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STREAMFLOW REQUIREMENTS FOR COTTONWOOD SEEDLING RECRUITMENT—AN INTEGRATIVE MODEL

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Abstract: This paper describes the 'recruitment box,' an integrative model that defines the stream stage patterns that enable successful establishment of riparian cottonwood seedlings. In western North America, cottonwood seed dispersal generally occurs after annual peak river flows. The receding stream exposes moist sites upon which seeds land after transport by wind and water. Germination is rapid, and initial seedling establishment is often prolific. However, the vast majority of seedlings die, primarily due to drought stress, as root growth is insufficient to maintain contact with the receding zone of moisture. Cottonwood roots grow about 0.5 to 1 cm per day or 60 to 100 cm in the first year. Along the 'losing' streams in semi-arid regions, the riparian water table is an almost horizontal extension from the stream stage. A capillary fringe exists above the water table and is often 30 to 40 cm in elevation, but can range from about 5 to 130 cm depending on substrate texture. The combination of root growth and capillary fringe define the successful recruitment band, which is usually from about 0.6 to 2 m in elevation above the late summer stream stage. Within this range, higher elevation establishment occurs (i) for the *Aigeiros* cottonwoods, *Populus deltoides*, and *P. fremontii*, which grow more rapidly than *Tacamahaca* species and occur in warmer areas with longer growing seasons; (ii) along larger rivers that are characterized by more gradual stage fluctuations; and (iii) along streams with finer substrate. The rate of stream stage decline is also critical for seedling survival and should not exceed 2.5 cm per day. The recruitment box model is consistent with dendrochronological interpretations that moderate flood events are naturally required for cottonwood recruitment. Flood events with recurrences of about 1 in 5 to 1 in 10 years often satisfy the model and provide stream stage patterns with a gradual decline through the recruitment box. The model will facilitate analyses of the reproductive ecology of riparian cottonwoods and also permit the prescription of stream stage patterns for cottonwood seedling recruitment along dammed rivers.

Key Words: cottonwoods, hydrology, modelling, *Populus*, riparian zone, seedlings

INTRODUCTION

The maintenance of riparian cottonwood populations relies on periodic recruitment to compensate for ongoing mortality. The recruitment can be through either seedlings or through clonal processes, particularly suckering (Rood et al. 1994). Seedling recruitment is probably the dominant means of replenishment for the section *Aigeiros* Duby cottonwoods, the prairie cottonwood (*Populus deltoides* Bartr. ex Marsh.) and the Fremont cottonwood (*P. fremontii* Wats.). Clonal processes are probably more common in the section *Tacamahaca* Spach. cottonwoods, the black cottonwood (*P. trichocarpa* T. & G. *ex* Hook (or *P. balsamifera* L., subsp. *trichocarpa* T. & G. *ex* Hook (Brayshaw 1965)) and the balsam poplar (*P. balsamifera* L.) (Gom 1996). The narrowleaf cottonwood (*P. angustifolia* James) may be intermediate between the other *Tacamahaca* species and the *Aigeiros* cottonwoods. Even for the *Tacamahaca* species, periodic seedling recruitment is essential since sexual recombination introduces the genetic diversity required to cope with gradual change in physical or biological conditions. Seedling recruitment is also a principal mechanism for dispersal and colonization of new islands and other recruitment sites.

One common major impact of river damming in western North America has been a reduction of cottonwood seedling recruitment (reviewed in Rood and Mahoney 1990, Braatne et al. 1996). This failure has been partially caused by the imposition of artificial patterns on stream flow (stage) in which (i) flood events are often attenuated, (ii) flow changes and par-

Table 1. Estimated flood recurrences associated with cottonwood recruitment based on dendrochronological analyses (chronological listing).

Flood Return Interval (yrs)	*Populus* Species	River	Source
5	*P. deltoides*	Milk, AB, MT	Bradley and Smith 1986
3	*P. angustifolia*[1]	Animas, CO	Baker 1990
10–15	*P. angustifolia*[2]	Animas, CO	Baker 1990
10	*P. balsamifera*	Bow, AB	Cordes 1991
3	*P. fremontii*	Rio Grande, NM	Howe and Knopf 1991
5	*P. deltoides*	Milk, AB	Reid 1991
7	*P. fremontii*	Hassayampa, AZ	Stromberg et al. 1991
10	*P. deltoides*	Red Deer, AB	Marken 1994
10	*P. fremontii*	Colorado, UT	Rood et al. 1997
9	*P. deltoides*	Missouri, MT	Scott et al. 1997
10	*P. deltoides*	Red Deer, AB	Cordes et al. 1997
5–10	*P. balsamifera*	Bow, AB	Rood et al. 1998a

[1] Seedlings.
[2] Stands.

ticularly declines can be abrupt, and (iii) insufficient flows may be delivered in mid- through late summer. These artificial patterns may prevent initial establishment of seedlings at appropriate streambank elevations and/or exaggerate drought stress, increasing mortality of the small, vulnerable seedlings. The attenuation of flooding also prevents the essential geomorphic disturbance that creates new nursery sites (Johnson et al. 1976, Rood and Mahoney 1990, 1995, Scott et al. 1997, Stromberg et al. 1997).

