FLOOD DEPENDENCY OF COTTONWOOD ESTABLISHMENT ALONG THE MISSOURI RIVER, MONTANA, USA

Michael L. Scott, Gregor T. Auble, and Jonathan M. Friedman

United States Geological Survey, 4512 McMurry Avenue, Fort Collins, Colorado 80525-3400 USA

Abstract. Flow variability plays a central role in structuring the physical environment of riverine ecosystems. However, natural variability in flows along many rivers has been modified by water management activities. We quantified the relationship between flow and establishment of the dominant tree (plains cottonwood, *Populus deltoides* subsp. *monilifera*) along one of the least hydrologically altered alluvial reaches of the Missouri River: Coal Banks Landing to Landusky, Montana. Our purpose was to refine our understanding of how local fluvial geomorphic processes condition the relationship between flow regime and cottonwood recruitment. We determined date and elevation of tree establishment and related this information to historical peak stage and discharge over a 112-yr hydrologic record. Of the excavated trees, 72% were established in the year of a flow >1400 m³/s (recurrence interval of 9.3 yr) or in the following 2 yr. Flows of this magnitude or greater create the necessary bare, moist establishment sites at an elevation high enough to allow cottonwoods to survive subsequent floods and ice jams. Almost all cottonwoods that have survived the most recent flood (1978) were established >1.2 m above the lower limit of perennial vegetation (active channel shelf). Most younger individuals were established between 0 and 1.2 m, and are unlikely to survive over the long term. Protection of riparian cottonwood forest along this National Wild and Scenic section of the Missouri River depends upon maintaining the historical magnitude, frequency, and duration of floods >1400 m³/s. Here, a relatively narrow valley constrains lateral channel movement that could otherwise facilitate cottonwood recruitment at lower flows. Effective management of flows to promote or maintain cottonwood recruitment requires an understanding of locally dominant fluvial geomorphic processes.

Key words: bottomland; dendrogeomorphology; disturbance; flood; Missouri River; Montana; patch dynamics; Populus deltoides; *riparian ecosystems; seedling establishment.*

INTRODUCTION

Variation in streamflow is central in structuring the physical environment of riverine ecosystems and in determining community composition of lotic and riparian environments (Hupp and Osterkamp 1985, Poff and Ward 1989). Flow regime influences species abundance by determining the spatial and temporal occurrence of suitable habitat patches (Bain et al. 1988, Johnson 1992, Auble et al. 1994, Poff and Allen 1995). Although extreme flow variation can eliminate species (Zimmerman 1969, Bain et al. 1988), floods or droughts are necessary for the persistence of some species of fish (Meffe 1984) and plants (Nilsson et al. 1991, Friedman et al. 1996).

The early successional woody plants that dominate newly formed surfaces along streams typically demonstrate rapid growth, intolerance of shade, tolerance of nutrient scarcity and sediment accretion, high seed production, seed release associated with peak flows, and lack of seed dormancy (Sigafoos 1964, White 1979, Hupp 1992). In more arid regions of the northern hemisphere, this functional group is dominated by members of the Salicaceae, including cottonwood (*Populus* spp.). More complete understanding of the relationship between flow regime and the spatial and temporal patterns of riparian tree establishment would allow water managers to maintain or adjust flows to sustain populations of this riparian forest species. Such efforts are complicated, however, because the response of riparian vegetation to changes in flow varies as a function of geomorphic setting (Malanson 1993, Hughes 1994). When the relation between flow and riparian vegetation establishment is placed in a geomorphic context, much of the observed variability in vegetation response is explained and management prescriptions are clarified (Johnson 1993, Hughes 1994, Scott et al. 1996).

Establishment of cottonwood seedlings is generally restricted to bare, moist sites protected from intense physical disturbance (Bradley and Smith 1986, Friedman et al. 1995). For species that reproduce vegetatively, such as *P. balsamifera* (Nanson and Beach 1977), establishment of new stems may not be as tightly restricted to bare, moist surfaces. However, root or shoot sprouts are relatively uncommon in plains cottonwood (*Populus deltoides* subsp. *monilifera*), and appear to be primarily limited to shoot suckering from flood-trained stems (Rood et al. 1994).

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TABLE 1. Fluvial processes producing sites suitable for cottonwood establishment.†

Fluvial process	Flow	Landform	Community patterns
Narrowing	one to several years of flow below that necessary to re-work channel bed	channel bed	spatial patterns variable; usually not even-aged stands; establishment surface at relatively low elevation of former channel bed
Meandering	frequent moderate flows	point bars	moderate number of even-aged stands, arranged in narrow, arcuate bands; strong left-bank, right-bank asymmetry in ages corresponding to meander pattern; flood training of stems common; establishment surface of mature trees often well below present ground surface and near channel bed elevation
Flood deposition	infrequent high flows	flood deposits	small number of linear, even-aged stands; flood training of stems rare; establishment surface of mature trees near present ground surface and well above channel bed elevation

† Based on Scott et al. 1996.

Three fluvial geomorphic processes are important in producing sites suitable for establishment of cottonwoods from seed: channel narrowing, channel meandering, and flood deposition (Table 1; Scott et al. 1996). At a site, these processes may act alone or in combination; their relative importance depends upon geologic and climatic factors, including flow variability, sediment load, and stream gradient.

The process of channel narrowing involves stream abandonment of a portion of the former channel bed. This includes reduction in width of a single channel or loss of flow in one or more channels of a multiple-channel stream. Although narrowing can occur along any stream, it is most important along braided channels typified by a high width : depth ratio and large areas of channel bed exposed for much of the growing season (Friedman et al. 1997). These conditions are maintained by high flow variability, high gradient, and a sediment load dominated by sand and gravel; such coarse sediment must be transported along the bed and forms highly erodible banks (Osterkamp 1978). Channel narrowing can occur in response to flood-induced widening (Schumm and Lichty 1963, Osterkamp and Costa 1987, Friedman et al. 1996), climate change (Schumm 1969), construction of upstream dams (Williams and Wolman 1984), establishment of exotic bottomland plant species (Graf 1978), or as part of a cyclic, autogenic process (Patton and Schumm 1981). Narrowing occurs during a period of relatively low flow, when stream power is insufficient to rework the entire channel bed. Exposed portions of the bed are ideal sites for establishment of vegetation, including cottonwood. This vegetation promotes deposition of fine sediment (Osterkamp and Costa 1987) and increases resistance to erosion (Smith 1976), thus stabilizing the channel at a narrower width. Cottonwood trees established during an episode of channel narrowing are often not even-aged, since establishment could occur at any time within the period of relatively low flow (Friedman et al. 1996). Stands usually have an irregular shape, with the longest axis parallel to the direction of flow. The establishment point of trees is low, at the elevation of the channel bed at the time the surface was abandoned by the stream (Friedman et al. 1996).

