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FLUVIAL DISTURBANCE PATCHES AND COTTONWOOD RECRUITMENT ALONG THE UPPER MISSOURI RIVER, MONTANA

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Abstract: The disturbance patches most suitable for seedling establishment of pioneer riparian trees are also subject to future disturbances that produce high seedling mortality. We are monitoring plains cottonwood seedling establishment and mortality along the Wild and Scenic reach of the Missouri River upstream of Fort Peck Reservoir, Montana at four sites subject to livestock grazing and four paired, ungrazed exclosures. New seedlings at these sites were largely restricted to surfaces inundated by spring and summer flows. Winter ice drives and livestock grazing are important mortality factors along the study reach. Livestock grazing reduced seedling densities, although the position of these seedlings in normal flow years means it is unlikely that they will survive future disturbance. Average values of the maximum density parameter of a Gaussian curve of seedling distribution along a hydraulic gradient of inundating discharge were 30 and 114 seedlings/m^2 on ungrazed sites in 1996 and 1997, compared to 19 and 18 seedlings/m^2 for grazed sites. Water-surface elevations produced by ice drives and damming in the severe winter of 1995–1996 corresponded to inundating discharges of 1,670 to 4,580 m^3/s. No existing trees at the study sites occurred at inundating discharges below 1,625 m^3/s. Seedlings established as a result of maximum summer flows of 827 and 1,201 m^3/s in 1996 and 1997 were all below the elevation of the 10-year return flow of 1,495 m^3/s. Recruitment of plains cottonwood trees along this reach of the Missouri River is strongly dependent on infrequent high flows that position moist, bare disturbed patches high enough for seedlings to establish and survive subsequent flooding and ice scour, in contrast to other reaches and streams where hydrogeomophic processes of channel meandering and narrowing produce different patterns of disturbance patches.

Key Words: dam, flood, livestock grazing, hydrogeomorphic, ice, *Populus deltoides*, riparian, seedling demography, streamflow

INTRODUCTION

Riparian forests represent critical structural habitat in arid and semi-arid landscapes throughout western North America and are valued for their role in supporting regional biological diversity, as well as a range of human economic and recreational activities (Brinson et al. 1981, Finch and Ruggiero 1993). Widespread declines in riparian forests of arid and semi-arid regions have been observed in association with a variety of human water- and land-use practices, including flow alteration (Johnson et al. 1976, Bradley and Smith 1986, Rood and Heinze-Milne 1989, Rood and Mahoney 1990, Johnson 1992) and heavy cattle grazing (Ames 1977, Boldt et al. 1978). Short-term increases in riparian tree recruitment have been noted along some semi-arid region rivers following flood-induced channel widening or flow reductions below dams (Johnson 1994, Friedman et al. 1996). Variation in the responses of riparian forest to similar flow modifications are largely a consequence of flow-related channel change and emphasize the importance of interpreting or predicting riparian forest response to flow in the context of the dominant fluvial geomorphic processes acting along a particular stream or reach (Scott et al. 1996, Johnson 1998).

Although sparse, stands of plains cottonwood (*Populus deltoides* Marsh. subsp. *monilifera* (Ait.) Eckenw.) along the Wild and Scenic reach of the upper Missouri River in Montana, USA are highly valued for wildlife habitat and human recreation. The majority of existing trees within this reach established as seedlings in association with infrequent, high-magnitude floods. Since the mid-1950s, flows within the Wild and Scenic reach of the Missouri have been influenced by the operation of two upstream Bureau of Reclamation dams, and cattle grazing has been ubiquitous since the turn of the century (Scott et al. 1997). Based on a retrospective study linking historical peak flows to establishment years of excavated cottonwood stems, Scott et al. (1997) concluded that because of limited channel

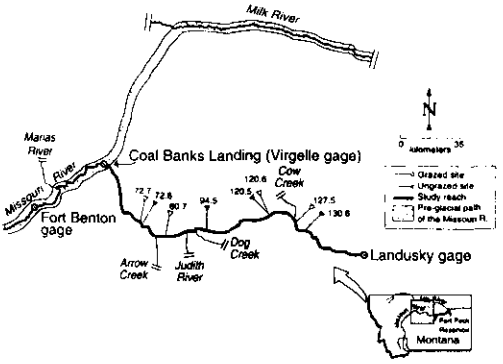

Figure 1. Study reach of Missouri River, MT indicating sampling sites and the pre-glacial course redrawn from Lemke et al. (1965) and Scott et al. (1996).

movement, only infrequent, large flows could create the physical site conditions required for seedling establishment at channel elevations that were high enough to allow for successful tree recruitment. However, their analysis did not account for the possible influence of widespread cattle grazing in this reach as a factor in cottonwood seedling establishment and survival.

