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Fluvial process and the establishment of bottomland trees

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

National Biological Service, Midcontinent Ecological Science, Fort Collins, CO 80525-3400, USA

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Abstract

The effects of river regulation on bottomland tree communities in western North America have generated substantial concern because of the important habitat and aesthetic values of these communities. Consideration of such effects in water management decisions has been hampered by the apparent variability of responses of bottomland tree communities to flow alteration. When the relation between streamflow and tree establishment is placed in a geomorphic context, however, much of that variability is explained, and prediction of changes in the tree community is improved.

The relation between streamflow and establishment of bottomland trees is conditioned by the dominant fluvial process or processes acting along a stream. For successful establishment, cottonwoods, poplars, and willows require bare, moist surfaces protected from disturbance. Channel narrowing, channel meandering, and flood deposition promote different spatial and temporal patterns of establishment. During channel narrowing, the site requirements are met on portions of the bed abandoned by the stream, and establishment is associated with a period of low flow lasting one to several years. During channel meandering, the requirements are met on point bars following moderate or higher peak flows. Following flood deposition, the requirements are met on flood deposits high above the channel bed. Flood deposition can occur along most streams, but where a channel is constrained by a narrow valley, this process may be the only mechanism that can produce a bare, moist surface high enough to be safe from future disturbance. Because of differences in local bedrock, tributary influence, or geologic history, two nearby reaches of the same stream may be dominated by different fluvial processes and have different spatial and temporal patterns of trees. We illustrate this phenomenon with examples from forests of plains cottonwood (*Populus deltoides* ssp. *monilifera*) along meandering and constrained reaches of the Missouri River in Montana.

1. Introduction

The first woody plants to dominate bare, wet sediment along streams often demonstrate rapid growth, intolerance of shade, tolerance of nutrient scarcity and burial, release of large numbers of seeds following peak flows, and lack of seed dormancy (Sigafoos, 1964; White, 1979; Hupp, 1992). In the more arid regions of the northern hemisphere, the dominant plants in this group are members of the family Salicaceae, including cottonwoods and poplars (*Populus*) and willows (*Salix*). Bottomland forests provide important habitat structure for wildlife, especially where bottomlands are the only locations in the landscape wet enough to support trees (Brinson et al., 1981).

A focus of our work is to understand how spatial and temporal patterns of bottomland cottonwoods, poplars, and willows are influenced by the flow regime. These patterns are determined to a large extent by flow during the establishment phase (Stromberg et al., 1991; Scott et al., 1993). The relation between flow and establishment, however, varies from site to site. Along one stream cottonwoods may establish following high flows, whereas along another they establish during low flows. The thesis of our paper is that this variation results from differences in the fluvial-geomorphic proc-

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esses that form surfaces suitable for establishment.

Several studies have addressed the relation between flow and establishment of cottonwoods, poplars, and willows in the context of a single fluvial process (Everitt, 1968; Nanson and Beach, 1977; Bradley and Smith, 1986; Hupp, 1992; Johnson, 1994; Friedman et al., 1996). In this paper, we synthesize these studies and provide an example of how different dominant fluvial processes produce different relations between flow and patterns of cottonwoods on different reaches of the same river.

The conditions associated with successful establishment of bottomland cottonwoods, poplars, and willows are well understood. An abundant crop of wind- and water-dispersed seeds is released early each summer in association with peak flow (Densmore and Zasada, 1983; Fenner et al., 1985). The seeds can germinate immediately, but lose germinability under field conditions within a few weeks (Moss, 1938; Ware and Penfound, 1949; Densmore and Zasada, 1983). Freshly deposited alluvium typically provides ideal substrate for germination and establishment. Because they are intolerant of shade and germinate poorly in plant litter, cottonwoods, poplars, and willows are incapable of becoming established from seed under an existing stand of trees (Johnson et al., 1976) or herbs (Friedman, 1993). This trait often leads to even-aged stands. Young seedlings require a continuously moist substrate during at least the first week of growth (Moss, 1938). Root growth during the first month is slow (Burns and Honkala, 1990), but later in the first growing season seedlings of some species are able to extend a taproot deep enough to survive declines in the water table of as much as 1 m (Fenner et al., 1984; Segelquist et al., 1993). Therefore, the vulnerability of these plants to dry conditions decreases rapidly with age (McLeod and McPherson, 1973; Sacchi and Price, 1992). Bottomland cottonwoods, poplars, and willows are tolerant of burial and able to sprout from stems or roots (Nanson and Beach, 1977; Krasny et al., 1988). Extensive mortality of young plants, however, has been reported as a result of floods (Zimmerman, 1969) and ice scour (Johnson, 1994).

In summary, successful establishment from seed occurs only in channel positions that are moist, bare, and protected from removal by subsequent disturbance (Sigafoos, 1964; Everitt, 1968; Noble, 1979; Bradley and Smith, 1986; Stromberg et al., 1991; Sacchi and Price, 1992; Johnson, 1994). In humid regions vegetation is dense and grows rapidly, and as a result the need for a bare surface is more restrictive than the moisture requirement (Johnson, 1965). The reverse is true in arid regions (Zimmerman, 1969; Friedman, 1993). Some bottomland cottonwoods, poplars, and willows are capable of forming root sprouts. Where this mode of reproduction is important, formation of new stems may not be restricted to bare, moist surfaces, and the rate of lateral root growth may influence the timing of colonization of new areas.

2. Geomorphic processes and tree establishment

A suitable environment for establishment of cottonwoods, poplars, and willows can be produced by many fluvial processes, but we concentrate on three processes — narrowing, meandering, and flood deposition (Table 1). These processes are complex and the distinctions among them are sometimes arbitrary. Nevertheless, the three processes produce different spatial and temporal patterns of trees and different relations between flow regime and establishment. Our goal is to develop the ability to predict how changes in river management will affect bottomland forests.

2.1. Narrowing

In this paper, channel narrowing refers to abandonment by the stream of a portion of former channel bed. Thus, we include establishment of trees and shrubs in a former channel following avulsion. Establishment by channel narrowing, important in streams subject to large fluctuations in width, occurs more in braided streams than in meandering streams (Schumm, 1969), and more in arid regions than in humid regions (Wolman and Gerson, 1978).