Fortunately, it is primarily the pattern of streamflow management rather than the presence of dams, *per se,* that determines impacts on downstream cottonwoods. With respect to cottonwood recruitment, informed stream-flow management should enable seedling recruitment and may even permit regulation of stream stage patterns to promote seedling recruitment for the conservation and restoration of the riparian cottonwood-based ecosystem. Here, we analyze the hydrologic pattern that is required for seedling recruitment of riparian cottonwoods and propose a model for assessing and predicting the impact of water-management strategies on riparian cottonwoods. This should contribute to the understanding of cottonwood reproductive ecology and also facilitate river resource management that is directed toward the conservation and restoration of riparian woodlands, particularly in semiarid regions of western North America.

HYDROLOGIC REQUIREMENTS FOR COTTONWOOD SEEDLING RECRUITMENT

Flood Flows

Cottonwood seedling recruitment is episodic and relatively rare even along free-flowing streams. It has been repeatedly concluded that flood events enable cottonwood seedling recruitment both through geomorphic impacts and direct hydrologic patterns (Johnson et al. 1976, Rood and Mahoney 1990, Scott et al. 1996, and citations in Table 1). The flood magnitude required for cottonwood recruitment has been estimated with a dendrochronological approach in which cottonwoods are aged and correlations (or in this case, 'core-relations') are investigated between recruitment years and high stream flows. The specific aging of cottonwoods may be problematic due to ambiguous annual rings, the occurrence of flood-training and other processes that topple seedlings and saplings, heart-rot which is common in middle-aged and older trees, variable growth rates up to the height at which increment cores are taken, and other biological and methodological complexities. Despite these problems, various researchers have reached relatively similar conclusions regarding the need for moderate flood events for successful cottonwood establishment (Table 1).

Studies have consistently suggested that a 1 in 5 to 1 in 10 year flood event is associated with cottonwood recruitment (Table 1). These moderate flood events drive the erosional and depositional processes associated with the creation of barren nursery sites on meander lobes, lateral bars, and islands and also provide a pattern of stream flow and stage that is suitable for seedling establishment. Larger floods may cause massive fluvial-geomorphic change that sets the framework for cottonwood recruitment over the next years and even decades (Friedman et al. 1996, Stromberg et al. 1997, Rood et al. 1998).

Pattern of Flow

The roles of specific components of the flood hydrograph relative to seedling establishment have been proposed (Bradley and Smith 1986, Mahoney and Rood 1991b, Scott et al. 1993). Agreement with respect to components by various researchers provides some confidence in the general process and also indicates common applicability for different cottonwood species and different streams. Following our review of the literature and field and greenhouse studies, we previously developed a general model describing the hydrologic requirements for cottonwood seedling recruitment (Mahoney and Rood 1991b). We subsequently applied the general model to assess potential impacts of different flow scenarios along dammed rivers (Mahoney and Rood 1993a, 1993b). By integrating subsequent results, we are now able to quantitatively define some features relevant to the model. The resultant quantitative model describes the streambank elevation and timing of stream stage patterns that are required for successful cottonwood seedling recruitment.

A Generalized Hydrograph for Rivers in Western North America

Along many rivers in the western prairie and mountain regions of western North America, a typical hydrograph includes low flows in the early spring and rising flows that accompany spring rains and mountain snow-melt (Figure 1). Annual hydrographs are rather jagged due to precipitation events and variations in temperature, which influence the rate of snow-melt. Peak flows typically occur in early June and persist for a few days. The recession component or 'falling limb' of the hydrograph is initially very rapid and becomes more gradual as the summer proceeds. Low flows typically occur in mid- to late summer when snow-melt is complete and rainfall is often sparse. At this time, temperatures are generally maximal, creating conditions of greatest water demand. This hot, dry period in mid- through late summer is also the period of greatest irrigation demand, and thus, offstream diversion is often greatest.

Riverine and riparian ecosystems have adapted to natural stream-flow conditions. While discharge is normally reported for stream-flow analyses, interpretations relative to riparian processes are more appropriately made relative to the stream stage, which represents the water-surface elevation. River stage is the parameter measured at hydrometric gauging stations, and these data are then converted to discharges using stage-discharge ratings curves. For analyses relative to cottonwood seedling recruitment, river stage data should be used. However, unlike discharge, stream stage is site-specific because channel geometry and gradient determines the stage-discharge function. Ratings curves from gauging stations can be used to initially estimate stage patterns, but gauging sites are generally selected based on ease of access and are often at points that do not display a cross-sectional geometry that is typical of the river reach. More appropriately, analyses should involve site-specific stage-discharge determinations at meander lobes and other sites that are suitable for cottonwood seedling recruitment. Analyses should also consider variations in channel width and slope and streambank geometry along the reach.