Maintenance of cottonwood forests along the Wild and Scenic Missouri river will be achieved through a long-term balance among physical processes that control patterns of recruitment and mortality. A more complete understanding of the interplay among these processes would be an important element of water and land-use management decisions that seek to protect the future of cottonwood forests along this reach of the Missouri. Accordingly, we initiated a seedling monitoring study to (a) examine the mechanisms responsible for the historical flood dependence of cottonwood recruitment along the Wild and Scenic reach of the Missouri River (Scott et al. 1996) by direct observations of seedling establishment and mortality over a range of flow conditions and (b) examine how cattle grazing acts as an additional control on cottonwood recruitment. This paper reports on the first two years of plains cottonwood seedling demography data.

STUDY REACH

Our study reach is the 172-km section of the Missouri River from Coal Banks Landing to the upper end of Fort Peck Reservoir (Figure 1). It is within the section of the upper Missouri River designated as Wild and Scenic. The channel in this geologically young reach has low sinuosity and is constrained within a narrow valley. Before the Pleistocene, the Missouri River diverged from its modern course near Coal Banks Landing, flowing north and east into Hudson Bay (Figure 1, Lemke et al. 1965, Wayne et al. 1991). Our study reach thus differs from the sections of the Missouri River above Coal Banks Landing and below the modern confluence with the Milk River downstream from Fort Peck Reservoir. These reaches typically have higher sinuosities, wider valleys, and more rapid channel migration, at least prior to regulation.

The Missouri River in Montana has a snow-melt-dominated hydrograph, with peak flows typically occurring in late May or early June and low flows occurring in fall and winter. A Log Pearson III analysis for the period 1936–1997 showed that the 2-, 5-, 10-, and 100-year return floods are 657, 1,119, 1,495, and 3,081 m^3/s, based on maximum annual value of daily discharge. Stages produced by winter ice jams are frequently higher than stages associated with the highest discharge of the year. Flow in the study reach is influenced by a number of diversions and upstream dams, principally Canyon Ferry dam on the mainstem and Tiber dam on the Marias River. Although large peak flows still occur, a reconstruction of unregulated flows indicated that, since 1954, dams have attenuated peak flows by 14–23% at Fort Benton, located above the confluence with the Marias, which is also regulated (Ramey et al. 1993, Rood and Mahoney 1995). Widespread timber cutting for steamboat fuel occurred along the Missouri River in Montana from 1860 to 1890 (Hansen 1989), and cattle grazing has occurred throughout most of the study reach since 1900.

The dominant riparian tree species along the study reach is plains cottonwood (*Populus deltoides* subsp. *monilifera*). Box elder (*Acer negundo* L.), green ash (*Fraxinus pennsylvanica* Marsh.), and peachleaf willow (*Salix amygdaloides* Anderss.) are also present. The riparian cottonwood forest consists of discontinuous, narrow, often single-ranked stands of trees. Historical accounts suggest that cottonwood stands in the study reach were also spatially restricted prior to European settlement of the region (Coues 1893).

METHODS

Study Sites

In collaboration with the Lewistown District, MT of the Bureau of Land Management, we began monitoring a set of four livestock grazing exclosures along the study reach in 1996 (Figure 1). Two of these exclosures were pre-existing but had not been effectively maintained prior to 1996. For each exclosure, we identified a paired grazed site. In two cases, the paired site was adjacent to the exclosure. In the other two cases, the valley geometry precluded a comparable adjacent

site, and the paired site was selected from aerial photos and ground reconnaissance to match the geomorphic setting of the exclosure. Location of the exclosures was influenced by the practicalities of fencing, maintenance, and grazing administration, as well as by interest in encouraging cottonwood recruitment. In particular, their location is biased towards more geomorphically active areas (e.g., near tributary junctions) where potential for cottonwood recruitment might be higher than for the reach as a whole.

At each site, we installed bench marks (galvanized pipe hand-driven to a depth of 1.5–3 m) on a high terrace and established three transect lines perpendicular to the channel. Rebar markers were placed at several locations on each transect to facilitate alignment and relocation of sampling plots along the transect. Transect locations within the site were determined by random selection from a set of 6–10 possible locations laid out with at least 10-m separation between transects. Exclosure areas were 1.0, 2.2, 4.8, and 12.9 hectares, with much of the variation due to how much upland area was fenced adjacent to the bottomland. For all sites, distance from the upstream to downstream transect averaged 65 m, with a range of 30 to 133 m. At 6 of the 8 sites, only two transects were sampled in 1996. In the analysis reported here, all sampled plots were pooled by site regardless of the transect on which they occurred. To standardize across sites, all transects were truncated to contain only the area below the elevation of an inundating discharge of 3,500 m^3/s. Transects were extended into the channel to a depth approximately 0.5 m below the water surface at the annual low flow. Transect lengths from the 250-m^3/s flow line to the 3,500-m^3/s flow line averaged 93 m, with a range of 48 to 162 m.