Meandering channels are generally characterized by low flow variability, low gradient, low width : depth ratio, and a sediment load dominated by silt and clay. During the process of meandering, cutbanks on the outside of channel bends erode outward and downstream, while the sediment removed is deposited downstream in point bars on the inside of bends. Most of this channel movement is produced by moderately high flows with recurrence intervals of <5 yr (Wolman and Miller 1960). Conditions suitable for establishment occur on portions of the point bar that are sufficiently moist and safe from riverine disturbance (Bradley and Smith 1986). Sediment accretion and movement of the channel away from the point bar protect vegetation from flood disturbance and ice scour. Stands produced by channel meandering typically exhibit arcuate bands of even-aged trees oriented parallel to the flow at the time of establishment (Everitt 1968, Noble 1979). These bands form relatively frequently, and each band occupies a small portion of the floodplain. The establishment point of these trees is at the moderate elevation of the point bar: above the channel bed but below the surface of the flood plain (Everitt 1968, Bradley and Smith 1986).

Floods can produce tree establishment by creating bare, moist deposits high enough above the channel bed to minimize future flow- or ice-related disturbance. Trees established on flood deposits along constrained channels occur as even-aged stands oriented along the direction of flood flow. The establishment point is high relative to the channel bed, and close to the present floodplain surface (Table 1). Flood deposition should

be particularly important for tree establishment where channel movement is constrained by a narrow valley (Scott et al. 1996). Because the channel is relatively immobile, the only positions safe from flow-related disturbances are on relatively high surfaces. Only the largest flows would be capable of producing bare, moist alluvial deposits at these elevations. Floods can induce tree establishment directly through the process of sediment deposition, or indirectly by initiating a process of channel narrowing.

Because channel meandering is accomplished in small increments by relatively frequent flow, the area occupied by an individual cohort is a small portion of the bottomland, and forest area and age structure can be relatively stable over time (Everitt 1968, Bradley and Smith 1986, Hughes 1994). In contrast, where flood deposition is the dominant mode of establishment, cohorts may be widely spaced in time, and forest area and age structure may, likewise, vary widely. Episodes of channel narrowing lasting for decades and separated by ≥50 yr can also lead to highly variable or punctuated age structures (Schumm and Lichty 1963, Hughes 1994, Friedman et al. 1997). These different modes of cottonwood establishment can be distinguished by examination of the elevation and year of establishment (Friedman et al. 1996; J. C. Stromberg et al., *personal communication*).

The dominant fluvial processes acting along a river control the response of riparian vegetation to flow alteration. Dam management characteristically decreases downstream sediment loads and peak flows, thereby reducing stream power and the movement of sediments along the channel bed. This can lead to channel narrowing and a temporary increase in riparian vegetation, as cottonwood and other early successional species become established on formerly active channel surfaces. Channel narrowing with forest recruitment resulting from flow alteration is most pronounced along formerly wide, shallow, braided channels and has been reported along the Rio Grande (Williams and Wolman 1984), Arkansas (Williams and Wolman 1984), South Platte (Nadler and Schumm 1981, Johnson 1994), Republican (Northrop 1965, Williams and Wolman 1984), North Platte and Platte Rivers (Johnson 1994). Along meandering channels, which have a low width : depth ratio, the primary effect of diminished peak flows and sediment loads is not narrowing, but a reduction in the meandering rate resulting from the river's decreased capacity to erode and deposit sediments. This decreases the formation of establishment sites and, thus, reduces the recruitment of cottonwood and other early successional species (Scott et al. 1996, Friedman et al. 1997). Such responses have been reported along the Missouri (Johnson et al. 1976, Johnson 1992), Milk (Bradley and Smith 1986), Marias (Rood and Mahoney 1995), and Bighorn Rivers (Akashi 1988). Along channels where lateral movement is constrained by a narrow valley or by channel stabilization, flood deposition may

be the only process that produces cottonwood establishment high enough to survive the effects of future damage from ice and floods (Scott et al. 1996). Thus, reductions in peak flows along a constrained channel may curtail cottonwood recruitment. In summary, management of flows to promote cottonwood recruitment requires an understanding of the locally dominant fluvial geomorphic processes.

The objective of this research was to refine our understanding of how local fluvial geomorphic processes condition the relationship between flow regime and cottonwood recruitment along the National Wild and Scenic reach of the Missouri River in Montana. A narrow valley constrains the channel throughout much of this section of river, suggesting that the dominant fluvial geomorphic process controlling cottonwood establishment is flood deposition. If so, the reproduction of cottonwoods should occur primarily at high elevations following infrequent large flows (Table 1). In previous analyses of cottonwood population age structure, trees have been dated by coring the stem above the ground surface. This approach can underestimate the age of the tree and provides no information on the elevation of establishment; this information is critical for determining the fluvial processes that created the establishment surface. To more precisely measure the age and elevation of establishment, we excavated trees and sampled them at the root collar. This approach has been used to date changes in channel morphology (Hereford 1984, Hupp 1992, Friedman et al. 1996) and to estimate sedimentation rates (Nanson and Beach 1977).

STUDY AREA

The Missouri River, formed by the confluence of the Jefferson, Madison, and Gallatin Rivers in southwestern Montana, flows north to Great Falls and then trends northeast and east through central Montana. Before the Pleistocene, the river flowed north and east into Hudson Bay. Pre-Wisconsinan continental glaciation diverted drainage southward into the Mississippi River (Wayne et al. 1991). The modern course of the Missouri River from Coal Banks Landing to the confluence with the Milk River, downstream of Fort Peck Reservoir (Fig. 1), corresponds roughly to the Late Illinoian ice margin (Wayne et al. 1991). Our study reach is the upstream 172 km of this postglacial channel extending from Coal Banks Landing to Landusky (Fig. 1). This comparatively young section of river is constrained by a narrow valley and exhibits low sinuosity. Comparison with detailed maps prepared by the Missouri River Commission between 1892 and 1895 indicates that little channel migration has occurred in this reach in the last 100 yr. In contrast, relatively high sinuosities, wide valleys, and more rapid channel migration are typical for the Missouri River upstream of Coal Banks Landing and downstream of the Milk River confluence.