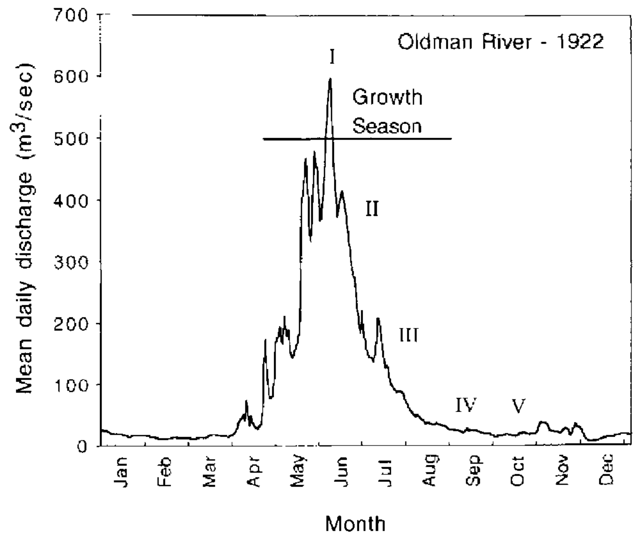

Figure 1. The daily hydrograph for the Oldman River, at Lethbridge, Alberta, for 1922, prior to the construction of major dams upstream. Roman numerals represent important components relevant to cottonwood seedlings recruitment: (I) high flows to drive geomorphological processes that create suitable moist and barren nursery sites, (II) falling flows to expose the nursery sites, (III) gradual flow decline after germination that permits the growing roots to maintain contact with the receding moisture zone, (IV) sufficient flows through the hot and dry period of mid- to late summer, and (V) sufficient flows in late summer and autumn to provide the seedlings with a favorable water balance to withstand the winter.

Despite latitudinal differences, the timing of annual peak flows is reasonably similar in the western prairie and Rocky Mountain regions of western North America (Figure 2). Southward from Alberta, Canada to New Mexico, the rivers that drain the southern and central Rocky Mountains usually peak in early June. Annual peaks that are substantially earlier or later than the normal period are generally relatively small and correspondingly less important for cottonwood seedling recruitment. The relative synchronization of the peak flows is partly explained by elevational patterns. The Rocky Mountains of Colorado are higher than those of Montana or Alberta, and this elevational increase compensates for the latitudinal gradient. However, this timing of peak flow is certainly not experienced by all western rivers. Those draining more

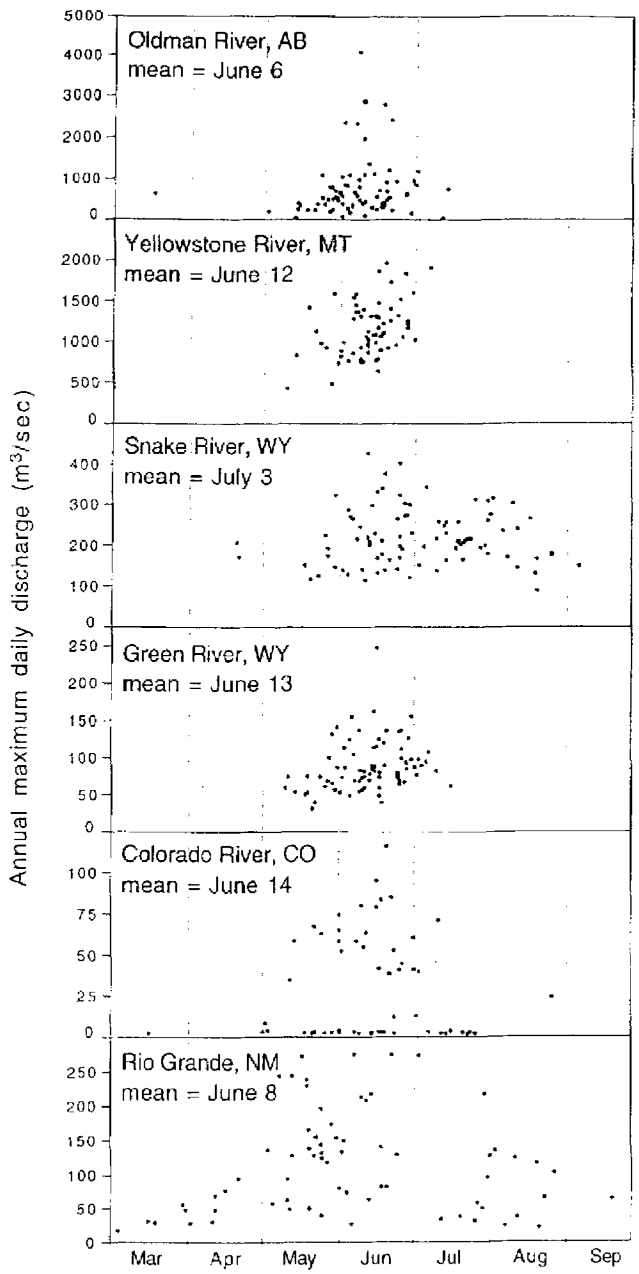

Figure 2. Dates and discharges of annual peak daily flows for six rivers draining the Rocky Mountains of western North America (north to south): the Oldman River at Lethbridge, AB (Water Survey of Canada station 05AD007; SD (standard deviation of the mean) = 17 days; median = June 7; years: 1912 to 1995); the Yellowstone River near Billings, MT (USGS station # 06214500; SD = 11; median = June 13; 1904 to 1994); the Snake River near Moran, WY (# 13011000; SD = 32; median = June 27; 1904 to 1994); the Green River near Daniel, WY (# 09191000; SD = 15; median = June 14; 1913 to 1994); the Colorado River near Granby, CO (# 09019500; SD = 26; median = June 16; 1908 to 1994); and the Rio Grande River near Taos, NM (# 08276500; SD = 48; median = May 31; 1926 to 1994). Of these rivers, the Oldman was dammed in (about) 1992, the Yellowstone remains free-flowing and the Green River is →

southerly and especially southwesterly areas or lower elevations peak earlier; more northern, glacier-fed streams peak more gradually and somewhat later; and many streams in Pacific regions are more responsive to seasonal rains that are often heavy in the autumn and winter.