Field Sampling

Cottonwood seedlings are counted during a single annual census between August 15 and September 1. Elevations at 1-m intervals along each transect were determined to within 1 cm with a total station and are checked annually to determine net erosion or deposition. Four age-size classes of *Populus deltoides* subsp. *monilifera* stems are distinguished: 1) new, young-of-the-year seedlings (identified in late August by the presence of cotyledons and lack of leaf scars); 2) older seedlings (with leaf scars, no cotyledons, and less than 1 m tall); 3) saplings (stem greater than 1 m tall and less than 2.5 cm in diameter); and 4) trees (stems greater than 2.5 cm in diameter, measured 1.2 m above the ground).

Seedlings and saplings are censused in plots at 1-m intervals within belt transects centered on each permanent transect line. Seedlings are censused in 1×5 m plots placed on alternate sides of the transect center line, while saplings are censused in a 1×10 m belt transect centered on each transect line. Relocation of the plots along each transect is facilitated by stretching a marked tag line between permanent, marked rebar. A collapsible, multiple-plot sampling frame of PVC pipe and cord is then aligned along the tag line to delineate plots. Alternating plots allow access to seedling plots with minimal trampling. Trees are censused every 2 to 3 years on the entire area between the upstream- and downstream-most transects. Zones of trees located on surfaces of similar elevation are circumscribed by the width of the surface perpendicular to the channel and the distance between the outermost transect lines where they intersect the surface supporting trees.

Water-surface elevations are marked by flagging or surveying the water's edge on specific days, representing a range of discharges throughout the year. High water lines associated with annual peak flow, or high stages associated with winter ice damming, are identified at each site based on the location of debris and freshly deposited sediment within several months of the event. Marked water lines are then converted to elevations at each site by surveying relative to the permanent bench marks.

Hydrologic Analysis

The most precise way to determine the inundating discharge of a point along a vegetation transect is to use local measurements of stage and discharge combined with a hydraulic model to determine the local stage-discharge relation. Where discharge varies between sites, a flow duration curve can be used to convert inundating discharge to inundation duration, or hydroperiod (Auble et al. 1994, 1997). Relative elevation can be a reasonable surrogate for inundation duration (Scott et al. 1997) but introduces error where stream gradient, channel shape, discharge, and roughness vary among cross-sections. Our approach for comparing locations within and between sites is a compromise because it was not feasible to develop, calibrate, and revise site-specific hydraulic models and measure discharge separately at each site over time. Thus, all plots were registered to a common gradient of inundating discharge based on site-specific empirical rating curves developed from measured water-surface elevations at each site and discharge at a single upstream gage (Virgelle gage at Coal Banks Landing, USGS gage 06109500, Figure 1).

Vegetation Analysis

The analysis reported here focuses on the relative position of cottonwood age-size classes along a com-

mon gradient of inundating discharge. Cottonwood distributions are summarized separately by year of sampling, livestock grazing treatment, and age-size class. Each 1×5-m seedling plot was assigned an inundating discharge from the hydraulic rating curve described above, and plots from the three transects at a site were pooled for a given year. A Gaussian response curve was then fit to seedling abundance by year, site, and age-size class as a function of inundating discharge, adapting the approach of Ter Braak and Looman (1986):

$$\mathrm{SEED} = c_{max} \cdot \exp[-0.5 \cdot (\mathrm{IQ}_{vir} - u)^2/t^2] \qquad [1]$$

where,

- SEED = seedling abundance at a plot
- IQ_{vir} = inundating discharge of a plot relative to Virgelle gage
- c_{max} = maximum abundance
- u = optimum value of inundating discharge, IQ_{vir}
- t = species tolerance, standard deviation on inundating discharge gradient.

The parameters of the response curve were derived from a maximum likelihood fit of a generalized linear model using the SAS GENMOD procedure (SAS Institute 1989) of Version 6.12. The regressions used a log link function, a Poisson error distribution, and an overdispersion scale factor calculated as the deviance divided by the degrees of freedom. In 4 of 16 cases, there were no seedlings in the older age class at a site in a given year. In these cases, a value of 0 was used for the aggregate maximum abundance (c_{max}) parameter, and the site was considered missing for estimation of u and t. The three parameters (c_{max}, u, and t) representing the distribution of a seedling age class for each site and year were averaged across the grazed (n=4) and ungrazed (n=4) sites to yield a composite distribution for each year, age-size class, and livestock grazing treatment. Pairing of the sites was ignored for this analysis.

The distribution of trees was calculated as weighted average densities within 50 m³/s-wide classes of inundating discharge. Inundating discharges were determined at 1-m increments along each transect, and tree densities along the transect were derived from the census of polygons containing trees, assigning zero density to sections of the transect outside these polygons.