The Missouri River in Montana is a snowmelt-dominated river, with peak flows occurring in spring, usu-
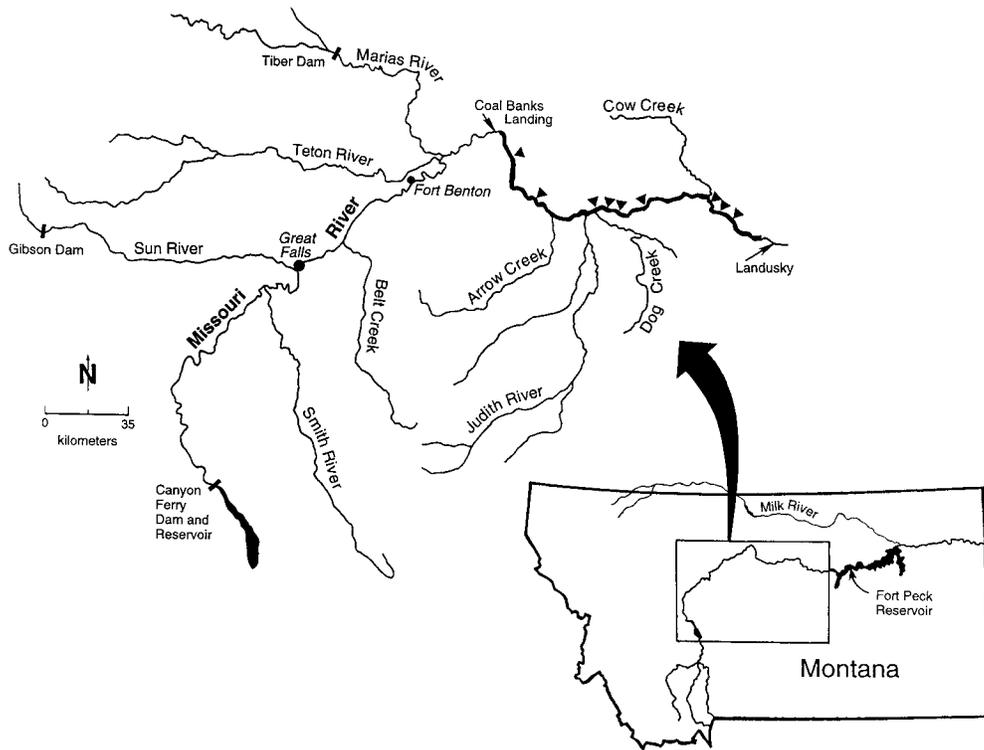
Fig. 1. Location of the study reach along the Missouri River, Montana. Study sites are indicated by triangles.

ally during late May or early June, and low flows occurring in late fall and winter. At the Fort Benton gage (U.S. Geological Survey gage 06090800), the Missouri River drains an area of 64 100 km² and has a mean annual discharge of 219 m³/s (EarthInfo 1994). Flows on this portion of the river are influenced by irrigation withdrawals and a number of upstream dams, principally Canyon Ferry (Fig. 1; Ramey et al. 1993). Many unregulated tributaries join the Missouri River below Canyon Ferry, including the Smith, Teton, and Judith Rivers and Belt, Arrow, Dog, and Cow Creeks (Fig. 1). The cumulative upstream reservoir storage is ≈51% of the annual flow at Fort Benton and ≈43% at Landusky (Ramey et al. 1993). Unregulated tributaries, the limited storage capacity, and the operation of dams for irrigation and hydropower, as well as flood control, all limit the influence of reservoir operations on peak flows. As a result, the study reach (Fig. 1) is the least hydrologically altered alluvial portion of the Missouri River. Below Landusky (Fig. 1), backwaters from Fort Peck Reservoir influence both hydrology and vegetation.

The dominant riparian tree species along the study reach is plains cottonwood, *Populus deltoides* subsp. *monilifera.* Also present are *Acer negundo, Fraxinus pennsylvanica,* and *Salix amygdaloides.* The shrub community includes *Salix lutea, S. exigua, Symphoricarpos occidentalis, Rosa woodsii, Cornus stolonifera,* and *Prunus virginiana.* Within the study reach, where

lateral channel movement is constrained, the cottonwood forest consists of discontinuous, often single-ranked stands of trees. In more geomorphically active locations, such as tributary junctions and channel islands, cottonwood stands and alluvial surfaces are wider. Upstream of the study area, the meandering preglacial river channel is associated with a broad floodplain and more extensive cottonwood stands (Hansen 1989).

The journals of the Lewis and Clark expedition (1804–1806; Coues 1893) indicate that cottonwood stands in the study area were spatially restricted before European settlement of the region. For example, in the constrained reach above Cow Creek (Fig. 1), they note that "there is, however, no timber on either side of the river, except a few pines on the hills." At a location above Arrow Creek, they state "There is now no timber on the hills, and only a few scattering cottonwood, ash, box elder, and willows along the water." In contrast, above Coal Banks Landing, where the river meanders within the broad preglacial valley, they reported that its "timber increases in quantity, the low grounds become more level and extensive," and they "came-to for the night in a handsome, low cottonwood plain on the south." Water management is not the only human activity that has affected riparian cottonwood forests. Native Americans used cottonwoods for fuel and forage for horses, which were introduced to North America in the 1500s (Winship 1904). From 1860 to 1890, there

was widespread timber cutting for steamboat fuel along the Missouri River in Montana (Hansen 1989), and cattle grazing has occurred along portions of the study reach since the turn of the century. Nevertheless, within the study area, cottonwoods now occur in small, scattered stands similar to those described in 1805. Cottonwoods along this reach of the Missouri River are considered important regional nesting habitat for Bald Eagles and migratory bird species (R. Hazlewood, *personal communication*). Between Fort Benton and Landusky (Fig. 1), the river has been designated Wild and Scenic; the historical significance of the river and the scenic qualities of the cottonwood forests are central to this designation.

Methods

Nine sites were selected to represent the range of geomorphic conditions that occur within the study reach, including channel islands, back channels, and small tributaries. The sites were identified by number of river kilometers (RK) downstream of Fort Benton, Montana (RK 90.4, 117.3, 144.4, 152.1, 153.2, 157.7, 209.2, 211.1, and 218.0: Fig. 1), as shown on maps of the Wild and Scenic River (Government Printing Office 1990). We avoided sites dominated by trees of >1 m diameter at breast height (dbh), assuming that many trees of this size predate the period of hydrologic record that began in 1891. Also, in order to minimize the complicating effects of tributary hydrology, we avoided sampling the relatively young populations at major tributary junctions.

At each site, a transect was established perpendicular to the channel. Distinct topographic surfaces along the transect were noted and surveyed. Elevations were determined relative to the lowest extent of perennial emergent vegetation, i.e., the active channel shelf of Osterkamp and Hedman (1982). Four size classes of cottonwoods were defined: seedling (0–1 m tall); sapling (1 m tall to 10 cm in diameter); pole (10–30 cm in diameter); and tree (>30 cm in diameter). On each surface, four stems in each size class, if available, were selected for determination of establishment date and elevation.

We estimated densities of cottonwoods on each surface by counting individuals by size class in rectangular quadrats downstream of the transect. The width of each quadrat was the width of the respective surface along the transect, and the downstream length was a distance from the transect sufficient to record at least 10 individuals of each size. Quadrat widths ranged from 1.5 m for a narrow surface with seedlings to 112 m for a high bench with poles and trees. Quadrat lengths parallel to the channel ranged from 1 to 108 m. We sampled the sites in October 1992 and from April to July 1993 (excluding seedlings that germinated in 1993).

Relating the origin of cottonwood stands to specific flows requires precise dating of individual stems. This can be difficult with cottonwood for two reasons. First,

the early years of growth are often well below the present ground surface because of sedimentation (Everitt 1968). Second, cottonwood has diffuse-porous wood and can exhibit false or missing rings. In order to find the oldest wood on the tree, we excavated each stem with hand shovels and sectioned or cored it above, below, and at the apparent point of establishment as indicated by the flared root collar (Sigafoos 1964). We also sampled each stem at the ground surface to gauge the improvement in age determination provided by tree excavation. In seven cases, we were not able to obtain accurate ages at the ground surface, and excluded these trees from analyses comparing ground and establishment ages.

