retarded seedling growth but many seedlings survived and future growth release is anticipated.
5. Welling ford 1	49.465°N 112.999°W	Cobble and gravel	Sparse leafy spurge and clover	–	Sheep grazing intended to control leafy spurge was substantial. The shoreline browsing, trampling and pugging killed all seedlings.
6. Welling ford 2	49.466°N 113.000°W			–	

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Following those impacts, Sites 3 and 4 contained the highest numbers of seedlings after the first growth season (Figure 6), with counts of 488 and 998, about 0.7% and 1.7% of the seeds supplied. These values were below the 7% establishment reported by Grabau *et al*. (2011) for seeding with a pre-wetted mixture of seed and mulch that was broadcast on a cultivated agriculture field and irrigated.

The seedling pattern of 2011 extended into 2012, when Site 3 appeared most successful (Figure 5). While abundant, the seedlings at Site 4 were apparently suppressed by the larger horsetail (*Equisetum arvense*) that provided shading and probably root competition. The spring count in 2012 indicated slight winter mortality, and there was some thinning through the summer, resulting in 70% and 37% survival from autumn 2011 to late summer 2012, for Sites 3 and 4.

For the 2011 and 2012 seedling counts, the assessments considered the sequential 20 × 50-cm quadrats that were directly along the initial transects and included the positions of the stuck cuttings. From July 2011, we observed seedlings outside of the band, and some were probably due to wind drift, and a very few were probably naturally occurring seedlings, because we observed a few seedlings in recruitment bands well away from our seeding zones. As the seedlings grew, species identification was more confident, and for 2013 and 2014, we expanded the quadrats to 1 × 1 m, but the primary bands of seedlings were still confined to narrower zones. This adjustment would only slightly alter the 2012 and 2013 inventories, and after the fourth summer in 2014, about 9% and 21% of the first-year seedlings remained at Sites 3 and 4, respectively (Figure 6).

The comparisons between the two species revealed a number of differences. Both produced about 33 capsules per catkin, but the prairie cottonwoods (*P. deltoides*) produced threefold more seeds per capsule and thus many more seeds per catkin (Table I). Seed viability was very high in both but slightly lower in the *P. angustifolia* clone number 6, suggesting slight differentiation. There were many more seedlings established below the stuck cuttings and along the seed spreading zone of the *P. deltoides*, and this increase was much larger than the difference in the numbers of seeds applied (Figure 6). Following the reduced establishment, there was also reduced survival of *P. angustifolia*. After 2013, only 6% of the *P. angustifolia* seedlings remained at the exposed Site 3 after the high flow summer of 2014 (Figure 3), while survival of *P. deltoides* was 10-fold higher, at 64%. At Site 4 that was less exposed to swift flood flows, there was increased survival of the *P. angustifolia* (52%), but this was still below that of the *P. deltoides* (75%). The *P. deltoides* appeared larger by the second growth season, and this was confirmed following the 2014 inventory by species, as the *P. deltoides* at Site 4 were about two-thirds taller than the *P. angustifolia* (37.3 ± 1.5 vs. 19.1 ± 2.9 cm).