Channel narrowing can occur as a response to flood-induced widening (Schumm and Lichty, 1963; Burkham, 1972; Osterkamp and Costa, 1987), climate change (Schumm, 1969; Gottesfeld and Johnson Gottesfeld, 1990), construction of upstream dams (Williams and Wolman, 1984), changes in land management (Nadler and Schumm, 1981), introduction of exotic bottomland plant species (Nevins, 1969; Graf, 1978), or as part of a cyclic, autogenic process (Patton and Schumm, 1981; Nanson, 1986). The

Table 1
Geomorphic processes associated with cottonwood establishment

Geomorphic process	Flow	Landform	Cottonwood community patterns
Narrowing	One to several years of flow below that which is necessary to rework channel bed	Channelbed	· 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 distribution corresponding to meander pattern · Flood training of stems common · Establishment surface of mature trees often well below current ground surface and near channel bed elevation
Flood deposition and erosion	Infrequent high flows	Flooddeposits	· Linear stands · Small number of even-aged stands · Establishment coincident with floods · Little flood training of stems · Establishment surface of mature trees near current ground surface and well above channel bed elevation

immediate cause of narrowing is usually a period of one to several years of flows lower than that necessary to rework the entire channel bed. This allows establishment of vegetation on the channel bed. The newly established 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.

The magnitude of flow necessary to produce channel narrowing depends upon antecedent conditions. After flood-induced widening, a stream is generally not competent to keep the entire bed free of vegetation. In this situation narrowing can occur under a wide range of low to moderate flows as has been observed on the Cimarron River in Kansas, the Gila River in Arizona, and Plum Creek in Colorado (Schumm and Lichty, 1963; Burkham, 1972; Osterkamp and Costa, 1987). Where the channel is closer to an equilibrium width, narrowing may occur only as a response to one to several years of exceptionally low peak flows. Thus, narrowing of the South Platte River in Colorado was associated with low flows during the 1930's (Nadler and Schumm, 1981).

Populations of cottonwoods, poplars, and willows established during channel narrowing are usually not strictly even-aged (Friedman, 1993); individuals in a stand may have been established at any time within a period of several years of relatively low flow. Stands usually have an irregular shape, of which the greatest dimension, or axis, is generally parallel to the direction of flow. Where narrowing occurs rapidly, young individuals are inundated infrequently and are usually not flood-trained (bent downstream into a decumbent position). The germination point of trees and shrubs established during channel narrowing is at the elevation of the channel bed at the time the surface was abandoned by the stream. This elevation may be different from the present bed-level because the process of channel narrowing sometimes involves bed-level changes (Friedman et al., 1996).

Most published examples of channel narrowing have involved the process discussed above. Channel narrowing, however, does not always involve establishment of vegetation on the channel bed. Channel narrowing can occur by lateral deposition at channel islands (Schumm and Lichty, 1963; Osterkamp and Costa, 1987) or at the channel bank (Nadler and Schumm, 1981). Where this process is important, establishment from seed will take place at higher elevations than the channel bed, as occurs along meandering channels. In addition, in the case of gradual narrowing by lateral deposition along an already vegetated surface, establishment of new individuals from root sprouts or sprouts from decumbent stems is likely to be important.

2.2. Meandering

Meandering streams are characterized by low width-to-depth ratios and progressive channel movement. The process of meandering is most important along low-gradient streams with low discharge variability and sediment load dominated by suspended sediment (Schumm, 1969). Infrequent events can have long-lasting effects on the geometry of meandering streams, especially in arid and semiarid regions (Schumm and Lichty, 1963; Burkham, 1972; Wolman and Gerson, 1978). Most of the sediment deposition on point bars, however, is carried out by moderate flows with recurrence intervals less than 5 years (Wolman and Miller, 1960). Forests produced as a result of meandering generally take the form of a series of parallel, arcuate bands of even-aged trees. These bands develop on point bars, and are, therefore, parallel to the direction of flow at the time they were established (Everitt, 1968; Nanson and Beach, 1977; Noble, 1979). On the point-bar side of the channel, the age of bands increases with distance from the channel. Stands on the cutbank side are older and not necessarily parallel to the present direction of flow. Because establishment is on a surface subject to frequent deposition, young stems may be repeatedly flood-trained (Everitt, 1968). The establishment surface of an adult tree is at the elevation of a young point bar — typically below the present flood plain, but above the channel bed. In some cases extensive flood-training may make it difficult to locate precisely the original root flare of a tree (Everitt, 1968).

Along a meandering stream, progressive movement of the channel protects trees and shrubs on former point bars from flood disturbance. This results in the preservation of a large number of bands on the flood plain. If a band is not removed by erosion, the cottonwoods, poplars, and willows are eventually replaced by shade-tolerant woody species (Weaver, 1960; Johnson et al., 1976; Nanson and Beach, 1977) or by grassland (Hefley, 1937; Lindauer, 1983).

Along the Little Missouri River in North Dakota, Everitt (1968) found establishment of plains cottonwood (*Populus deltoides* ssp. *monilifera*) seedlings at about 2 m above the low-water level. Adult trees occurred on surfaces as high as 5 m above low water. When trees were excavated, the establishment surface was found to be at approximately the elevation now occupied by seedlings. Cottonwoods were arranged in arcuate bands, and the stems in each band at ground level were generally even-aged. Because of extensive damage caused by flood-training, it was often impossible to find or date the establishment point.

On the Milk River in Alberta and Montana, Bradley and Smith (1986) counted rings in cores of plains cottonwood trees and found that establishment took place at approximately 5-year intervals, when flows of 2-year recurrence interval or greater occurred during the period of seed release. Cottonwood trees were arranged in parallel, arcuate bands, each spanning a range of ages of one to a few years. No consistent pattern of tree presence occurred relative to flood-plain ridges and swales. Seedlings were established approximately 0.5 m above the channel bed and then experienced 0.5 to 2 m of sediment deposition during flood-plain development.