We photographed and sketched each excavated stem, indicating the apparent establishment surface, its distance below the present ground surface, and the positions of the slabs (or cores) removed from the stem. In addition, we recorded the sediment stratigraphy associated with each excavated stem, noting the depth and texture of each stratum. Finally, we collected samples of flood or ice scars found on trees near our cross sections.

All stem sections, cores, and scar samples were returned to the laboratory and air-dried. Cores were mounted on wooden blocks (Phipps 1985), and all slabs and cores were sanded with progressively finer sandpapers to a median particle size of 15 μm (600 grit). Ring number and width were recorded using a University Model incremental measuring machine (obtained from Curt Zahn, formerly of Fred C. Henson Company) and the TRIMS (Version 1.2) software system from Madera Software. Each core or slab was interpreted by at least two readers.

We detected and accounted for both false and partial rings (i.e., rings that were not continuous around the stem circumference). False rings were generally identifiable by an incomplete transition between early- and late-wood vessels through some portion of the stem. Where possible, false and missing rings were confirmed by cross dating (Stokes and Smiley 1968) both within and between trees. However, cross dating was reliable only after approximately the first 30 yr of growth. Presumably, for younger trees, effects of shading and local soil conditions obscured the hydrologic and climatic influences on annual growth increment (Stromberg and Patten 1996).

Flow records for three U.S. Geological Survey gaging stations on the main stem of the Missouri River were obtained from CD-ROM (EarthInfo 1994). Most of our analyses were based on the Fort Benton gage (06090800) at the upstream end of the study reach, because of its long period of record. The currently accepted period of record starts in water year 1891. We also used records for water years 1881 to 1890 (U.S. Geological Survey 1922), and estimated maximum daily discharge for water year 1890 from incomplete records for that year. Although these earlier records ex-
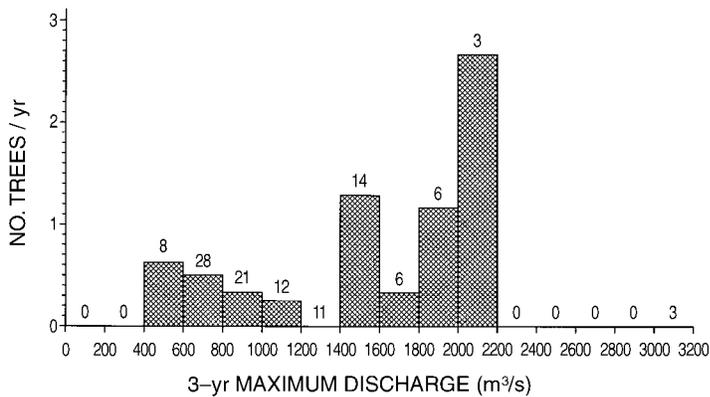
FIG. 2. Frequency distribution of mean rate of tree establishment vs. 3-yr maximum discharge. Mean rate of tree establishment equals no. trees established in years with 3-yr maximum discharge in the given range, divided by no. years in that range. The 3-yr maximum discharge is the maximum daily discharge of the given year and two preceding years. The number of years in each range of 3-yr maximum discharge is given above the bars.

clude winter months and are less accurate, we judged that they would be acceptable for identification of flood years.

We used least squares linear regressions to examine the following relations: (1) age at establishment surface vs. age at ground surface; (2) age at establishment surface vs. burial depth; and (3) age vs. dbh. We compared flood hydrographs from establishment and non-establishment years using the Fort Benton USGS gage records for the period 1891–1992. The analyses, based on water year (1 October to 30 September), examined growing-season flow volume (1 May through 30 September), minimum and maximum values for highest mean daily flow by date, and recession limb characteristics of total days with flow >1400 m^3/s, 1050 m^3/s, and 700 m^3/s.

We determined whether the channel had downcut within the study reach by comparing the relation between stage and peak instantaneous discharge at the Fort Benton gage for the pre- and post-dam periods; stages associated with ice jams were excluded from this analysis. If significant downcutting had occurred, we would expect a downward shift in the stage–discharge relationship with lower stages associated with given discharges. To identify ice-related events not reflected in the Fort Benton gage, we used the Landusky gage (061152; 1934–1992) at the downstream end of the study reach.

We evaluated the significance of the association between high flows and cottonwood establishment by comparing our data to expectations from a null hypothesis that individuals were independently and randomly established over time. In the null hypothesis, all individuals have an equal chance of being established in any year, regardless of the flow in that year. Seedling establishment can occur 1–3 yr following a flood on bare, alluvial deposits (J. Stromberg and M. Merigliano, *personal communication*). In addition, age underestimates may result from failure to detect small, annual increments in the first 1–2 yr of growth. Therefore, we defined a suitable establishment year as the year of a flood (≥1400 m^3/sec) or the following two years. Using the binomial distribution, we calculated the

probability that the observed proportion of individuals established in suitable years could have occurred by chance alone (Snedecor and Cochran 1980).

If four stems of all size classes present had been dated from all surfaces at all sites, there would have been a total of 216 dated stems; we dated 157. Failure to date stems resulted from: (1) the presence of large trees, especially those likely to predate the hydrologic record; (2) failure to recognize a second size class within an apparently even-aged stand; and (3) occurrence of heartrot. Four of the dated stems were excluded from the data set because they were identified as sprouts from buried roots or stems. Because of variability in the incidence of undated stems, dated stems do not perfectly represent riparian forest on a per-unit-area basis. To investigate the influence of undated stems, we created and analyzed an alternative data set, in which each dated stem was replaced by the area of forest it represented and was normalized across sites in units of hectares of forest established in a given year per kilometer of river.

RESULTS

Temporal patterns of establishment

Establishment of plains cottonwood along this reach of the Missouri River was strongly associated with floods exceeding 1400 m^3/s (Fig. 2). Of 64 saplings, poles, and trees that were established during the period of record at Fort Benton, 35 (55%) dated to years in which flow exceeded 1400 m^3/s (recurrence interval of 9.3 yr) or to the two years following these flood years (Fig. 3A and C). This large proportion of cottonwoods dating to the 32 flood and postflood years in the 112-yr record was inconsistent with the null hypothesis that all years had an equal likelihood of producing cottonwoods regardless of flow ($P = 1.1 \times 10^{-5}$).