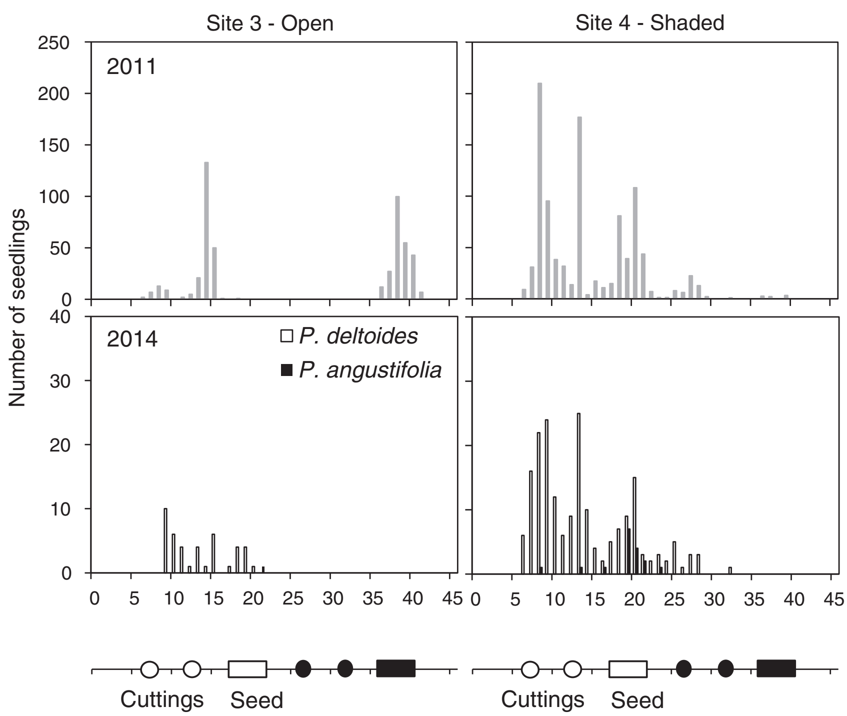

Figure 6. Seedlings along study transects for Sites 3 and 4 in the establishment year 2011 and in 2014, when seedlings were large enough for identification. The transects treatments are indicated in the following and estimated seed numbers for Site 3 were (from left): 23 200 seeds number 31 branch, 10 300 seeds second *Populus deltoides* branch and 20 600 mixed seeds spread; and for *Populus angustifolia*: 5100 (number 6), 2900 and 10 000 seeds. For Site 4: ~23 200, 460 and 20 600 *P. deltoides* seeds, and 5500, 3900 and 10 000 *P. angustifolia* seeds

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DISCUSSION

This novel, twofold field application clearly supported our three hypotheses. There was extensive cottonwood seedling establishment following the branch sticking or seed spreading but almost no seedlings along the non-seeded reference zones. This indicated that the lack of cottonwood seedlings along the lower St Mary River was due to the lack of parental trees and seeds, supporting our first hypothesis.

After germination, there was substantial seedling survival, and this reflected the favourable moisture condition that followed from the gradual flow ramping (Segelquist *et al*., 1993; Sprenger *et al*., 2002; Bhattacharjee *et al*., 2006; 2008). We have previously demonstrated strong correspondence between river stage and the alluvial groundwater along this river reach with piezometers situated near Sites 5 and 6 (Rood *et al*., 1995). The seedling survival through the first summer was thus probably promoted by the deliberate flow ramping, and this supported our second hypothesis that the functional flow regime would promote seedling establishment and survival.

Seedling survival through the third summer may be considered as the transition from 'establishment' or 'colonization' to 'recruitment' (Polzin and Rood, 2006) because the root systems should be sufficiently deep and complex to enable survival through the subsequent seasonal groundwater variations (Rood *et al*., 2013). Conversely, there was substantial removal of seedlings at the exposed Site 3 in the fourth year, 2014, including almost complete removal of the *P. angustifolia* seedlings. The 2014 peak provided about a 1-in-10-year high flow that would have produced substantial sediment erosion and shear stress that combined to uproot the seedlings. Consistent with this interpretation, there were fewer seedlings lost at the more protected Site 4.

Supporting our third hypothesis, we observed differentiation across the two species (Table I and Figure 6, Wilding *et al*., 2014). Seed viabilities were almost complete, but there might be a slight reduction in *P. angustifolia*. Following either the cut branch sticking or direct seeding, we observed many more *P. deltoides* seedlings than those of *P. angustifolia*. After establishment, the *P. deltoides* seedlings' survival was higher, and those seedlings grew taller. All of these traits could benefit seedling establishment in *P. deltoides*, and this superior sexual reproduction might compensate for the relative deficiency in clonal or asexual reproduction (Gom and Rood, 2000). The study thus supported our prediction that there would be greater seedling recruitment of *P. deltoides* relative to *P. angustifolia*.

With a broader perspective, these results expand our understanding of the reproductive ecology of riparian cottonwoods. Seedling reproduction requires three conditions: (1) suitable colonization sites, which are generally well-draining substrates of sands and gravels, barren of competing vegetation; (2) sufficient viable seeds; and (3) water to support germination and subsequent growth and survival. Along rivers, these three requirements converge particularly along arcuate bands of meander lobe point bars and also along lateral bars and the fringes of islands or other floodplain features (Kalischuk *et al*., 2001; Benjankar *et al*., 2014).