RESULTS

Example Transect

The distribution of young-of-the-year seedlings (SEED_{new}) in 1997 at the middle transect of the grazed site near Cow Island (Site 127.5, Figure 1) illustrates our field sampling and data analysis for one of the three transects annually sampled at each site. Surveyed elevations (Z_{adj}) at 1-m intervals along the transect characterize the topography and define the edges of the vegetation sampling plots (Figure 2A). Elevations of the high and low flow during the summer germination period from May 15 to September 1, 1997 and the end of the transect corresponding to the calculated 3,500-m³/s flow line are also indicated on Figure 2A. Data points on Figure 2B represent densities of new seedlings on individual 1×5-m plots arrayed at 1-m intervals along the transect. At higher elevations, the

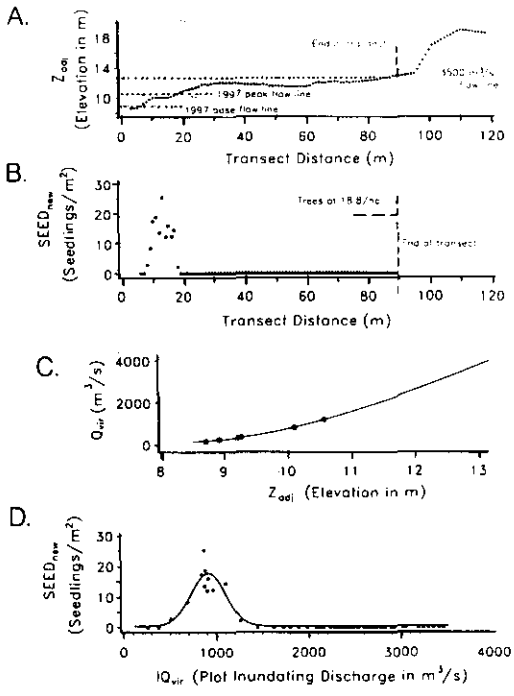

Figure 2. Topography, rating curve, and new cottonwood seedling densities from 1997 sampling at middle transect of grazed Site 127.5. (A) Elevations, Z_{adj}, are adjusted to local benchmark. Peak and base flow lines are maximum and minimum between May 15 and September 1. (B) Densities of seedlings germinating in 1997, SEED_{new}, are from 1×5 m² plots at specified distances along transect. Tree densities were determined by sampling entire zone of occurrence as a single plot. (C) Rating curve of Virgelle daily discharge, Q_{vir}, as a function of adjusted site water surface elevation, Z_{adj}. Calibration points are from a combination of daily observations and high water lines. (D) Distribution of 1997 plot seedling densities, SEED_{new}, as a function of plot inundating discharge.

transect intersected a polygon of trees that extended slightly beyond the upland edge of the transect to the base of a high bank defining the edge of the bottomland. The density of trees in the polygon was 18.8/ha, and this value was assigned to all the 1-m intervals of the transect intersecting the zone of tree occurrence.

The rating curve used to determine the discharge at the Virgelle gage (Q_{vir}) that inundates plots at given elevations at Site 127.5 is depicted in Figure 2C along with the calibration data points used to fit the curve. Application of the rating curve (Figure 2C) to the relative elevations of transect plots (Z_{adj}) produces a data set of plot seedling densities ($SEED_{new}$) by inundating discharge as measured at Virgelle (Q_{vir}). Thus, the distribution along an elevational gradient depicted in Figure 2B can be converted to the distribution along the hydraulic gradient of inundating discharge depicted in Figure 2D. A Gaussian response curve (Eq. 1), fit to the plot data for this individual transect using a generalized linear model, is also shown in Figure 2D. The fit parameter values for the curve of Figure 2D are: c_{max} = 17.4 seedlings/m^2; u = 902 m^3/s; and t = 188 m^3/s.

Aggregated Distributions

The 1996 and 1997 distributions of seedlings by age-size class and livestock grazing treatment along the gradient of inundating discharge are summarized in Figure 3, along with the distribution of trees from all sites, the position of ice-related stages from the winter of 1995–1996, and the discharge ranges of the 1996 and 1997 summer germination periods. Although Figure 3 depicts several complex relations, the portrayal is highly aggregated from the raw data. Each of the seedling distribution curves was derived by averaging (n=4) parameter values from individual curves fit to each site using data from 1-m intervals along three transects at each site. The parameters of the distribution for the individual paired sites are given in Table 1.

The age-size classes of cottonwood differ in density by roughly four orders of magnitude (Figure 3). There were substantially fewer seedlings of both seedling classes at grazed sites. Average values of maximum abundance (c_{max}) for new seedlings on ungrazed sites (n=4) were 30.0/m^2 in 1996 (site range of 0.16 to 85.8/m^2) and 113.8/m^2 in 1997 (site range of 0.17 to 250.2/m^2). Grazed sites (n=4) had lower average densities of new seedlings, with c_{max} values of 19.0/m^2 in 1996 (site range of 1.1 to 70.8/m^2) and 18.2/m^2 in 1997 (site range of 0.16 to 48.5/m^2). The contrast between grazed and ungrazed sites was greater for older seedlings. Older seedlings had c_{max} values of 1.3/m^2 in 1996 and 0.92/m^2 in 1997 (site ranges of 0 to 3.9/m^2 and 0.16 to 2.1/m^2, respectively) at ungrazed sites, compared to grazed site values of 0.11/m^2 in both 1996 and 1997 (site ranges of 0 to 0.40/m^2 and 0 to 0.24/m^2, respectively).