An additional 11 saplings, poles, and trees were established from 1978 to 1980, following an ice jam that occurred between the Fort Benton gage and the study reach in March 1978 (Fig. 3A). This ice jam produced the highest stage of record at Landusky. When the jam released, the Landusky gage recorded an instantaneous
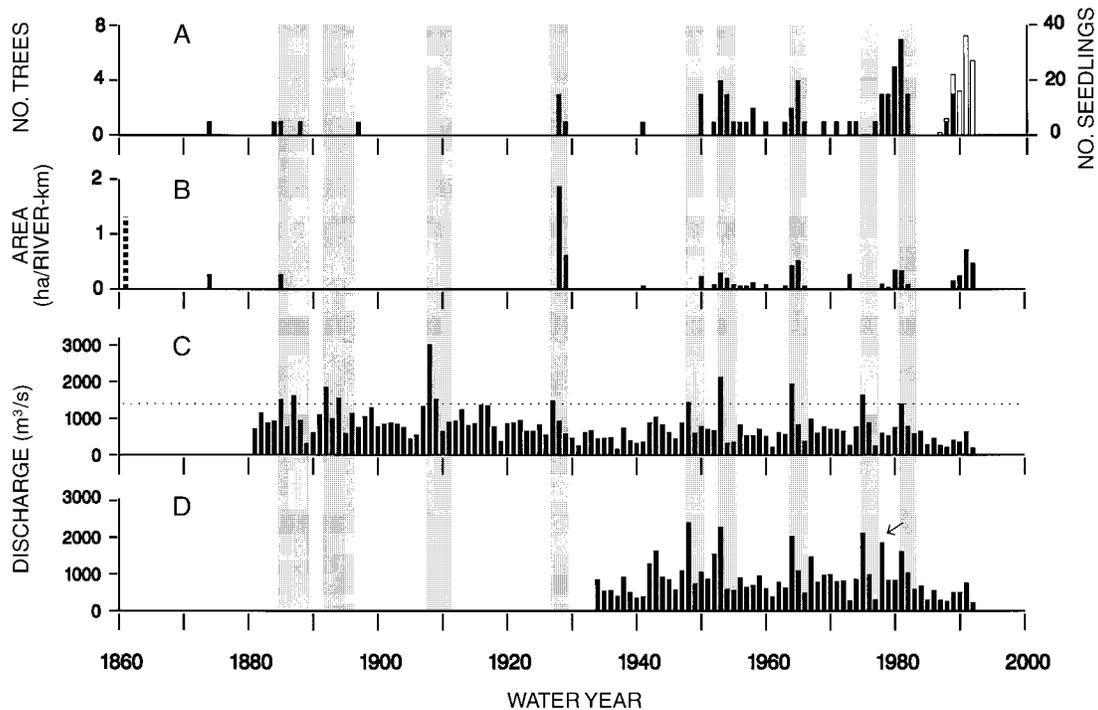
FIG. 3. (A) Number of sampled cottonwood trees and seedlings established in each year along the Missouri River, Montana. Solid bars represent tree, sapling, and pole size classes. Open bars represent seedling size class, with a different scale. (B) Area established in a given year per kilometer of river, based on weighting sampled cottonwoods (all size classes combined) by forest area. The dashed bar at 1861 represents the area occupied by older trees that could not be aged. (C) Maximum daily discharge for each water year at Fort Benton, Montana. The dotted line indicates a discharge of 1400 m³/s. Shaded vertical sections are years with maximum discharge >1400 m³/s and the two following years. (D) Maximum daily discharge for each water year at Landusky gage. The ice-related stage at Landusky in 1978 is indicated with an arrow.

discharge of 3060 m³/s, the third highest discharge of record (Fig. 3D). Considering 1978 as a flood year, there were 35 flood or postflood years out of a total of 112, and 46 of 64 cottonwoods (72%) established in these years (Fig. 3A).

When stems were weighted by the area of riparian forest they represent, the relative importance of individual years was changed, but the relation between flood years and establishment remained strong. During the 112-yr flow record, 62% of the sampled cottonwood forest area was established in the 32 years (29% of all years) that were associated with flows >1400 m³/s (Fig. 3B). Including the ice-related high stage of 1978, 68% of the cottonwood forest area was established in 31% of the years.

Eighteen of 64 sampled trees, poles, and saplings (28%) and all of the 88 seedlings exhibited no relation between establishment and high discharge. Seedlings dated to all years since the ice jam of 1986, and most postdated the lesser ice jam of 1989 (Fig. 3A).

During the 102-yr period of the published USGS record (1891–1992), there were 10 years in which flows exceeded 1400 m³/s. Five of these flood years were associated with establishment of sampled trees and five were not; we found no clear or consistent differences between the hydrographs in terms of growing-season

volume, maximum daily discharge, flood duration, date of peak, or rate of recession following the peak. This analysis was not extended to the flood years of 1885 and 1887 (Fig. 3A), because daily flow data prior to 1891 were incomplete and, therefore, less precise.

The highest flows almost always occurred during the ice-free period, but the highest stages usually occurred during ice jams (Fig. 4). A similar pattern has been observed along the Turtle River in North Dakota (Harrison and Reid 1967). Most flood scars collected were produced by ice jams rather than ice-free floods. Two or more of the 21 collected scars dated to each of four years: 1978, 1979, 1986, and 1989 (Fig. 4). These were the four years of highest ice-related stage at Landusky since 1972. Only one scar dated to a year (1953) of discharge >1400 m³/s at Fort Benton (Fig. 4). In almost all cases, the wound generating the scar tissue occurred between growth rings, indicating that the tree was dormant at the time of the event. Although ice jams were more likely than ice-free floods to produce scars on pre-existing trees, ice-free floods were more likely to produce establishment of new trees. The only ice jam clearly associated with cottonwood establishment was that of 1978. Unlike most other ice jams, this event resulted in high discharge (Fig. 4).
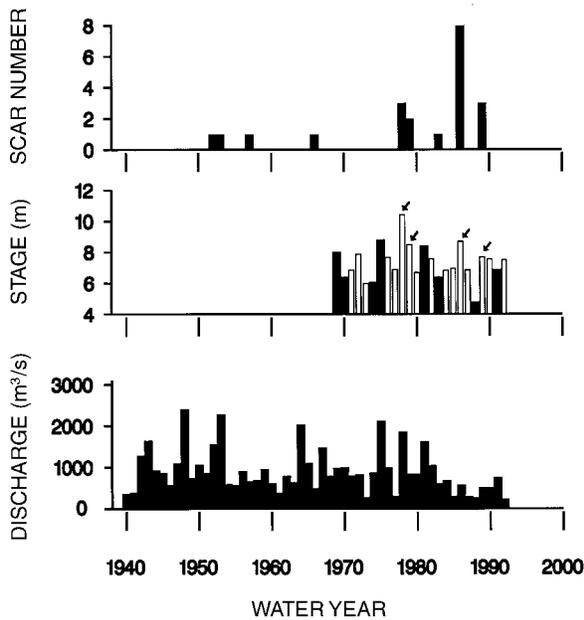
FIG. 4. Dates of injury (as indicated by scar tissue) for trees along the Missouri River, Montana, in relation to peak stage and maximum daily discharge at Landusky. Dark bars indicate ice-free stages. Open bars indicate high stages in the presence of ice. Stages in years that produced two or more sampled scars are indicated by arrows.
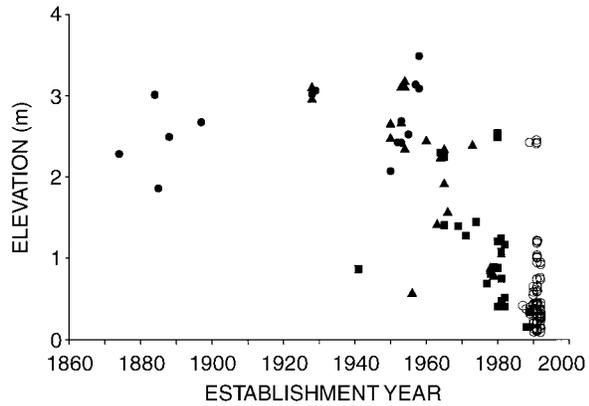