The natural river dynamic is responsible for the first requirement, the formation of the barren colonization sites (Scott *et al*., 1996; Polzin and Rood, 2006). High and swift river flows scour away vegetation and provide the sediment erosion, transport and deposition that build new nursery sites. Flood flows are especially competent for the geomorphic disturbance, and as a consequence, there are typically pulses of cottonwood colonization after moderate or major floods (Scott *et al*., 1997; Polzin and Rood, 2006)—floodplain forests require occasional floods.

For seed availability, cottonwoods display an r-selection reproductive strategy as vast numbers of seeds are produced, but very few ultimately contribute to the woodland population (Dixon, 2003; Polzin and Rood, 2006). The period of seed release is limited to around 3–8 weeks, and viability of the tiny seeds falls quickly after dispersal (Herbison *et al*., 2015). There is no year-round seed bank, and the interval of seed dispersal and viability must coincide with the availability of suitable colonization sites. The spatio-temporal convergence of the viable seed and suitable, barren sites is only satisfied in very specific riparian zones (Scott *et al*., 1996; Rood *et al*., 2003 Dixon, 2003; Benjankar *et al*., 2014).

The third requirement, moisture for germination and seedling survival, may also result from the instream flow pattern, particularly in semi-arid regions where summer precipitation is sparse. Thus, along rivers like the lower St Mary River, the seedlings are dependent upon moisture that is provided by the capillary fringe above the alluvial groundwater table (Rood *et al*., 2011; 2013), and this is why flow ramping is essential for seedling survival. Conversely, in more humid ecoregions, rain provides an alternate moisture supply, and consequently the summer flow regime is less critical (Polzin and Rood, 2006; Rood *et al*., 2011; Herbison *et al*., 2015). For all riparian woodlands, the flow regime is essential for the fluvial geomorphic disturbance and sediment movements that produce the barren colonization sites (Scott *et al*., 1996; Polzin and Rood, 2006).

DIRECTIONS FOR RIPARIAN RESTORATION

Our study confirmed that a deficiency of cottonwood seeds because of the loss of parental trees will prevent cottonwood colonization, even if suitable nursery sites were available and a favourable instream flow regime was provided. We thus investigated the prospect of direct seeding, and the

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result was promising. Because of the quick collection and implementation, and the broader seedling establishment interval and spatial extent, we conclude that the cut branch method could be very effective. We might recommend larger branches that would provide more seeds and a higher source of dispersal.

After seeding, the functional flow regime enabled seedling survival through the critical first summer, and we encourage continued flow ramping in all years to promote growth and survival. In our study, in the flood flow year of 2014, there was another delivery of the functional flow regime (Figure 4) that should benefit cottonwood and willow colonization along the downstream river segments, where mature trees persist to provide seeds (Rood *et al*., 1995; Rood and Mahoney, 2000).

With the combination of direct seeding and the delivery of a favourable functional flow regime, we anticipate that it should be possible to restore riparian woodlands along severely degraded reaches such as the canyon segment of the lower St Mary River. We would anticipate modest cost for seeding, and this could be ideal for 'citizen science' (Silvertown, 2009) whereby youth or volunteer groups would contribute to the branch collection, sticking and seedling monitoring. Following seedling establishment, the riparian land-use must be managed, and this should limit livestock grazing and recreational use.

As a practical strategy, we recommend staggered implementation, whereby particular meander lobes are identified for initial recolonization and over time, different meander lobes would be seeded. There are also other considerations such as deer browsing that can be severe for sparse saplings and beaver cutting that would likely advance as the saplings grow in size. We thus anticipate that there would be a number of physical and biotic influences, and woodland restoration would require long-term commitment.

Finally, the lower St Mary River represents a case study in which the conservation and restoration efforts would have been much more practical before the mature trees had been lost. The woodland decline was measureable in air photos from 1961 vs. 1951, and if functional flow patterns had been implemented following the natural high-flow years between 1961 and 2000, the woodlands would probably have persisted. This twofold restoration strategy might thus be regarded as a desperate measure, and earlier efforts for conservation and restoration would be more practical.

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