Patterns of Seed Release

The phenology of cottonwood flowering and seed release is partly determined by photoperiod (day length) and, hence, is relatively constant across years at a given site. However, temperature also influences development, often hastening or delaying seed release by one or two weeks. Temperature patterns also influence the duration of seed dispersal, which typically occurs over about one month. The phenology of seed release has been reviewed by Braatne et al. (1996); release tends to extend from May into July for most cottonwood species. The exception is *P. fremontii*, which occurs in warmer areas and generally releases seed earlier than the other species.

Cottonwoods are prolific seed producers, with large females producing hundreds of thousands (Kapusta 1972) or even millions of seeds (Bessy 1904). Initial viability is almost complete but declines completely over a one-to-four-week period (Braatne et al. 1996). Thus, there is no carryover seed bank from previous years, and the seeds must land on suitable sites for successful establishment. Cottonwoods have thus adopted a reproductive strategy in which many propagules are produced, but each has been provided with minimal resources, and very few survive. The limited period of seed dispersal and viability defines the period for cottonwood seedling establishment. The total period can reach about six weeks but has a more limited period of maximal seed release of about three weeks (Lee et al. 1991, Virginillo et al. 1991, Johnson 1994). Thus, a model describing stream-flow requirements for cottonwood seedling establishment begins with a temporal framework related to cottonwood phenology (Figure 3 (top)).

Seed release generally occurs after peak flows and during the falling limb of the hydrograph. This timing is appropriate since the receding stream exposes moist sites that are suitable for seedling establishment. The seeds are initially wind-dispersed and may land on the stream-side lateral or point bars. Alternately, the seeds

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free-flowing at the gauging site used. Conversely, the Snake and Colorado gauging sites are below dams and a number dams exist on the Rio Grande and its tributaries upstream from the gauging site used.

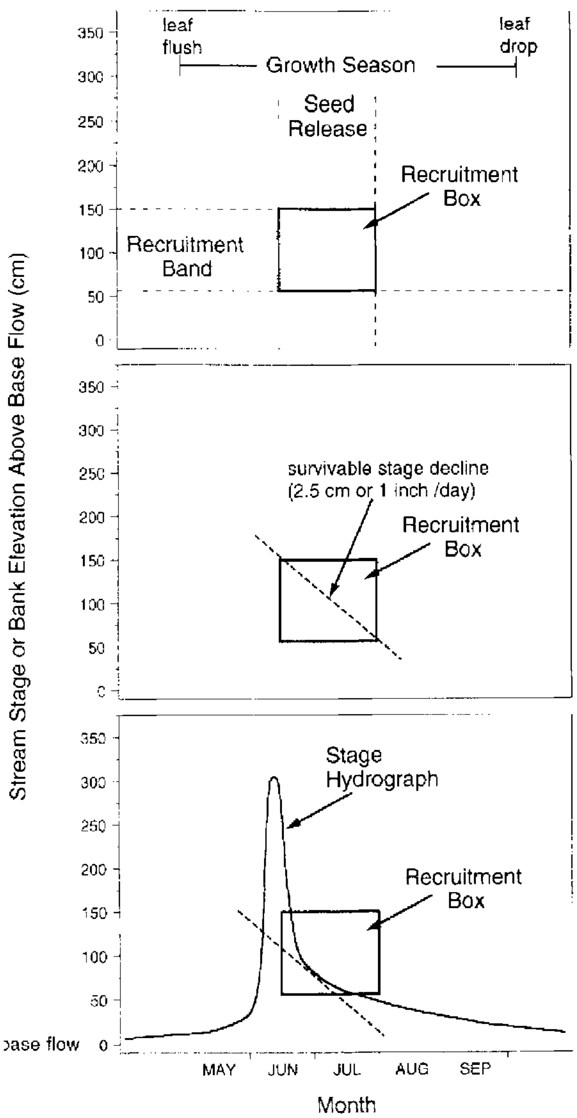

Figure 3. The 'Recruitment Box,' a zone defined in elevation and time in which riparian cottonwood seedlings are likely to become successfully established if stream flow patterns are favorable. The graphs represent phenology of components (top), survivable rate of stage decline (middle), and a hydrograph that satisfies requirements for seedling establishment (bottom).

may land on the stream and be deposited by the receding stream edge in bands along the shoreline. This combination of wind and water dispersal increases the chances that the small seeds will land on appropriate recruitment sites.

The process of seed dispersal partially explains the banding that is common in riparian woodlands (Braatne et al. 1996). Moist sites occur at specific elevations paralleling the receding stream, and thus, seedlings are more likely to survive in bands. The floating seeds deposited directly along the stream edge are also deposited in bands of constant elevation, again favoring a banded distribution. The arcuate banding is emphasized by the processes of seedling mortality and scouring. Seedlings initially established at higher elevations are likely to succumb to drought stress, and those established at low elevations are likely to be scoured away by subsequent high stream flows or ice. Thus, both seedling establishment and seedling survival tend to produce banding patterns in riparian cottonwoods.