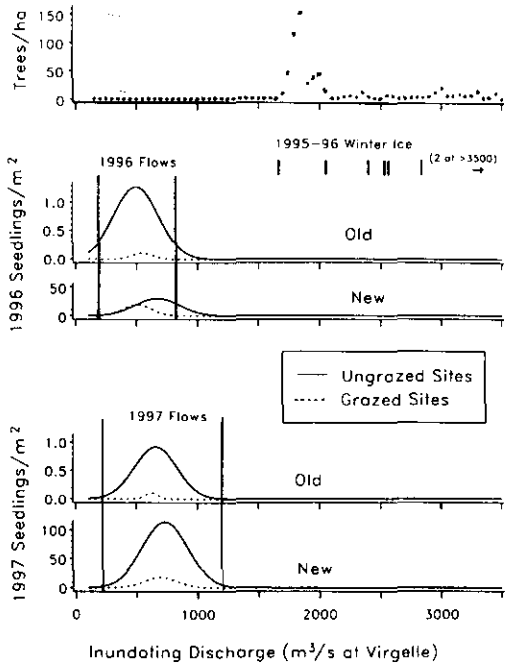

Figure 3. Cottonwood distribution on gradient of inundating discharge. Trees are average densities for narrow ranges of inundating discharge across all sites. Seedling curves are derived from fit site-specific normal distributions of seedling counts as a function of the inundating discharge (text Eq. 1) by averaging the maximum density, mean, and standard deviation parameters from the sites (n=4) for each combination of age class, livestock grazing treatment, and year. Note different units of density. New, young-of-the-year seedlings germinated in the current year, old seedlings (<1 m tall) germinated in a previous year, and trees are >2.5 cm diameter. All inundating discharges are with reference to the Virgelle gage near Coal Banks Landing. The flow recommendation for cottonwood regeneration is registered to the Virgelle gage from the Fort Benton gage used by Scott et al. (1997) as described in text. Ice lines from the winter of 1995–96 are high water lines of elevated stages from ice damming. Ice-related stages in winter 1996–97 did not exceed the maximum summer flow. Summer flow ranges are the maximum and minimum daily flows from the period May 15–September 1.

New seedlings were strongly restricted to the zone between the high and low water lines during the period May 15 to September 1 (Figure 3). The mean gradient

Table 1. Parameters of Gaussian distribution (Eq. 1) of seedlings at paired study sites (U = Ungrazed, G = grazed).

		Site		c_{max} (#/m²)		t (m³/s)		u (m³/s)	
Year	Age	U	G	U	G	U	G	U	G
1996	New	72.8	72.7	23.36	0.44	166	167	776	696
		94.5	80.7	10.69	70.79	113	82	543	458
		120.5	120.6	0.16	1.15	168	31	1278	229
		130.8	127.5	8.58	3.56	280	186	92	657
1996	Old	72.8	72.7	0.86	0.40	315	84	117	413
		94.5	80.7	0.36	0.04	170	—	517	675
		120.5	120.6	0.0	0.0	—	—	—	—
		130.8	127.5	3.89	0.0	59	—	866	—
1997	New	72.8	72.7	27.50	2.07	163	143	820	838
		94.5	80.7	250.18	48.54	162	111	681	673
		120.5	120.6	0.17	0.16	219	84	627	441
		130.8	127.5	177.39	21.91	209	205	812	826
1997	Old	72.8	72.7	2.09	0.05	172	42	668	433
		94.5	80.7	0.53	0.14	235	63	480	521
		120.5	120.6	0.16	0.0	180	—	676	—
		130.8	127.5	0.90	0.24	111	49	799	914

position parameter, u, was 672 m³/s for grazed sites and 510 m³/s for ungrazed sites in 1996, which had a May 15 to September 1 flow range of 163 to 827 m³/s. Higher flows in 1997 (222 to 1,201 m³/s) shifted the distribution upward to u values of 734 m³/s for ungrazed sites and 694 m³/s for grazed sites. In grazed and ungrazed sites in 1997 and in ungrazed sites in 1996, the summer flow range contained at least $u \pm 2.5 \cdot t$, corresponding to more than 98% of the distribution of new seedlings. New seedlings were more dispersed in the ungrazed sites in 1996, but the range of summer flow still contained $u \pm 1.16 \cdot t$, corresponding to over 75% of the seedling distribution. Distributions of older seedlings were also centered within the summer flow ranges, with u values of 500 and 544 m³/s for grazed and ungrazed sites in 1996 and values of 656 and 623 m³/s for grazed and ungrazed sites in 1997.