On the Beatton River in British Columbia, establishment of balsam poplar (*Populus balsamifera*) occurred on the tops of scroll bars (Hickin and Nanson, 1975; Nanson and Beach, 1977). These bars were formed on average once every 27 years, but the periodicity varied from one bar to the next depending on the local rate of channel migration (Hickin and Nanson, 1975). Poplars became established on bars that had exceeded approximate bankfull stage. Subsequent deposition of sediment then buried the establishment surface by about 2.5 m (Nanson and Beach, 1977). Seasonality of individual flows was probably relatively unimportant in this case because establishment was not from seed but from root sprouts. As the scroll bars grew laterally, new stems were added on the streamward side. Therefore, the ages of stems on an individual scroll bar encompassed several years.

2.3. Flood deposition

Flood deposition and erosion occur along most streams, but are especially important for cottonwood establishment where lateral channel movement is constrained by a narrow valley. Because the channel is not moving, the only locations that are safe from subsequent scouring are those at high elevations. Only the greatest flows produce bare, moist substrate at these high elevations. Therefore, along a constrained channel trees occur in a small number of even-aged groups. The germination point of individuals is at a high elevation relative to the channel bed and close to the present ground surface. Flood-training is rare because the high establishment surface is rarely inundated.

For several reasons, the oldest trees along a constrained channel do not always date to the greatest recent discharge. First, the area of bare surface generated by flood deposition or erosion is a function not only of discharge but also of sediment load, type and age of pre-existing vegetation, local channel geometry, and flow history. Second, a bare surface will not support establishment unless it is moist during the time of seed viability. Flow timing, flow duration, subsequent precipitation, and sediment particle size may also be important. Finally, trees are susceptible to removal by subsequent floods, drought, fire, grazing, or competition from other plants.

Along the Animas River, a montane stream in western Colorado, establishment of narrow-leaf cottonwood (*Populus angustifolia*) occurred about once every 10 years, when peak snowmelt flows of recurrence interval over 3.6 years coincided with cool, wet weather (Baker, 1990). This combination of events produced the locations necessary for establishment — bare, moist surfaces high enough to be safe from future scouring. Because seedlings need cool moist conditions in the first growing season, high spring flows did not always result in cottonwood establishment.

Stromberg et al. (1991) observed successful recruitment of Fremont cottonwood (*Populus fremontii*) and Goodding willow (*Salix gooddingii*) about every 12 years along the Hassayampa River in Arizona. Flows with a recurrence interval of at least 7 years appeared to be necessary to create suitable bare surfaces. In this system, peak flows usually occurred months after the March through May period of seed release. As a result establishment took place 1 to 3 years after the year of peak flow and appeared to depend on moisture from precipitation. In the two cases just described, the river valley was wide enough to allow movement of the channel. This protected established trees from flood disturbance and explains the relatively large number of age classes observed.

Floods can cause tree establishment either directly, through the process of flood deposition, or indirectly, by initiating an episode of channel narrowing. For example, along a sandbed stream in the Great Plains, deposits left on low terraces by a catastrophic flood in 1965 were too high, and, therefore, too dry, to allow establishment of cottonwood from seed; however, the flood widened the stream, and during subsequent decades of narrowing, extensive establishment occurred at or near the elevation of the channel bed (Friedman et al., 1996).

3. Case example from the Missouri River in Montana, USA

The fluvial processes previously discussed can act alone or in combination. Where the dominant process changes along a stream, patterns of trees may change accordingly. We examined patterns of cottonwood (*Populus deltoides* ssp. *monilifera*) establishment within a post-glacial section of the upper Missouri River in Montana, USA (Fig. 1), where the river is variously constrained by a narrow valley (Lemke et al., 1965).

We present data from two sites within the post-glacial section (Fig. 1). At Site A, 153.3 km downstream of Fort Benton, Montana, lateral migration is prevented by the narrow valley (Fig. 2A and Fig. 3). At Site B, 237.5 km downstream of Fort Benton, the valley is wider and some meandering occurs (Fig. 2B and Fig. 4). In 1992, a transect was surveyed perpendicular to the channel at each site. Distinct fluvial surfaces along the transect were noted and the nearest four to ten trees on each surface downstream of the transect were selected for sampling. We excavated these trees to the root flare and sectioned and aged the stem above, below, and at the root flare. For trees larger than 60-cm diameter, we extracted cores instead of stem sections. We cross-dated all trees at a site to identify false or missing rings (Phipps, 1985).

Flow records were obtained from the United States Geological Survey gages at Fort Benton and Landusky, upstream and downstream, respectively, of our study sites (Fig. 1). Because patterns of discharge at these two gages are similar, only data from Fort Benton are presented here. Canyon Ferry Dam, approximately 220 km upstream of Fort Benton (Fig. 1), has been in operation since 1953. The dam, however, has limited storage capacity, and several unregulated tributaries enter the Missouri River between the dam and the study area.