Elevation of Successful Seedling Recruitment

As already introduced, bands of riparian cottonwood seedlings typically occur at common streambank elevations. These bands are partially a result of the moist and barren zones that are exposed during the falling limb of the hydrograph. Initially, broad bands of seedlings are established, but mortality restricts the elevational range in which seedlings survive to grow into saplings and mature trees.

The elevation of successful cottonwood seedling recruitment can be determined by (i) direct observation of seedling elevations along various streams, (ii) excavation of seedlings to determine root length and moisture depth, and (iii) physiological studies to determine root growth and establishment potential. The three methods are somewhat independent, and quantitative agreement would strengthen their collective interpretation.

Various researchers have determined recruitment elevations, although primarily for *Aigeiros* cottonwoods (Table 2). Direct comparison of the data is complicated by differences in reference elevations. As much as possible, the values in Table 2 have been converted to a common reference, with '0' representing the growing season 'base-flow,' which is the typical low flow at the end of the growing season. This conversion was particularly problematic for the Reid (1991) data due to interbasin transfers that artificially elevated summer flows for much of the period of record.

Recognizing the complexity of a common reference stage, the observed elevations across eight streams are relatively consistent in indicating that successful seedlings tended to establish at elevations from about 60 to 150 cm above the base flow. These data are limited but also suggest that cottonwoods are successfully established at slightly higher elevations along larger rivers. This conclusion would be consistent with the knowledge that larger rivers tend to have more gradual stage changes since multiple tributaries combine to produce the overall river flow. Abrupt flow fluctuations along individual tributaries are attenuated by flow patterns from other tributaries. The larger rivers also tend to have finer substrates and occur at lower elevations with longer growing seasons and warmer

Table 2. Elevation of cottonwood seedlings established along various rivers in western North America (chronological listing).

Elevation[1] (cm)	*Populus* Species	River	Source
150–180	*P. deltoides*	Little Missouri, ND	Everitt 1968
100–130	*P. deltoides*	Minnesota, MN	Noble 1979
20–100	*P. fremontii*	Dry Creek, CA	McBride and Strahan 1984
100–120	*P. deltoides*	Milk, AB	Redi 1991
60–100	*P. fremontii*	Hassayampa, AZ	Stromberg et al. 1991
40–70	*P. deltoides*	Platte, NB	Johnson 1994
60–120	*P. deltoides, P. angustifolia, P. balsamifera*	Marias, MT	Rood and Mahoney 1995 and unpublished
20–230[2]	*P. deltoides*	Missouri, MT	Scott et al. 1997
40–240[3]	*P. deltoides*	Missouri, MT	Scott et al. 1997
60–260[4]	*P. deltoides, P. angustifolia, P. balsamifera*	Oldman, AB	Rood et al. 1998b

[1] Elevation is expressed relative to base flow, which usually represents the typical low stream stage during the late summer or autumn.
[2] Seedlings.
[3] Saplings.
[4] Following an exceptional 1 in 100 year flood.

temperatures, additional physical factors that enable cottonwood establishment at higher bank elevations.

The second approach, the excavation of cottonwood seedlings along various rivers, also provided general consistency with respect to root length (Table 3). Seedlings situated close to the stream edge would be expected to have shorter roots since the depth to the moist zone would be relatively shallow. It is most useful to compare the longer root data and data from actual riparian zones rather than from artificial studies. In these cases, roots of first year seedlings were less than 1 m in length and tended to be about 60 cm long. The limited data also reveal shorter roots for the *Tacamahaca* seedlings, which would further limit the establishment elevation of these slower-growing cottonwood species.

Rates of root elongation have been measured in artificial or experimental systems, and values of about 4 to 10 mm per day have been observed (Table 3). Assuming seedling establishment in early June and a first year growth period of about 60 to 90 days, this growth rate would result in root lengths of about 60 cm. This

Table 3. First-year root growth rates for cottonwood seedlings (chronological listing).

Growth Rate	*Populus* Species	System/River	Source
Per day (mm - rounded off to 1 mm)			
6–13	*P. fremontii*	artificial	Fenner et al. 1984
13	*P. fremontii*	artificial	McBride et al. 1988
4	*P. deltoides* × *P. balsamifera*	artificial	Mahoney and Rood 1991
3	*P. angustifolia*	Oldman, AB	Virginello et al. 1991
6–8	*P. balsamifera*	upland	Peterson and Peterson 1992
4	*P. deltoides*	artificial	Segelquist et al. 1994
4–12	*P. trichocarpa*	artificial	Reed 1995
After first year (cm - rounded off to 5 cm)			
60	*P. deltoides*	S. Canadian, OK	Ware and Penfound 1949
70–165	*P. fremontii*	artificial	Fenner et al. 1984
10–60	*P. deltoides*	Milk, AB	Bradley and Smith 1986
10–15	*P. balsamifera*	Belly, AB	Reid et al. 1992
40	*P. deltoides*	artificial	Segelquist et al. 1994
15[1]	*P. trichocarpa*	Elk, BC	Rood 1995
40[1]	*P. deltoides*	Coal Ck, CO	Friedman et al. 1997

[1] Estimated from photograph.