Trees occurred on surfaces with different and higher inundating discharges than seedlings. The lowest inundating discharge range with trees was 1,625 to 1,675 m³/s, with a density of 8.7/ha. No seedlings of either age class in 1996 or 1997 were found in plots with discharge greater than 1,500 m³/s. Maximum tree density of 150.5/ha was in the discharge range of 1,825 to 1,875 m³/s. Less than 10 total plains cottonwood saplings were observed in either 1996 or 1997. These occurred at only two sites, were all obvious root or stump sprouts from trees, and occurred at locations with inundating discharges of 1,800 m³/s or larger. The winter of 1995–96 had severe river ice. Water-surface elevations produced by ice drives and damming were identified at each site from scoured vegetation, sediment deposition, debris, and relict blocks of ice remaining in mid-May. These elevations were transcribed to the gradient of inundating discharge using the site rating curve, understanding that they do not reflect an actual discharge and that the rating curve for these discharges is questionable because of the extent of extrapolation. Ice elevations corresponded to inundating discharges of 1,670 to 4,580 m³/s, generally within the range of positions occupied by existing trees. There was no evidence or observation of ice in the winter of 1996–97 at elevations higher than those inundated by the high summer flow of 1,201 m³/s.

DISCUSSION

Fluvial disturbance patches of freshly deposited or reworked alluvium typically provide ideal substrate for establishment of plains cottonwood. Seedlings require a continuously moist surface during the first week or more of growth (Moss 1938). Abundant seeds are released early each summer (Scott et al. 1993, Johnson 1994) and lose germinability within a few weeks (Moss 1938, Ware and Penfound 1949). Cottonwoods rarely recruit successfully from seed under an existing stand of trees (Johnson et al. 1976) or herbs (Friedman et al. 1995). By the end of the first growing season, seedlings are able to survive declines in the water table of 1 m or more (Fenner et al. 1984, Mahoney and Rood 1991, Segelquist et al. 1993). However, drought mortality in arid regions may impose an upper limit on height of seedling recruitment above the river or ground-water surface. Recruitment of seedlings to trees depends on protection of seedling establishment

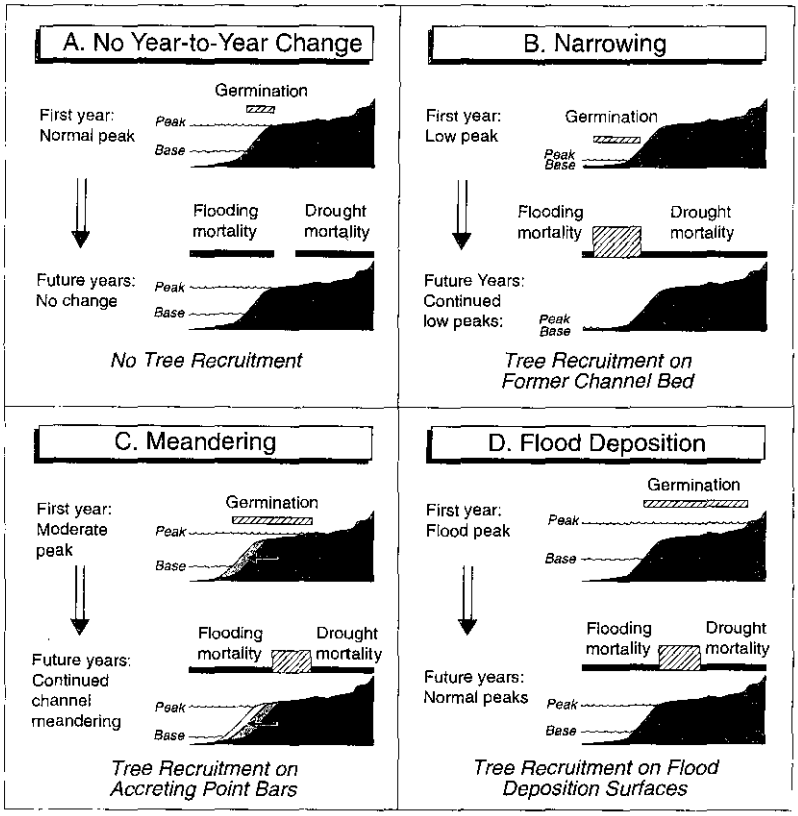

Figure 4. Hydrogeomorphic control of cottonwood recruitment: diagrammatic representations of cottonwood seed germination, early seedling mortality, and tree recruitment in relation to annual high and low flow lines along a bottomland elevational gradient. Four idealized situations are depicted using a single bottomland cross-section: (A) little or no tree recruitment in the absence of inter-annual flow variability and channel movement, (B) channel narrowing with recruitment on the former channel bed, (C) recruitment on point bars of a meandering river, and (D) tree recruitment at high elevations associated with infrequent floods and no channel movement.

sites from subsequent intense disturbances that kill or remove seedlings (Stromberg et al. 1997).