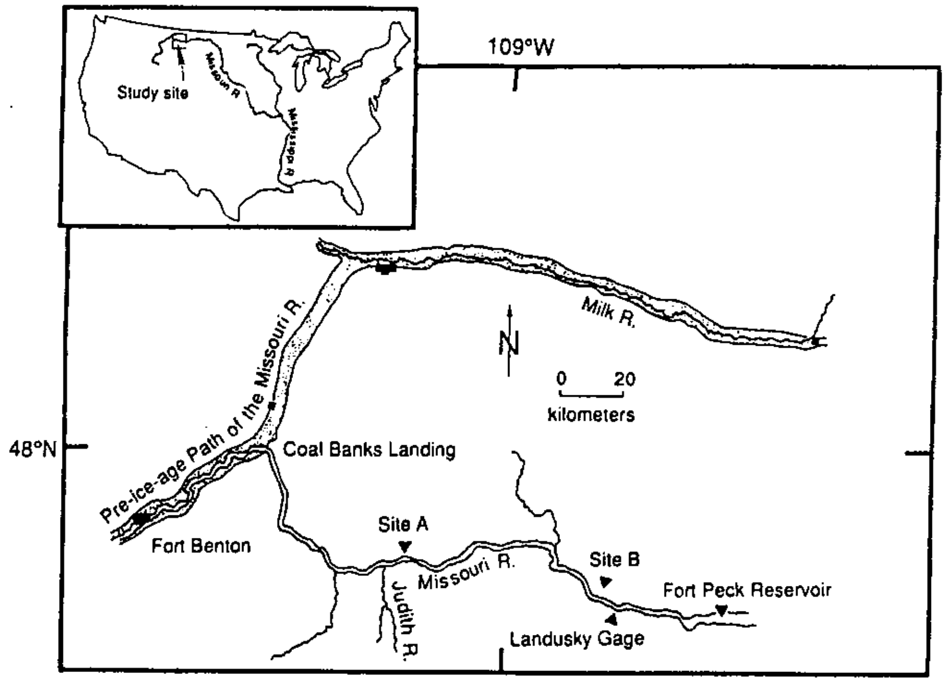

Fig. 1. Map of the study reach on the Missouri River, Montana. The stippled area represents the pre-Illinoian channel of the Missouri River (redrawn after Lemke et al., 1965).

As a result, the reduction in peak flows caused by Canyon Ferry Dam is small in this part of the river.

At Site A, where a narrow valley (0.4 km) limits channel meandering, we found a narrow single band of trees at a high position adjacent to the valley wall (Fig. 2A and Fig. 3). These trees became established at an elevation of 3 m above the low-water stage (measured at a discharge of approximately 115 m^3/s), on a layer of coarse sand apparently deposited by the flood of 1927 (Fig. 3); none of these trees were flood-trained (Fig. 5). Three of four sampled trees dated to the year following a flood of 1500 m^3/s in 1927, and the fourth tree was established in the second year following the flood (Fig. 6). The only other cottonwoods present were seedlings (individuals less than 1 m tall) established during the last two growing seasons at elevations less than 1.5 m above the low-water surface. Such seedlings, present along much of the study reach, are not likely to survive future high flows. Others researchers have reported that cottonwood seedlings occupying low-channel positions are prone to flood-related mortality from scour, burial, and inundation (McBride and Strahan, 1984; Asplund and Gooch, 1988; Stromberg et al., 1991).

At Site B the point-bar and cut-bank characteristics of a meandering channel were associated with several arcuate bands of cottonwoods distributed across a relatively broad bottomland (1.2 km) (Fig. 2B and Fig. 4). We sampled trees in the three bands closest to the channel. The band adjacent to the channel consisted of seedlings established in 1991 and 1992. Trees sampled on the other two bands included 15 individuals established up to two years after flows of 1400 to 2000 m^3/s in 1964, 1978, and 1981 (Fig. 6); the 1978 flood was recorded at the Landusky gage, following breakup of an ice jam between Fort Benton and Landusky (Fig. 1). Four other trees were apparently established following lesser flows from 1968 to 1970 (Fig. 6). The root flares of all sampled trees were within 2 m of the low-water surface and at or below the elevation occupied by seedlings at this cross-section (Fig. 4). These trees had experienced 0.5 to 1.0 m of sediment accretion since establishment (Fig. 4) and most stems were flood-trained (Fig. 7).

In summary, the frequency of cottonwood establishment in the post-glacial section of the Missouri River is determined by the locally dominant fluvial processes. Where lateral movement of the channel is prevented by