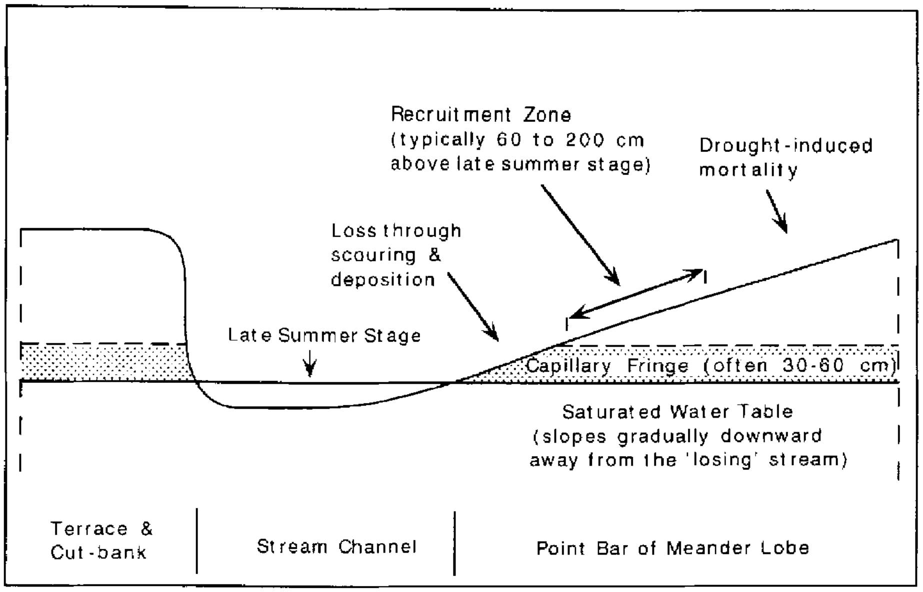

Figure 4. Cross section of a stream and riparian zone at the point bar of a meander lobe, showing the riparian water table, the capillary fringe, and the suitable band for cottonwood establishment and survival.

physiological analysis is thus consistent with the actual field measurements.

These analyses of seedling establishment elevation and seedling root growth provide relatively consistent results but also indicate that the seedlings' roots often do not reach the saturated water table. The roots would grow to about 60 cm or less in the first year, but the successful seedlings are situated from 60 to 150 cm above the late summer stream stage. The difference between root length and establishment elevation reflects the presence of an important subsurface moisture band above the water table, the capillary fringe or 'tension saturated zone.'

The Capillary Fringe

Alluvial floodplains along streams in western North America contain relatively coarse substrates consisting of sand, gravel, cobble, and boulders, along with silts and other finer materials. The collective substrates are generally relatively freely permeable, and consequently, infiltration and drainage are very rapid (Mahoney and Rood 1991, Mahoney 1996). In semi-arid regions, influent systems occur in which the streams tend to be 'losing' streams during the hot, dry period of midsummer. At this time, the riparian water table is provided with water percolating or discharging from the stream. This results in a relatively horizontal riparian water table that slopes gently downwards away from the stream edge (Kondolf et al. 1987, Rood et al. 1995, Mahoney 1996). Within the seedling recruitment zone that typically occurs within about 50 m of the stream edge, the summer riparian water table is approximately level with the stream stage, and as the stream stage recedes, the riparian water table declines correspondingly (Rood et al. 1995, Mahoney 1996).

The capillary fringe is a zone of moisture that extends above the saturated riparian water table (Figure 4). This moisture moves upwards due to water 'wicking,' resulting from adhesive and cohesive forces associated with the polarity of water and its resulting surface tension (Gordon et al. 1992). Observations of root architecture indicate that the fine cottonwood roots that are primarily responsible for water uptake especially occur in the capillary fringe. At depths below the water table, conditions are relatively anaerobic and, hence, unfavorable for root functioning. This alters a conception of phreatophytes. Rather than having drinking straw-like linkages with the saturated water table, the phreatophyte roots probably favor the moist and aerobic capillary fringe.

The extent of the capillary fringe is determined by substrate texture and ranged from about 5 cm in a mixture dominated by coarse gravel to 70 cm in medium textured sand (Mahoney and Rood 1991). Finer textured sand and silts have even greater capillary capacity. The capillary zone can be seen as a moist band above the stream stage (Rood et al. 1995), particularly if the stream site is visited in the morning before the surface is dried by sunshine and warmth. The extent of this apparent capillary fringe was associated with substrate texture along rivers in Alberta and Montana (Table 4). For coarse-textured substrates along streams that typically support *Tacamahaca* cottonwood species, the capillary fringe was typically about 20 to 40 cm. For finer-textured substrates along streams that are

Table 4. Apparent extent of the capillary fringe on point bars of meander lobes with differing substrate textures along rivers in Alberta and Montana.