Hydrogeomorphic Recruitment Model

Scott et al. (1996) introduced a hydrogeomorphic recruitment model to describe some of the ways rivers generate the sequence of site establishment and survival conditions necessary for cottonwood recruitment. The model assumes a minimal set of physical requirements for seedling recruitment, including establishment sites that are bare, moist, and relatively safe from physical disturbance. Complexity in the pattern and extent of seedling recruitment emerges from the ways in which riverine hydrologic and geomorphic processes create suitable establishment sites on the landscape. Many fluvial processes produce suitable recruitment sites, and actual reaches may have combinations of these processes operating with their relative importance changing over time. Scott et al. (1996) and Friedman et al. (1997) described how the contrasting geomorphic processes of meandering, narrowing, and flood deposition produce different spatial and temporal patterns of riparian forest. These three cases are illustrated in Figure 4. This illustration uses a single bank geometry, typical of our study reach, and compares cases of successful tree recruitment patterns with the null case of No Year-to-Year change, where no recruitment to sapling or tree size classes occurs.

Suitable combinations of disturbance and moisture

are present each year in the wetted edge zone between summer peak flow and late summer base flow. When there is no year-to-year change, seeds germinate each year and survive the summer only to be eliminated by next year's flooding or winter ice in the repeatedly disturbed zone adjacent to the channel (Figure 4A). In situations of severe flow stabilization (e.g., in a highly regulated river with a large storage capacity relative to annual discharge) or along a highly confined or bank-stabilized channel, young-of-the-year seedlings are present every year, but there are no saplings. The inner banks of irrigation delivery canals often fit this case, as do flow-regulated and stabilized urban reaches (Auble et al. 1997).

Some combination of flow variability and channel change different from the No Year-to-Year change case of Figure 4A is necessary to produce successful tree recruitment. Some of the possible combinations are Channel Narrowing (Figure 4B), Channel Meandering (Figure 4C), and Flood Deposition (Figure 4D). Correspondence of the ages of extant trees with historic floods led Scott et al. (1997) to suggest that Flood Deposition (Figure 4D) was the dominant mode of cottonwood recruitment along the constrained Wild and Scenic reach of the Missouri River. The two years of demography data reported here support that conclusion. Seedling establishment observed in the moderate flow years of 1996 and 1997 (Figure 3) was concentrated in the zone occupied by the water's edge from May 15 to September 1. Furthermore, this zone was well below the high position of trees on the inundating discharge gradient (Figure 3). Because the channel is not moving, the only locations safe from subsequent scouring are high on the bank.

In the Flood Deposition mode of Figure 4D, floods produce bare, moist surfaces that are high above the channel bed and therefore relatively safe from future fluvial disturbance. Floods occur along most streams and also play important roles in other fluvial processes that create suitable establishment sites. Infrequent floods may produce large episodic channel movement in a meandering pattern with consequently larger patches of even-aged cottonwood establishment (Figure 4C). Floods may temporarily widen the channel, setting the stage for recruitment during subsequent narrowing (Figure 4B).

Ice and Livestock Grazing

The importance of ice drives along our study reach strengthens the flood dependence of cottonwood recruitment by increasing the mortality of seedlings established at positions inundated at low flows. The resulting pattern is similar to Smith's (1980) generalized description of an enlarged, 2-bench channel geometry for northern rivers subject to ice drives. This geometry consists of a low bench corresponding to the elevation of the 2-year summer flow and a higher bench corresponding to the 9-year return summer flow but maintained by ice drives. He found that trees were limited to the higher bench but were typically ice scarred. Along our study reach, Scott et al. (1997) found that most surviving cottonwood trees were established in association with flows greater than the 9–10 year return flow. Even at these high positions, trees had ice scars dating to years with large ice jams (Scott et al. 1997). This is consistent with the overlap between the zone occupied by trees and the zone subject to ice scour during the extreme ice events of 1995–1996 (Figure 3).

In 1997, the maximum daily Virgelle gage flow of 1,201 m^3/s was the largest since 1981 but did not exceed the 10-year return flow of 1,495 m^3/s. Upstream dams (principally Canyon Ferry and Tiber) reduce high flows, which complicates determination of flood frequencies and diminishes cottonwood recruitment potential. The reduction in peak discharge has decreased the frequency and extent of overlap between the zone inundated by high flow where seedlings might become established and the zone above frequent ice disturbance where those seedlings might survive to become trees (Figure 3).