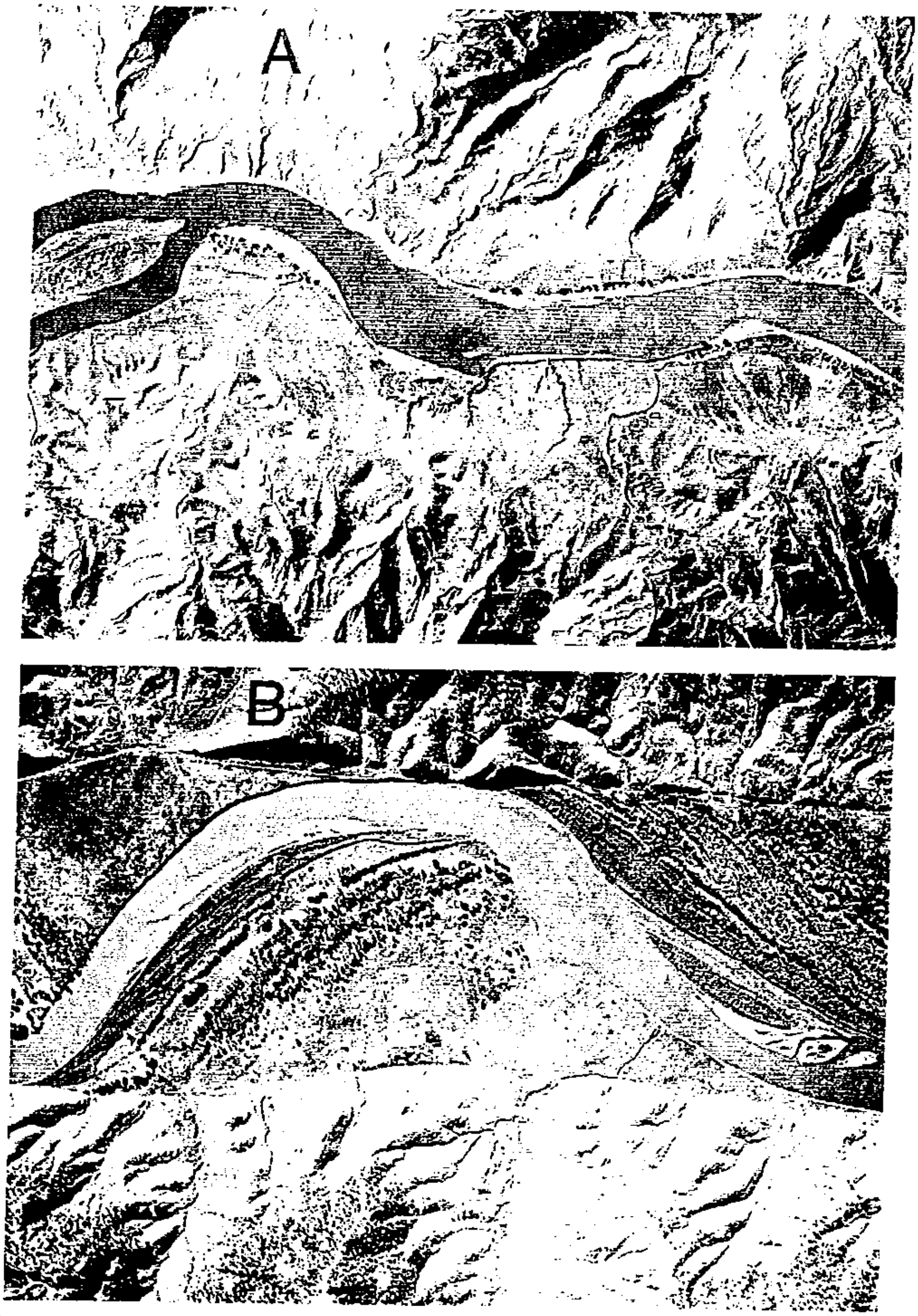

Fig. 2. Aerial photographs of (A) the constrained channel at Site A with associated narrow band of trees, and (B) the less constrained, meandering channel at Site B with a broad zone of bottomland trees arranged in arcuate bands.

a narrow valley, mature cottonwoods are few and largely restricted to narrow, elevated deposits of infrequent floods. On the other hand, in a less constrained reach cottonwood establishment occurs more frequently and at relatively low elevations. These conclusions are supported by preliminary examination of

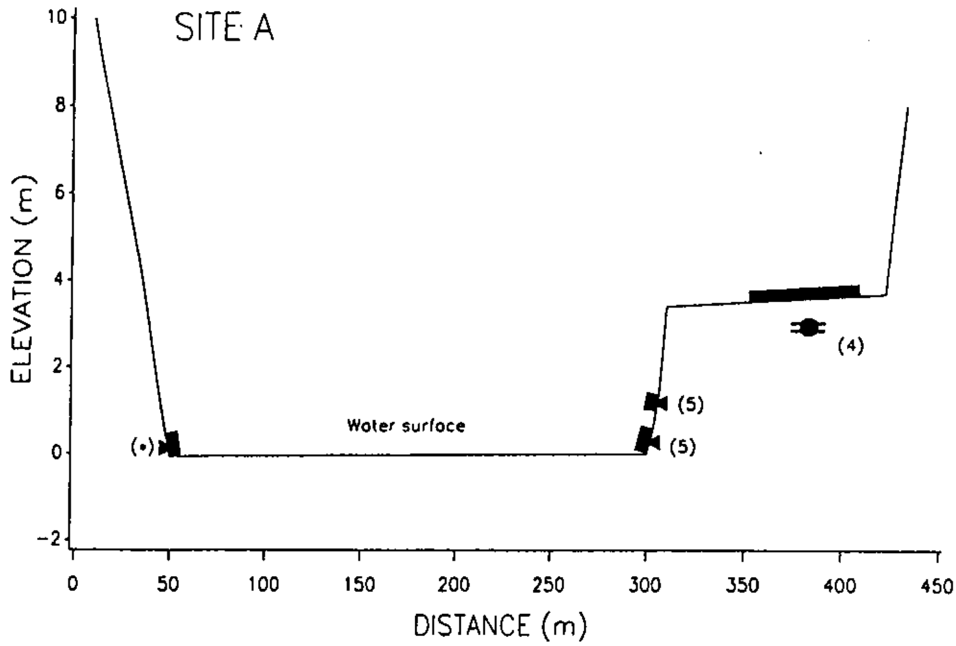

Fig. 3. Cross-section at Site A, Missouri River, Montana. Surfaces occupied by cottonwood are marked by thick bars. Triangles are seedlings and circles are trees. Bars attached to circles show the range of root-flare elevations. All seedlings had root flares within 10 cm of the present surface. The number of trees aged on a surface is given in parentheses. The asterisk indicates a surface on which seedlings were surveyed but not aged.

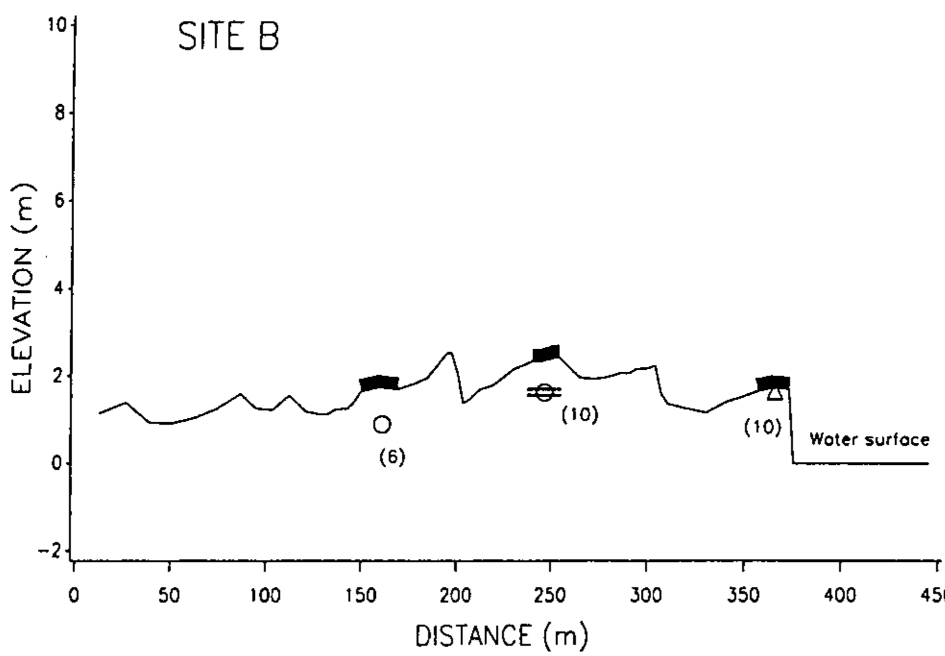

Fig. 4. Cross-section at Site B, Missouri River, Montana. Surfaces occupied by cottonwood are marked by thick bars. Triangles are seedlings and circles are trees. The number of trees aged on a surface is given in parentheses. Bars attached to circles show the range of root-flare elevations. On the surface at 160 m six trees were aged, but depth to root flare was measured for only one. All seedlings had root flares within 10 cm of the present surface.

