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**Biology of *Populus* and its Implications
for Management and Conservation**

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CHAPTER 3

***Life history, ecology, and conservation of
riparian cottonwoods in North America***

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CHAPTER 3

Life history, ecology, and conservation of riparian cottonwoods in North America

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Introduction

The life history and ecology of plants are closely related to the natural dynamics of their environment. In the case of poplars, the life history and ecology of riparian cottonwoods are interrelated with the patterns and processes of riverine systems. In this chapter, we describe some of the key features of riverine environments and the life history of riparian cottonwoods from seed dispersal and germination through maturity and senescence. Our intent is to reveal the fundamental ecological relationships between riparian cottonwoods and the alluvial floodplains they inhabit. On the basis of these relationships, we propose some approaches to the conservation and restoration of riparian cottonwoods.

The riparian cottonwoods of North America include: *P. angustifolia*, *P. balsamifera*, and *P. trichocarpa* from the *Tacamahaca* section; and *P. deltoides*, and *P. fremontii* from the *Aigeiros* section. These dioecious species are widely distributed throughout North America (see Eckenwalder in Chapter 1). In general, members of the *Tacamahaca* section are found at higher elevations and latitudes (i.e., high gradient riverine systems of montane and young piedmont valley floodplains), whereas members of the *Aigeiros* section are primarily limited to lower elevations and latitudes (i.e., lower gradient riverine systems of mature piedmont valley floodplains). Contact zones between species, particularly between members of different sections, occur at critical ecotones (see Whitham in

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Chapter 11) where contact gives rise to a broad range of natural hybrid complexes (see Eckenwalder in Chapter 1).

Environmental characteristics of riverine systems

The river systems and alluvial floodplains inhabited by riparian cottonwoods are the product of a complex array of interrelated fluvial geomorphic processes (Leopold 1994; Leopold et al. 1964). Given the complexity of fluvial processes, this chapter can present only a brief description of the hydrogeomorphic features of riverine systems. A more in-depth treatment and summary of fluvial geomorphology can be found in Leopold et al. (1964), Dunne and Leopold (1978), Leopold (1994), and Rosgen (1994).

The physical appearance and character of a river and its floodplain are a product of the continual modification of the river channel by streamflow and sediment regime (Leopold 1994; Rosgen 1994). Local and regional differences in fluvial geomorphology result in a broad range of river types (i.e., meandering to braided channels) with variable width, depth, and rates of lateral migration (Rosgen 1994). As shown in a generalized view (Fig. 1), river channels meander within the alluvial floodplain. These meanders reflect a balance between erosional and depositional processes within the river channel. Erosion of the concave bank is balanced by deposition on the adjacent convex bank (Fig. 1). As the concave bank recedes due to erosion, the point bar builds outward from the convex bank into the channel (Fig. 1). As a result, the form of the channel remains, but its position changes. Floodplains are typically built and continually modified by this process of point-bar extension (Leopold 1994).

Although portions of the floodplain may be far removed from active channel processes, they remain hydrologically linked to the main channel by the alluvial water table. The floodplain is directly linked with main channel processes (erosion and accretion of sediments) primarily during flooding events (flows exceeding bankfull stage, Fig. 1). Historical patterns of channel movement and processes of floodplain formation are readily apparent in aerial photos of extant floodplains and riparian forests (Figs. 2 and 8).

Most erosional and depositional events that affect channel morphology occur in high flow periods, typically during spring snowmelt and periodic stormflows. Such flows are characterized as either bankfull stage (Fig. 1), which occurs approximately every other year (1.5–2 yr intervals), or the less frequent over-bank flooding events (5–10+ yr intervals; Leopold 1994; Rosgen 1994). After high flow events, water levels decline, exposing bare mineral soils within the alluvial floodplain, commonly along point and gravel bars (see Fig. 1). These barren, yet moist, alluvial soils are critical microsites for colonization by cottonwoods via wind- and water-dispersed seed (see Figs. 1 and 6). These

Fig. 1. Generalized view of river channel and floodplain dynamics. Diagrammatic plan view and cross section indicating the relative balance between erosion of the concave bank and accretion of material in a building point bar. Bankfull condition shows that the level of the floodplain is the same as the top of the point bar. (Modified from Leopold 1994.)