Cattle grazing can strongly affect riparian plant communities, and dramatic re-establishment of woody riparian vegetation has been observed following elimination or reduction of livestock grazing along some streams and rivers (Chaney et al. 1990, Green and Kauffman 1995). Along our study reach of the upper Missouri River, ungrazed exclosures have higher overall densities of both new and old cottonwood seedlings at the end of the summer than do grazed sites. However, the position of those seedlings along the inundating discharge gradient and the Flood Deposition mode of cottonwood recruitment operating along this reach suggest that livestock grazing may not matter in most years. The frequently disturbed patches where the majority of seedlings are observed in most years are unlikely to produce tree recruitment regardless of livestock grazing pressure. Livestock grazing could be considerably more important in the years following an infrequent, high magnitude flood that provided hydrogeomorphically suitable sites for tree recruitment.

Additional Considerations

We believe that the Flood Deposition model of Figure 4D with the superposition of livestock grazing and ice mortality is the dominant process controlling cottonwood recruitment dynamics and forest stand pattern along the constrained Wild and Scenic reach of the

Missouri River. Nonetheless, there are some alternative explanations and unanswered questions.

(1) Analysis of the inundating discharges of trees reported here is based on elevations at the base of the tree. If these elevations were substantially higher than the establishment elevations of the tree, our data could reflect the Meandering case of Figure 4B, rather than Flood Deposition. In their excavation of 65 trees along our study reach, Scott et al. (1997) did excavate a few trees that had experienced substantial aggradation in geomorphically active positions such as accreting island edges. However, 98% of the trees more than 15 years old had establishment elevations greater than 1.2 m above the lower limit of perennial vegetation. Seedling establishment on low surfaces that subsequently aggrade to positions of high inundating discharge is occurring along our study reach but is not the dominant situation.

(2) Livestock grazing may interact with streamflow in ways that we have not yet measured. For example, we have not yet directly observed livestock grazing effects on a disturbance patch produced by an infrequent flood. Differences in livestock grazing may or may not have an important effect on tree recruitment when combined with a high flow and spatially extensive seedling establishment. It is also possible that a reduction in livestock grazing pressure would produce more overall woody and herbaceous vegetation on disturbance patches inundated at low discharges. This could result in more sediment trapping and aggradation and enhance cottonwood seedling establishment and tree recruitment on these patches.

(3) Trees might be recruited from seedlings established in years when high rainfall, low temperatures, and side slope drainage provide sufficiently moist conditions on bare patches created by winter ice scour at high inundating discharges. In this situation, the close dependence observed between seedling establishment and surfaces inundated by streamflow would not be the mechanism producing trees. The strong association Scott et al. (1997) observed between ages of existing trees and historic high flows might thus result from a general correlation between high flow years and climatic conditions that provide adequate moisture, rather than a direct dependence on streamflow inundation. We have no clear evidence to reject this possibility. However, we have seen few examples along this reach of seedlings establishing substantially above the location of the wetted edge during the summer, even in particularly advantageous, bare microsites with fine-textured soils and high moisture-holding capacity.

The scale of cottonwood demography is daunting. Given tree ages of 100 to 200 years, existing trees might be survivors of 100 annual cohorts of germinating seedlings. Combining these two orders of magnitude with the four orders of magnitude difference between densities of new seedlings and trees means that we are trying to determine what is different about the seedlings that become trees from the 99.9999% of seedlings that die without becoming trees. Practically, one has to track large numbers of seedlings for a long time to observe one become a tree, and it is difficult to measure anything about that many individuals with any precision. Retrospective analyses of historical conditions survived by existing trees powerfully extend the time scale but provide limited information on the vast majority of individuals that have died.

Clearly, much of this mortality is density-dependent. Seedling densities of 100/m^2 are not physically possible for trees whose individual basal areas often exceed 0.75 m^2. Inter- and intra-specific competition for light, moisture, nutrients, and space are thus responsible for much of the density reduction. Some of this competition is evident in very early stages; several cottonwood seedling studies have reported lower densities in the presence of more interspecific competition (Friedman et al. 1995, Auble et al. 1997, D.J. Cooper, pers. comm.).

The relative importance of physical factors incorporated in our hydrogeomorphic model may vary considerable over space and time. The generalization that bare, moist sites are most suitable for cottonwood seedling establishment is an accurate and powerful summary of observations. However, it fails to define exactly what about those sites is important and how those details vary across space and time. For example, the Recruitment Box model (Mahoney and Rood 1998) emphasizes drawdown rate as determining seedling drought mortality, which is especially important in arid climates and on sites with coarse substrates and low moisture holding capacity. At the other extreme, in the eastern portion of cottonwood's range, a humid climate and fine-textured substrate with high moisture-holding capacity may minimize the importance of moisture from the river in making a disturbance patch wet and emphasize the relative importance of creating bare sites free of competition (Johnson 1965). Furthermore, mortality factors such as ice and livestock grazing operating along the upper Missouri River, or beaver herbivory, may be superimposed on the simple fluvial processes depicted in Figure 4 in ways that mask or alter the spatial and temporal patterns predicted by that model. Nonetheless, the consideration of how riverine processes create bare, moist disturbance patches that are undisturbed long enough to support trees is a critical foundation for understanding the full set of factors regulating cottonwood recruitment.

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