Fig. 5. Photograph of an excavated cottonwood tree on a flood deposit along a narrow, highly constrained reach of the Missouri River.

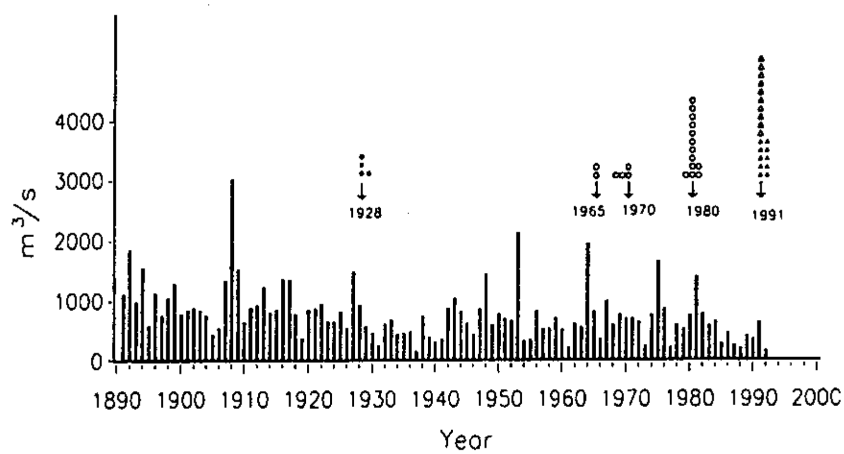

Fig. 6. Years of cottonwood establishment along the Missouri River, Montana, and peak mean daily discharge at the Fort Benton gage. Each circle or triangle indicates the establishment date of one cottonwood. Closed symbols are from Site A and open symbols are from Site B. Circles are trees and triangles are seedlings.

results from eight additional cross-sections examined along the Missouri River, Montana, in 1992 and 1993.

4. Discussion

Impacts of water development and river regulation on bottomland tree communities in western North America have generated substantial concern because of the important habitat and aesthetic values of these communities. Consideration of these impacts in water management decisions has been hampered by variability of responses of bottomland tree communities to flow alteration. Placing the relation of flow to vegetation in the appropriate geomorphic context helps explain this

Fig. 7. Photograph of an excavated, flood-trained stem from a meandering reach of the Missouri River. Note the prostrated, buried stem from which a new stem has arisen.

variability and may improve prediction of the effects of proposed flow alterations on bottomland vegetation.

Where meandering is the dominant fluvial process, a reduction in peak annual flows could decrease the rate of meandering, leading to decreased establishment. This phenomenon has been observed downstream of several dams in North America (Johnson, 1992; Bradley and Smith, 1986; Rood and Mahoney, 1990). On the other hand, reduction of peak flows in a braided stream could lead to narrowing and a one-time pulse of establishment during a period of low flow. After this pulse, additional establishment would occur infrequently, at higher elevations, and following higher flows. Thus, the extensive cottonwood forests that have developed during channel narrowing along the Platte and North Platte Rivers in Nebraska and along the South Platte and Arkansas Rivers in Colorado in the 1900s may be transient features. As the trees of these forests die they will probably be replaced by shade-tolerant tree species in relatively humid regions (Johnson, 1994), and by shrubland and grassland in more arid regions, where shade-tolerant bottomland trees do not occur.

If management of a stream prevented lateral migration of a formerly meandering channel, then the dominant fluvial process could shift from meandering to flood deposition and erosion. In other words, the discharge necessary for establishment could increase, because saplings on point bars would no longer be protected by lateral migration of the channel.

In this paper we have described a reach of the upper Missouri River in which sections of constrained channel alternate with sections where lateral migration occurs. In the former situation establishment occurs only at high flows, but in the latter situation establishment occurs at both moderate and high flows. Therefore, the constrained reaches would be more likely to exhibit cottonwood forest decline following construction of a dam that decreased the magnitude of flows with a recurrence interval of ten years or greater.

A better appreciation of the relevant geomorphic processes can help establish appropriate management objectives for bottomland forests. Often environmental objectives are formulated in terms of protecting the current situation from degradation. Bottomland cottonwood, poplar, and willow, however, are disturbance-dependent pioneer species. The current locations and extents of these bottomland forests do not always represent reasonable management objectives. Over the long-term, the natural extent and distribution of bottomland trees are limited by the geomorphic processes creating suitable establishment locations, and existing stands may be relicts of the geomorphic processes associated with a former flow regime. In the case of channel narrowing following a reduction in peak flows, extensive cottonwood and willow woodland is a transient response representative of neither the old nor the new flow regime.

Even in an unregulated situation, establishment along some constrained streams may occur only once in several decades. Bottomland cottonwoods, poplars, and willows do not live more than one or occasionally two centuries (Burns and Honkala, 1990). Thus, punctuated age distributions and large changes in densities from one decade to the next are the norm, and are not necessarily the result of human influence. Furthermore, the frequency of floods has varied naturally in some areas over the last several centuries (Webb et al., 1991; Knox, 1993). This has led to large changes in abundance of trees along streams where regeneration occurs on flood deposits (Baker, 1990) and along some streams in arid and semiarid regions prone to flood-related fluctuations in width (Schumm and Lichty, 1963; Burkham, 1972).

Quantifying many of the differences we have identified in the relations between flow and bottomland forests (Table 1) depends on accurate determination of the date and elevation of tree establishment. These data cannot be obtained without excavating the original root flare. Along the Missouri River, we have found that trees are often many years older below ground than above ground. The number of extra years below ground varies considerably from tree to tree within sites because it is influenced by factors such as flood injury and beaver attack. In this situation a core taken above the ground surface is a misleading indicator of the age of a tree.