River	Latitude (N)/ Longitude (W); and Date	Surface Substrate Composition[1]	*Populus* Species[2]	Apparent Capillary Fringe[3] Distance (m)	Apparent Capillary Fringe[3] Elevation (cm)
Bow, AB	50°49'/113°46'; 24.7.1996	medium cobble	*P. balsamifera*	1.1	3
	50°51'/113°36'; 24.7.1996	coarse sand, coarse gravel, medium cobble	*P. balsamifera*	3.8	39
St. Mary, AB	49°36'/112°54'; 12.6.1996	fine cobble, silt	*P. angustifolia*	1.7	12
	49°36'/112°54'; 12.6.1996	medium sand, fine cobble	*P. angustifolia, P. deltoides*	8.6	33
Oldman, AB	49°42'/112°52'; 14.8.1996	medium gravel, silt, fine cobble	*P. deltoides, P. angustifolia, P. balsamifera*	7.9	38
South Saskatchewan, AB	50°25'/110°24'; 30.6.1996	medium sand	*P. deltoides*	2.7	21
	50°02'/110°38'; 7.8.1996	fine sand, silt	*P. deltoides*	1.6	65
	50°02/110°39'; 11.8.1995	silt	*P. deltoides*	18.5	138
Missouri, MT	48°01'/110°07'; 16.7.1996	silt	*P. deltoides*	3.2	131

[1] In accordance with Gordon et al. (1992): silt: <0.06 mm; sand: 0.06 to 2 mm; gravel: 2 to 64 mm; cobble: 6 to 25 cm; boulder: >25 cm. Sand, gravel and cobble categories are split (equally) into fine, medium and coarse. Component materials are listed in descending order of abundance.

[2] Multiple species are listed in descending order of abundance.

[3] The apparent capillary fringe is the zone of moisture extending away from the stream edge, distance and elevation are relative to the stream stage.

dominated by *Aigeiros* species, the capillary fringe ranged from 30 to more than 100 cm.

The combination of the capillary fringe (Table 4) plus the root growth potential (Table 3) does result in elevation predictions consistent with the observed values in published reports (Table 2). Roots would extend downwards about 60 to 100 cm and penetrate into the capillary fringe which would range from about 50 to 100 cm above the riparian water table for most of the study streams with sandy substrates. The combination of root growth plus capillary fringe, would enable seedlings to become established up to about 200 cm above the stream's base flow. Thus, the different research approaches involving measurements of elevational position or root length plus capillary fringe, provide reasonable consistency (Figure 3 (top)).

The lower elevational limit of successful cottonwood recruitment is probably defined by erosional (physical) rather than physiological processes. Seedlings established at low elevations would be particularly prone to scouring during subsequent high stream flows or by ice (McBride and Strahan 1984, Johnson 1994, Scott et al. 1997, Rood et al. 1998b). Consequently, a lower limit of the seedling recruitment zone is probably about 60 cm above the base stage (Figure 4). Lower elevation establishment may occur if the stream flows remain low for a few years following seedling establishment. However, the prospects for survival are reduced as streambank elevation is lowered. Consequently, the typical recruitment band probably extends from about 60 to 150 cm above the base flow for coarse-textured substrates and from about 60 to 200 cm above base flow for streams with finer substrates (Figure 3 (top)). For both cases, the higher elevations are probably most applicable to larger rivers.

Survivable Rate of Stream Stage Decline

As already indicated, seedling survival through the first summer is relatively rare. The vast majority of seedlings die, primarily due to drought-stress, and those that survive probably do so because they are able to maintain a functional root contact with the receding moisture zone. Although root elongation is typically 1 cm per day or less, manipulative studies have demonstrated that many seedlings can survive water-table-decline rates of 2 to 4 cm per day (Segelquist et al. 1993, Mahoney and Rood 1991, 1992, McBride et al. 1988). The presence of a moist zone remaining temporarily above the receding water table may explain the difference between root growth rate and survivable water-table-decline rate.

For purposes of the recruitment box model, a value of about 2.5 cm per day decline in the water table is included as the maximal survivable stream stage decline rate (Figure 3 (middle)). This rate is very probably too rapid if particularly hot and dry conditions persist or if the riparian substrate is coarse. Conversely, even more rapid rates of stage decline may be survivable during periods that are cool and cloudy or if rain events occur to recharge the root zone from above.

The Cottonwood Recruitment Box Model

Following the preceding analyses, a seedling recruitment box model is proposed that outlines the timing and pattern of stream stage change that should permit seedling recruitment of cottonwoods. The stream stage should be declining to expose saturated sites for initial seedling establishment during the period of seed dispersal (mid-June). Ideally, streambanks between 0.6 and 2.0 m above the base stage should be exposed at this time. Subsequent gradual stage decline of less than 2.5 cm per day should permit seedling survival, with improved health and survival accompanying more gradual rates of stage decline.

Figure 3 (bottom) shows favorable hydrologic conditions for cottonwood seedling establishment based on the recruitment box model. The annual peak flow has passed prior to the onset of seed release, and the river stage is declining rapidly. The river-stage decline through the recruitment box exposes new areas for seedling establishment over a range of elevations. The rate of river-stage decline in the latter part of the recruitment box is favorable for cottonwood seedling establishment. Seeds germinating at the start of the period of seed release will have a low probability of survival due to high rates of river stage decline that will contribute to drought stress and mortality. Seeds germinating at the end of the seed release period will also have a low probability of survival due to mortality from ice scour and subsequent flooding.