FIG. 5. Elevation of establishment surface and year of establishment for sampled cottonwoods. Size classes are represented as trees (●), poles (▲), saplings (■), and seedlings (○).

charge for pre- and post-dam periods at the Fort Benton gage showed no downward shift in the stage–discharge relation, and indicated that the channel has not downcut in the post-dam (Canyon Ferry) period (Fig. 6).

Spatial patterns of establishment

Cottonwood age is strongly related to elevation of the establishment surface (Fig. 5). Thirty-seven of 40 cottonwoods (98%) that predated 1978 were established between 1.2 and 3.4 m above the lower limit of perennial vegetation. In contrast, 21 of the 25 cottonwoods larger than seedlings (84%) postdating the ice-related high flow of 1978 were established below 1.2 m. The root flares of excavated poles and trees were typically associated with relatively coarse alluvial deposits of gravel or sand. However, across-site variance in stratigraphic sequences and depths was high, indicating a spatially complex depositional environment throughout the study reach.

Nonflood cottonwoods were established across a range of elevations and sites. Five trees were established at elevations between 2.7 and 3.1 m at two sites. These trees occurred on surfaces where nearby stems dated to flood years. At another site, four nonflood poles and saplings were established in a former back channel at elevations between 1.2 and 1.4 m. Six non-flood poles and saplings were established at elevations between 0.15 and 0.8 m on depositional surfaces at the downstream end of an island and the inside of a channel bend. Eighty-four of 88 seedlings (95%) were established at elevations below 1.2 m and 60 (68%) were established below 0.5 m (Fig. 5).

Temporal changes in the elevation of establishment did not appear to be related to changes in channel bed elevation. Plots of stage at peak instantaneous dis-

Stem size structure and distribution

All size classes were present at only two of the nine sites (RK 144.4 and RK 218.0). Trees were absent at RK 152.1. Poles were absent at three sites and saplings were absent at five of the nine sites. Seedlings were not found at RK 90.4, where high water on the day of sampling may have obscured seedlings in low positions. Seedlings occurred on both banks (and both island edges) at all sites except for RK 90.4 and RK 209.2. Trees, poles, saplings, and seedlings occupied areas of 3.9, 2.3, 2.0, and 1.6 ha/river-km. Most surfaces had a single size class; where two size classes occupied the same surface, they were usually similarly aged poles and trees. Nonzero stem densities averaged across surfaces were 212 stems/ha ($n = 8$) for trees,
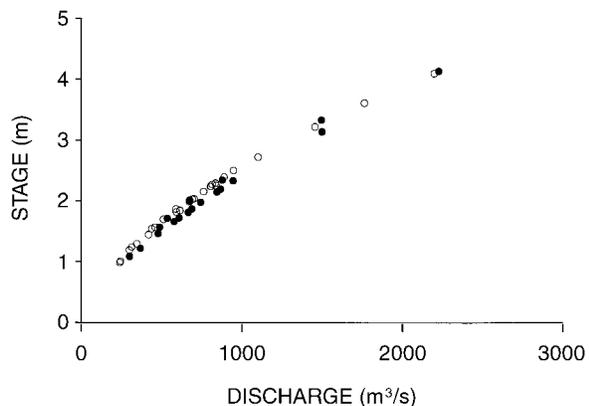

FIG. 6. Peak stage in relation to peak instantaneous discharge at Fort Benton, Montana, before and after presence of the Canyon Ferry Dam. Closed circles are water years before 1954; open circles are after 1954. Years in which peak stage was associated with ice jams are excluded.
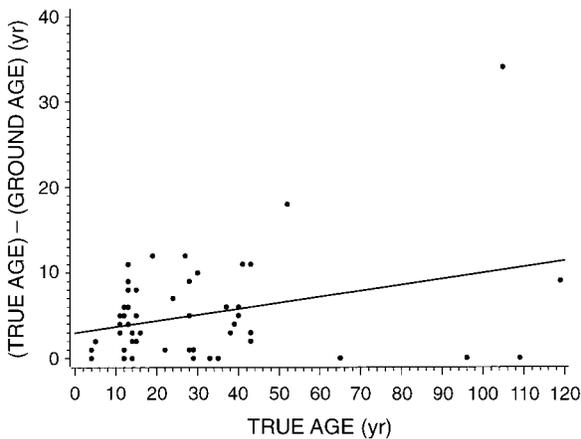
FIG. 7. The difference between true age and age at the ground surface vs. true age for cottonwood trees harvested along the Missouri River, Montana. The plotted line equation is $y = 2.97 + 0.070x$ ($F_{1,55} = 6.28$, $P = 0.02$, $r^2 = 0.10$, $n = 57$).

299 stems/ha ($n = 6$) for poles, 1428 stems/ha ($n = 4$) for saplings, and 16 217 stems/ha ($n = 8$) for seedlings.

Sources of error in dating cottonwood stems

Cottonwoods dated from 1862 to 1992. The difference in age between the establishment surface and the ground surface was 0–18 yr ($\overline{X} = 4.8$ yr, $n = 29$) for saplings, 0–12 yr ($\overline{X} = 4.3$ yr, $n = 18$) for poles, and 0–34 yr ($\overline{X} = 7.1$ yr, $n = 10$) for trees. All sampled seedlings were established within ≈ 2 cm of the present ground surface, and no difference in age between establishment and ground surfaces was observed. A linear regression of difference in age on true age was significant ($P = 0.02$, $n = 57$), but explained only 10% of the variance (Fig. 7). Differences in age were also significantly ($P = 0.02$, $n = 57$) related to depth of burial, but the relationship explained <10% of the variance. There was a highly significant relationship ($P = 0.0001$) between dbh and age at the establishment surface for saplings, poles, and trees (Fig. 8). However, the dispersion of points ($r^2 = 0.80$) and displacement from the origin limit the utility of this relationship for predicting age from size.

DISCUSSION

Fluvial processes and cottonwood establishment

Patterns of cottonwood establishment and survival within the study reach support the conclusion that successful recruitment of trees along constrained alluvial channels occurs following infrequent floods on elevated flood deposits. A significant majority of the trees, poles, and saplings was established in years when flows exceeded 1400 m³/s (recurrence interval of 9.3 yr), or in the following 2 yr. Cottonwoods that survived the most recent ice-related flood (1978) were established ≥ 1.2 m above the lower limit of perennial vegetation. In contrast, saplings and seedlings that postdate 1978

were established between 0 and 1.2 m; most seedlings were established below 0.5 m.