We have emphasized the importance of establishment in determining patterns of woody plants and further have focused on how stream discharge operates through different geomorphic processes to produce suitable establishment surfaces. Discharge, however, is not an infallible predictor of the bottomland disturbance necessary for establishment. Along some streams ice jams during relatively low flow can result in inundation of areas otherwise rarely flooded (Butler, 1979). Slumps, debris flows, and tributary alluvial fans may provide bare, moist surfaces for establishment independently of discharge. Such surfaces are often high above the channel, and can provide important safe havens during destructive floods (Osterkamp and Costa, 1987).

Cottonwoods, poplars, and willows do not always establish when suitable locations are present. One reason is the absence of viable seeds. Abundant seeds of these species are produced almost every year and they can be transported large distances by air or water. Seeds, however, are produced during a period of a few weeks, usually in early summer, and remain germinable only for a few weeks more. Floods occurring outside of the seed dispersal period may not lead to establishment, especially in arid regions where moisture provided by flood water is critical. Similarly, dams that delay the occurrence of peak flows can decrease establishment opportunities (Fenner et al., 1985). Grazing and trampling by cattle can also prevent establishment (Kauffman et al., 1983).

Adult mortality also influences the pattern of bottomland trees and shrubs. Geomorphic processes that create new establishment opportunities may also remove existing adults; such processes include flood scouring (Yanosky, 1982), cutbank erosion of a meandering river, ice impact (Sigafoos, 1964), fire (Nanson and Beach, 1977), drought (Albertson and Weaver, 1945), ground-water pumping (Stromberg et al., 1992), and beaver damage (Bradley and Smith, 1986), as well as timber harvest and land clearing. These factors dominate patterns of some populations, but in most cases the underlying pattern determined through establishment is still clear.

5. Conclusions

Establishment of bottomland cottonwoods, poplars, and willows from seed occurs almost exclusively on bare, moist surfaces protected from disturbance. These conditions can be produced by several different fluvial processes, including narrowing, meandering, and flood deposition. These processes are associated with different flows and produce different spatial and temporal patterns of trees. Because of the importance of bottomland forests as habitat, managers need to be able to predict how a flood-plain landscape would be affected by a change in flow regime. Such predictions require an understanding of the locally dominant fluvial processes.

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References

Albertson, F.W. and Weaver, J.E., 1945. Injury and death or recovery of trees in prairie climate. Ecol. Monogr., 15: 395–433.

Asplund, K.K. and Gooch, M.T., 1988. Geomorphology and distributional ecology of Fremont cottonwood (*Populus fremontii*) in a desert riparian canyon. Desert Plants, 9: 17–27.

Baker, W.L., 1990. Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado. J. Biogeogr., 17: 59–73.

Bradley, C.E. and Smith, D.G., 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. Can. J. Bot., 64: 1433–1442.

Brinson, M.M., Swift, B.L., Plantico, R.C. and Barclay, J.S., 1981. Riparian ecosystems: their ecology and status. U.S. Fish and Wildlife Service Biological Report 81/17, 155 pp.

Burkham, D.E., 1972. Channel changes of the Gila River in Safford Valley, Arizona 1846–1970. U.S. Geol. Surv. Prof. Pap., 655-G, 24 pp.

Burns, R.M. and Honkala, B.H. (Technical Coordinators), 1990. Silvics of North America, volume 2, hardwoods. United States Department of Agriculture, Forest Service, Agriculture Handbook 654, 877 pp.

Butler, D.R., 1979. Dendrogeomorphological analysis of flooding and mass movement, Ram Plateau, Mackenzie Mountains, Northwest Territories. Can. Geogr., 23: 62–65.

Densmore, R. and Zasada, J., 1983. Seed dispersal and dormancy patterns in northern willows: ecological and evolutionary significance. Can. J. Bot., 61: 3207–3216.

Everitt, B.L., 1968. Use of the cottonwood in an investigation of the recent history of a flood plain. Am. J. Sci., 266: 417–439.

Fenner, P., Brady, W.W. and Patton, D.R., 1984. Observations on seeds and seedlings of Fremont cottonwood. Desert Plants, 6: 55–58.

Fenner, P., Brady, W.W. and Patton, D.R., 1985. Effects of regulated water flows on regeneration of Fremont cottonwood. J. Range Manage., 38: 135–138.

Friedman, J.M., 1993. Vegetation establishment and channel narrowing along a Great-Plains stream following a catastrophic flood. Dissertation, University of Colorado, Boulder, Colorado, 156 pp.

Friedman, J.M., Osterkamp, W.R. and Lewis, W.M., Jr., 1996. The role of vegetation and bed-level fluctuations in the process of channel narrowing. Geomorphology, 14: 341–351, this issue.

Gottesfeld, A.S. and Johnson Gottesfeld, L.M., 1990. Floodplain dynamics of a wandering river, dendrochronology of the Morice River, British Columbia, Canada. Geomorphology, 3: 159–179.

Graf, W.L., 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. Geol. Soc. Am. Bull., 89: 1491–1501.

Hefley, H.M., 1937. Ecological studies on the Canadian River floodplain in Cleveland County, Oklahoma. Ecol. Monogr., 7: 345–402.

Hickin, E.J. and Nanson, G.C., 1975. The character of channel migration on the Beatton River, northeast British Columbia, Canada. Geol. Soc. Am. Bull., 86: 487–494.

Hupp, C.R., 1992. Riparian vegetation recovery patterns following stream channelization: a geomorphic perspective. Ecology, 73: 1209–1226.

Johnson, R.L., 1965. Regenerating cottonwood from natural seedfall. J. For., 63: 33–36.

Johnson, W.C., 1992. Dams and riparian forests: case study from the upper Missouri River. Rivers, 3: 229–242.

Johnson, W.C., 1994. Woodland expansion in the Platte River, Nebraska: patterns and causes. Ecol. Monogr., 64: 45–84.

Johnson, W.C., Burgess, R.L. and Keammerer, W.R., 1976. Forest overstory vegetation and environment on the Missouri River floodplain in North Dakota. Ecol. Monogr., 46: 59–84.

Kauffman, J.B., Krueger, W.C. and Vavra, M., 1983. Impacts of cattle on streambanks in northeastern Oregon. J. Range Manage., 36: 683–685.