MANAGEMENT IMPLICATIONS

Riparian cottonwood forests are rich aesthetic, environmental, and recreational resources in the semi-arid regions of western North America (Braatne et al. 1996). These woodlands provide prime habitat for a range of terrestrial animals and abundant and diverse bird species and thus comprise some of North America's richest wildlife habitats (Finch and Ruggiero 1993). The riparian woodlands are linked to and benefit the adjacent riverine aquatic ecosystems by providing shade that reduces water temperature and by contributing organic matter, leaves, and woody debris that provide a basis for the aquatic food web (Wallace et al. 1997). However, although being especially valuable, the riparian woodlands are especially vulnerable to impacts of human development. These impacts include direct clearing for agriculture and domestic settlement, trampling and grazing by livestock, and influences of river-damming and diversion. The latter two major impacts, livestock and river damming, often particularly impede recruitment of the riparian trees. Many woodlands have declined due to insufficient replenishment to compensate for ongoing tree aging and mortality. The restoration of degraded woodlands and the conservation of the remaining cottonwood groves is reliant on reestablishing cottonwood recruitment that often particularly involves seedling recruitment. This integrative report reviews the hydrologic processes underlying cottonwood seedling establishment and develops the recruitment box model, a quantitative model that can provide the basis for developing instream flow prescriptions for cottonwood conservation and restoration.

The recruitment box model also contributes to the understanding of cottonwood reproductive ecology. The hydrologically-based model partially explains why moderate and large flood events directly enable cottonwood recruitment, whereas smaller flood events are often insufficient for cottonwood replenishment. Although smaller peaks moisten the suitable recruitment zone, the falling limb of the hydrograph is very rapid after the peak flow, and thus, the rate of stage decline is too abrupt for seedlings to retain root contact with the descending moist zone. In contrast, with moderate flood events, the peak is well above the recruitment box, and the rapidly falling portion of the falling limb of the hydrograph occurs while the hydrograph stage is above the recruitment zone. As the hydrograph descends into the recruitment box, the rate of stage decline will have slowed to a rate that is gradual enough that the seedlings can maintain root contact.

This analysis also provides a management opportunity with respect to cottonwood recruitment. If the rate of stage decline can be artificially managed as a gradual stage recession, it should be possible to promote cottonwood seedling recruitment. It should also be possible to deliver a stage pattern satisfying the recruitment box model, even without a major flood event. Such a strategy will only succeed if suitable recruitment sites exist; geomorphological disturbance and the creation of recruitment sites is one reason major flood events are required to ensure long term cottonwood forest survival.

The present integrative model is built on established principles of hydrology and physiology and should be applicable for a range of cottonwood species and for various streams, large and small. The quantitative coefficients with respect to the timing of seed release, suitable elevation, and survivable rate of stage decline will undoubtedly undergo some refinement and some specific fine-tuning for different stream systems (Shafroth et al. 1998). However, the principles of hydrology and physiology are universal, and thus, it is likely that the 'recruitment box' will be applicable across a range of streams. Although developed with data from western North American rivers, the model is likely to be broadly applicable because riparian woodlands in semi-arid regions of North America, Africa, and Europe share common conditions (Hughes 1994).

It is also likely that the recruitment box model will be applicable across plant species and even genera. For example, an artificial hydrologic pattern that closely followed the recruitment box model resulted in a major cottonwood recruitment event along the Truckee River, downstream of Reno, Nevada, USA (Gourley, pers comm). In addition to the establishment of *P. fremontii* seedlings, abundant willows (*Salix exigua* Nutt.) were also established and, regrettably but not surprisingly, a few Russian olive (*Elaeagnus angustifolia* L.) and tamarisk (*Tamarix chinensis* Lour.) seedlings were also established. Riparian cottonwoods provide the foundation for the riparian woodland ecosystems across western North America, and the fate of these rich ecosystems follows the fate of the cottonwoods. The health and abundance of other riparian plants, especially willows, that are influenced by similar hydrologic characteristics will most closely follow the fate of the cottonwoods. Some differences do exist across species with respect to the timing of seed dispersal and the tolerance of flooding and water-table-decline rate, and these differences may be used to favor recruitment of native cottonwoods and willows over exotic species such as tamarisk or Russian olive (Shafroth et al. 1995).

The cottonwood recruitment box model has been successfully applied to dammed rivers in Alberta and Nevada. In another paper in the present issue, we describe a case study of the Oldman River, Alberta, in which dams were operated to deliver a gradual stage recession after a major natural flood, and this permitted extensive cottonwood seedling recruitment (Rood et al. 1998b). Along the Truckee River through Nevada, artificial flow regulation directed towards the recovery of an endangered fish coincidentally provided a stream stage pattern that satisfied the cottonwood recruitment box model and this permitted an extensive cottonwood seedling recruitment event (Gourley, pers comm). Subsequently, dams in the Truckee River basin were deliberately managed to deliver a stream stage pattern that satisfied the cottonwood recruitment box model and the optimistic results from that novel project will be described in subsequent reports. The successful implementation of instream flows developed with the recruitment box model provide some validation of the model and also provide some optimism for the conservation and partial restoration of riparian cottonwood forests.

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