The nearly ubiquitous occurrence of seedlings on bare, moist surfaces near the water's edge strongly suggests that the sparse pattern of older size classes cannot be explained by a shortage of seed. The strong correlation between cottonwood age and elevation of the establishment surface (Fig. 5) could be explained by recent channel degradation and associated changes in river stage (Hereford 1984) resulting from dam construction (Williams and Wolman 1984). However, our stage and discharge analysis shows that such channel degradation has not taken place in the study reach (Fig. 6). Thus, observed patterns of cottonwood establishment and survival indicate that, in most years, seedlings germinate on low, bare surfaces created by localized scour and deposition associated with winter ice or spring flows. However, these stems are unlikely to survive future ice jams and high discharges. Long-term survival is usually possible only for seedlings established on the higher bare, moist sites produced by extreme floods (Scott et al. 1996, Johnson 1994), or in protected depositional microsites like the downstream end of islands or the inside of large channel bends.

Although the instantaneous peak stage in most years is associated with ice jams, and most tree scars result from ice damage, cottonwood establishment is more closely associated with late-spring floods (Fig. 3). This may be because the large volume of water in a flood transports more sediment than the relatively low volume resulting from release of an ice jam. As a consequence, floods deposit a more spatially extensive, bare, alluvial surface necessary for cottonwood estab-
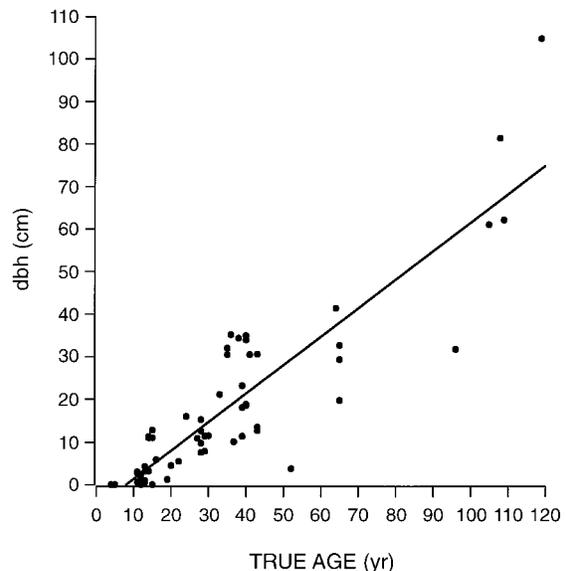

FIG. 8. Diameter at breast height (dbh) vs. true age for cottonwood trees along the Missouri River, Montana. The equation of the plotted line is $y = -5.35 + 0.67x$ ($F_{1,63} = 244$, $P = 0.0001$, $r^2 = 0.80$, $n = 65$).

lishment than do ice jams. Another important difference is associated with the timing of these events relative to the seed dispersal period for cottonwoods; typically, ice jams occur between January and March, well before seed release, whereas flood peaks occur during, or immediately before, the period of seed dispersal in late May through June. The association of peak and recession flows with seed release can be an important element of successful cottonwood establishment (Read 1958, Fenner et al. 1985, Mahoney and Rood 1993, Scott et al. 1993, Stromberg et al. 1993). Although ice jams seldom enable establishment, they can be an important cause of mortality, especially for smaller stems in relatively low channel positions (Fig. 3A; Johnson 1994).

Of the 12 floods with discharge >1400 m³/s at Fort Benton, only seven (1885, 1887, 1927, 1948, 1953, 1964, and 1981) resulted in cottonwood establishment in the year of the flood or in the two following years (Fig. 3). We detected no establishment following the floods of 1892, 1894, 1908, 1909, and 1975. Several factors could explain the absence of apparent establishment following these five floods. The first is our relatively small sample; there may be unsampled cottonwoods in the study area that date to these floods. A second factor could be subtle differences in the shape of the flood hydrograph. However, we observed no clear or consistent differences between the flood years that produced sampled trees and those that did not. A third factor is scouring by subsequent floods or ice jams. For example, the ice jam of 1978 may have removed young trees that had become established on surfaces deposited by the flood of 1975. Similarly, the flood of record in 1908 may have removed young trees established following the floods of 1892 and 1894. Other possible explanations include droughts (Albertson and Weaver 1945, Baker 1990), climate-related failures of the seed crop, or periods of intense grazing by livestock. The most interesting apparent failure of establishment occurred following the flood of record at Fort Benton in the period 1908–1911 (Fig. 3). It is possible that the high flows of 1907–1909 destabilized existing vegetation and initiated a period of widening. Such postflood widening has been observed elsewhere (Schumm and Lichty 1963, Osterkamp and Costa 1987). Alternatively, widespread cottonwood reproduction following cessation of cutting for steamboat operation may have resulted in extensive recruitment in the 1890s, thereby preempting sites that might otherwise have been occupied following the 1908 flood.

The study area has been grazed by livestock since the 1800s. We observed many seedlings that had been damaged by grazing. Recent reproduction of cottonwood seems to be more abundant at sites where cattle are excluded. It seems likely that grazing has decreased cottonwood establishment and survival. However, this effect has not obscured the significant relationship between cottonwood establishment and flood years. Con-

struction and long-term monitoring of livestock exclosures would help to determine the importance of grazing within the study reach.

Apparent establishment in the two years following a flood year could be an artifact resulting from failure to discern small, inner rings or to locate the precise point of establishment. Alternatively, if these trees are dated precisely, they indicate that survival of seedlings along the study reach is not always dependent upon the moisture left in a flood deposit by the flood. Similar age distributions of adult *Populus* spp. in Idaho have been attributed to establishment from seed 1–3 yr following a flood (M. Merigliano, *personal communication*). In Arizona, limited establishment in the 2nd yr following a flood was facilitated by high soil moisture on new fluvial surfaces located near the water table (J. C. Stromberg et al., *personal communication*). The best way to determine whether establishment in the study reach occurs in years following a flood year would be to monitor seedling establishment in permanent plots following floods (cf., Johnson 1994).

Although the majority of cottonwood trees, poles, and saplings was established at high elevations following floods, ≈30% of the sampled stems were not. Therefore, although floods have a dominant influence on cottonwood establishment along this section of the Missouri River, other factors also produce bare, moist sites suitable for seedling establishment. Such factors could include tributary floods, local slope failures, and cultivation. A few trees became established in nonflood years at low-to-moderate elevations in sites protected from floods and ice. Finally, it is possible that some dated stems were undetected sprouts from stems or roots; such sprouts may not have as strong a dependence on bare, moist substrate as do seedlings.