Knox, J.C., 1993. Large increases in flood magnitude in response to modest changes in climate. Nature, 361: 430–436.

Krasny, M.E., Vogt, K.A. and Zasada, J.C., 1988. Establishment of four Salicaceae species on river bars in interior Alaska. Holarctic Ecol., 11: 210–219.

Lemke, R.W., Laird, W.M., Tipton, M.J. and Lindvall, R.M., 1965. Quaternary geology of northern Great Plains. In: H.E. Wright, Jr. and J.C. Frye (Editors), The Quaternary of the United States. Princeton University Press, pp. 15–27.

Lindauer, I.E., 1983. A comparison of the plant communities of the South Platte and Arkansas River drainages in eastern Colorado. Southwest. Nat., 28: 249–259.

McBride, J.R. and Strahan, J., 1984. Establishment and survival of woody riparian species on gravel bars of an intermittent stream. Am. Midl. Nat., 112: 235–245.

McLeod, K.W. and McPherson, J.K., 1973. Factors limiting the distribution of *Salix nigra*. Bull. Torrey Bot. Club, 100: 102–110.

Moss, E.H., 1938. Longevity of seed and establishment of seedlings in species of *Populus*. Bot. Gazette, 99: 529–542.

Nadler, C.T. and Schumm, S.A., 1981. Metamorphosis of South Platte and Arkansas Rivers, eastern Colorado. Phys. Geogr., 2: 95–115.

Nanson, G.C., 1986. Episodes of vertical accretion and catastrophic stripping: a model of disequilibrium flood-plain development. Geol. Soc. Am. Bull., 97: 1467–1475.

Nanson, G.C. and Beach, H.F., 1977. Forest succession and sedimentation on a meandering-river floodplain, northeast British Columbia, Canada. J. Biogeogr., 4: 229–251.

Nevins, T.H.F., 1969. River training —the single-thread channel. N. Z. Eng., 1969: 367–373.

Noble, M.G., 1979. The origin of *Populus deltoides* and *Salix interior* zones on point bars along the Minnesota River. Am. Midl. Nat., 102: 59–67.

Osterkamp, W.R. and Costa, J.E., 1987. Changes accompanying an extraordinary flood on a sandbed stream. In: L. Mayer and D. Nash (Editors), Catastrophic Flooding. Allen and Unwin, Boston, pp. 201–224.

Patton, P.C. and Schumm, S.A., 1981. Ephemeral-stream processes: implications for studies of Quaternary valley fills. Quat. Res., 15: 24–43.

Phipps, R.L., 1985. Collecting, preparing, crossdating, and measuring tree increment cores. United States Geological Survey Water-Resources Investigations Report 85-4148, 48 pp.

Rood, S.B. and Mahoney, J.M., 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. Environ. Manage., 14: 451–464.

Sacchi, C.F. and Price, P.W., 1992. The relative roles of abiotic and biotic factors in seedling demography of arroyo willow (*Salix lasiolepis*: Salicaceae). Am. J. Bot., 79: 395–405.

Schumm, S.A., 1969. River metamorphosis. J. Hydraul. Div. Am. Soc. Civ. Eng., 95: 255–273.

Schumm, S.A. and Lichty, R.W., 1963. Channel widening and floodplain construction along Cimarron River in southwestern Kansas. U.S. Geol. Surv. Prof. Pap., 352-D: 88 pp.

Scott, M.L., Wondzell, M.A. and Auble, G.T., 1993. Hydrograph characteristics relevant to the establishment and growth of western riparian vegetation. In: H.J. Morel-Seytoux (Editor), Proc. Thirteenth Annual American Geophysical Union Hydrology Days. Hydrology Days Publications, Atherton, Cal., pp. 237–246.

Segelquist, C.A., Scott, M.L. and Auble, G.T., 1993. Establishment of *Populus deltoides* under simulated alluvial groundwater declines. Am. Midl. Nat., 130: 274–285.

Sigafoos, R.S., 1964. Botanical evidence of floods and flood-plain deposition. U.S. Geol. Surv. Prof. Pap., 485A: 35 pp.

Smith, D., 1976. Effect of vegetation on lateral migration of anastomosed channels of a glacial meltwater river. Geol. Soc. Am. Bull., 87: 857–860.

Stromberg, J.C., Patten, D.T. and Richter, B.D., 1991. Flood flows and dynamics of Sonoran riparian forests. Rivers, 2: 221–235.

Stromberg, J.C., Tress, J.A., Wilkins, S.D. and Clark, S.D., 1992. Response of velvet mesquite to groundwater decline. J. Arid Environ., 23: 45–58.

Ware, G.H. and Penfound, W.T., 1949. The vegetation of the lower levels of the floodplain of the South Canadian River in central Oklahoma. Ecology, 30: 478–484.

Weaver, J.E., 1960. Flood plain vegetation of the central Missouri valley and contacts of woodland with prairie. Ecol. Monogr., 30: 37–64.

Webb, R.H., Smith, S.S. and McCord, V.A., 1991. Historic channel change of Kanab Creek southern Utah and northern Arizona. Grand Canyon Natural History Association Monograph Number 9, 91 pp.

White, P.S., 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev., 45: 229–299.

Williams, G.P. and Wolman, M.G., 1984. Downstream effects of dams on alluvial rivers. U.S. Geol. Surv. Prof. Pap., 1286: 84 pp.

Wolman, M.G. and Gerson, R., 1978. Relative scales of time and effectiveness of climate in watershed geomorphology. Earth Surf. Process., 3: 189–208.

Wolman, M.G. and Miller, J.P., 1960. Magnitude and frequency of forces in geomorphic processes. J. Geol., 68: 54–74.

Yanosky, T.M., 1982. Effects of flooding upon woody vegetation along parts of the Potomac River flood plain. U.S. Geol. Surv. Prof. Pap., 1206: 21 pp.

Zimmerman, R.C., 1969. Plant ecology of an arid basin, Tres Alamos–Redington area southeastern Arizona. U.S. Geol. Surv. Prof. Pap., 485-D: 51 pp.