Nevertheless, the relationship between infrequent, large floods and cottonwood regeneration observed along this constrained channel reach of the Missouri River is clear, and is consistent with results of other recent studies that describe the importance of low-frequency, high-magnitude floods in the establishment of riparian trees (Friedman et al. 1996; J. C. Stromberg et al., *personal communication*). Flood deposition can facilitate establishment along a broad array of stream types by enabling germination at elevations that are infrequently flooded. Long-term cottonwood establishment along some nonmeandering stream types is associated with infrequent large floods with recurrence intervals of 30–50 yr (Hughes 1994). Along the section of the Missouri River examined in this study, a narrow valley severely restricts channel movement. Physical disturbance by ice and higher flows removes almost all seedlings established at lower elevations. As a result, establishment of tree-sized cottonwoods occurs chiefly on high-elevation fluvial surfaces created by floods with recurrence intervals >9 yr.

To dig or not to dig

In previous studies relating dates of establishment of riparian cottonwood trees to flow, investigators have dated cores taken above ground (Everitt 1968, Bradley and Smith 1986, Baker 1990, Howe and Knopf 1991). Our results demonstrate that dating cottonwoods at the ground surface can underestimate the age of a tree by as much as 34 yr, with a mean underestimate of 5.1 yr. The error introduced by sampling above ground could falsely strengthen or weaken a relationship between high flow and establishment. Microsite differences in environment or herbivory can cause different apparent rates of growth in buried portions of a stem. As a result, two trees established following the same flood may have widely different ages at the present ground surface. On the other hand, two trees established in different years may have the same age at the present ground surface if they were cut back to ground level in the same year by a flood or by beaver. In this study, if trees had been aged at the ground surface instead of the establishment surface, no significant relationship between floods and establishment would have been detected. In upland and riparian forests, attempts have been made to correct for the age discrepancy between the establishment surface and the point from which a core sample is taken by estimating the years necessary to grow to this height (Henry and Swan 1974, Stromberg et al. 1991). Although we found a significant correlation between depth of the establishment surface and the age underestimate at the ground surface, a low r^2 suggests that depth of burial is an unreliable predictor of the age difference between the ground and establishment surface. We recognize that, in some situations, the error introduced by coring at or above the ground surface is not as large as at our study area, and that this level of error is acceptable for some objectives. However, excavation is required in any study that depends on precise dates of establishment for riparian trees.

Excavation of trees to the establishment surface decreases by as much as an order of magnitude the number of trees that can be sampled per unit time. In this study, excavation time for trees ranged from two to 16 person–hours. However, information about the elevation and precise date of establishment is important for distinguishing between different modes of establishment. For example, without such data, the correlation between age and elevation observed at this site could be explained by accretion: cottonwoods established at low elevations survive over the long term as a series of moderate high flows raise the occupied surfaces without removing the trees. Such a process is typical of meandering and narrowing streams, where sediment accretion and progressive channel movement away from growing trees protects even those established at low elevations (Everitt 1968, Nanson and Beach 1977, Bradley and Smith 1986, Scott et al. 1996, Friedman

et al. 1997). If this process were common along the study reach, there would be many trees that had established outside of extreme flood years (Fig. 3), and there would be many old trees with low elevations of establishment (Fig. 5). Outside of the constrained postglacial reach of the river, the valley is wider and the presence of point bars containing arcuate, even-sized bands of cottonwoods indicates that meandering is an important process (Everitt 1968, Noble 1979, Bradley and Smith 1986). In these areas, we would expect that establishment would occur more frequently and that the elevation of establishment would be relatively low (Scott et al. 1996).

Hydrologic alteration

Ramey et al. (1993) used recorded daily changes in reservoir storage to reconstruct what flows would have occurred at Fort Benton without dams. Comparison of this derived record with the actual flow since 1954 indicates that dams have decreased the magnitude of flows >1400 m³/s by 14–23%, but have not decreased the actual number of flow events >1400 m³/s (Ramey et al. 1993). Operation of the dams has decreased the expected frequency of flows necessary for cottonwood establishment, but the decrease in flows >1400 m³/s has not yet been expressed in the short post-dam record. On alluvial rivers, channel degradation is sometimes observed downstream of dams as a result of sediment removal by the dam (Williams and Wolman 1984). We observed no evidence of degradation within the study reach (Fig. 6).

Classification of cottonwood stands in the study reach by size class (Hansen 1989) shows a relative scarcity of smaller, and presumably younger, trees within a portion of the study reach, implying a future decrease in the area of mature trees. Hansen (1989) interprets this apparent shortage as an impact of upstream dams. However, results of the present study indicate that cottonwood reproduction has been highly episodic; therefore, size class ratios at one point in time may not be a reliable predictor of future trends. Furthermore, dams have not yet altered the observed number of flows exceeding 1400 m³/s in the 38 yr since Canyon Ferry was completed. Therefore, if the present scarcity of young trees does represent the beginning of a long-term decline in forest area, the present level of flow regulation is unlikely to be the principal cause.

Management implications

By demonstrating the dependency of riparian cottonwood establishment and survival on floods, this study supports the central role of floods in structuring large riverine ecosystems (Welcomme 1979, Junk et al. 1989, Power et al. 1995). On the Missouri River, high flows in late May and June have been shown to stimulate spawning migrations of shovelnose sturgeon (*Scaphirhynchus platorynchus* Rafinesque) and paddlefish (*Polyodon spathula*) (Berg 1981). Flood flows

also are important in creating and maintaining geomorphic features such as side channels or back channels, sandbars, chutes, and pools that serve as essential habitat for native terrestrial and aquatic species, including the endangered pallid sturgeon (*Scaphirhynchus albus*), the sturgeon chub (*Macrhybopsis gelida*), sicklefin chub (*Macrhybopsis meeki*), blue sucker (*Cycleptus elongatus*), and paddlefish (Hesse et al. 1993). Cottonwood is a dominant tree species along rivers and streams throughout arid and semiarid regions of North America, and provides structural habitat for a diversity of wildlife species (Brinson et al. 1981). Therefore, identifying flows associated with the maintenance of cottonwood forests is consistent with management efforts emphasizing preservation of processes that support a diversity of riparian species (Nilsson 1992, Sparks 1995).

Complex interactions among flow regime, channel processes, and vegetation life history traits contribute to considerable apparent variability in the response of riparian vegetation to flow alteration (Pettis 1980, Johnson 1994). This apparent variability constrains the effectiveness of traditional vegetation analyses in assessing and predicting future change. Consideration of riparian vegetation in water management decisions must be balanced against competing needs for limited water and operational mandates such as flood control and power generation. In this context, flow prescriptions for cottonwoods benefit from specification of flows that maximize potential recruitment (Hughes 1994). By placing relations between flow and cottonwood establishment in a geomorphic context (Table 1), some of the observed variability of response can be explained and predictions can be improved. Demonstration of the primacy of flood deposition processes in the establishment and persistence of riparian cottonwoods within this constrained reach of the Missouri River provides a sharp focus for management prescriptions aimed at maintaining riparian cottonwoods. Protecting the frequency, timing, and duration of flows >1400 m³/s throughout this reach is central to maintaining the current abundance and distribution of much of its cottonwood forest.

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