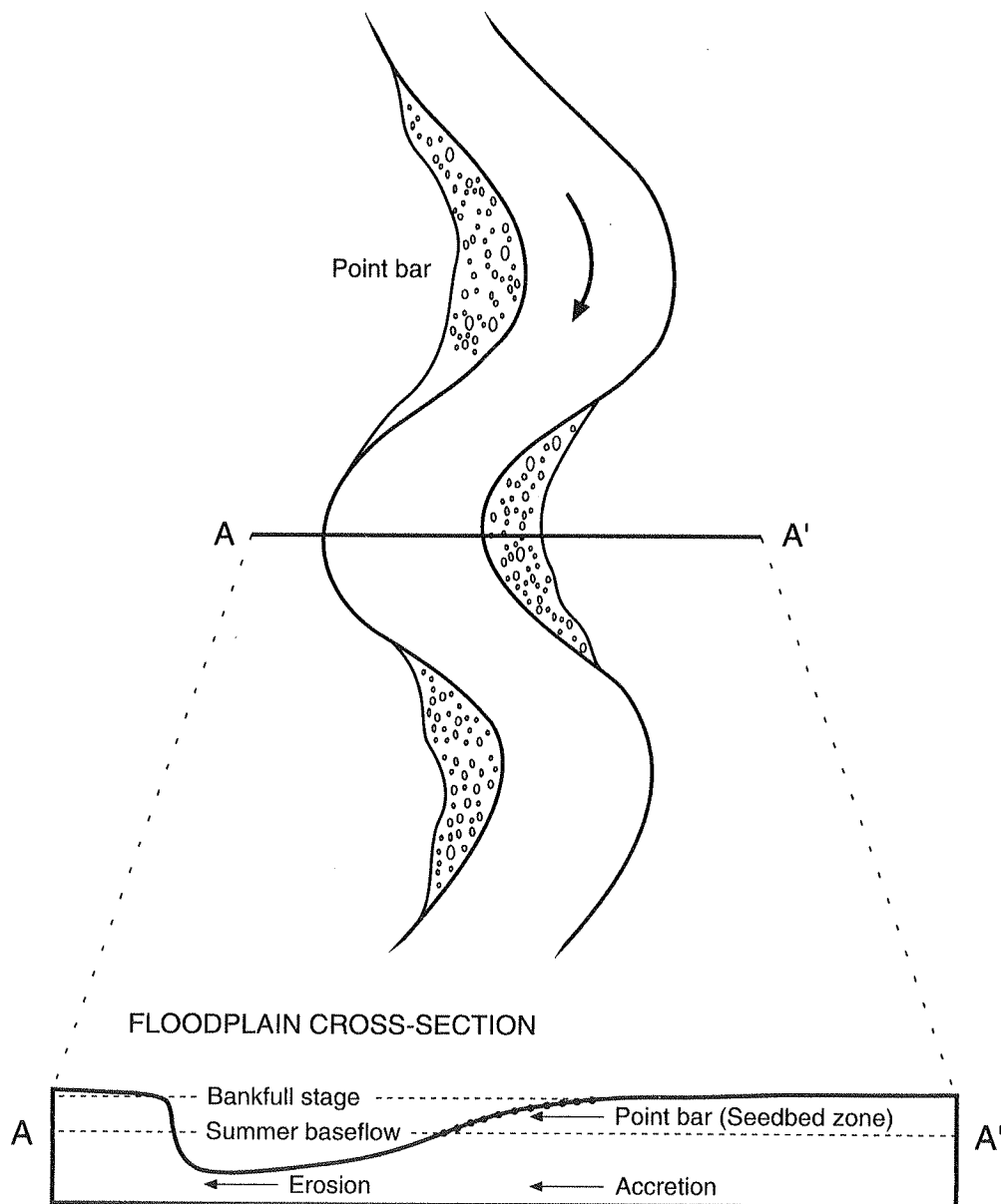
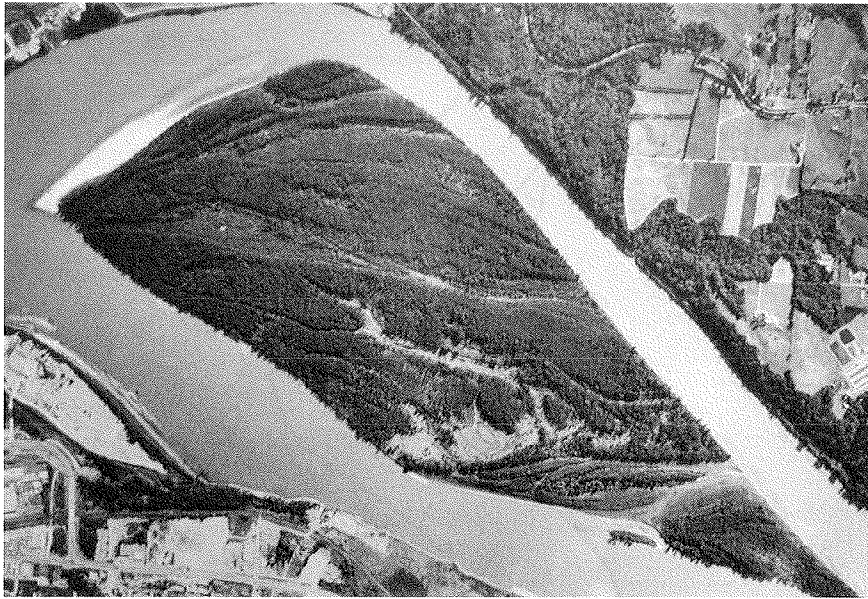


Fig. 2. Aerial photograph of Fraser River Island, British Columbia showing sequential patterns of establishment for Black Cottonwood (*Populus trichocarpa*) in relation to historical routes of river channel movement. (Photo by Scott Paper Ltd.)

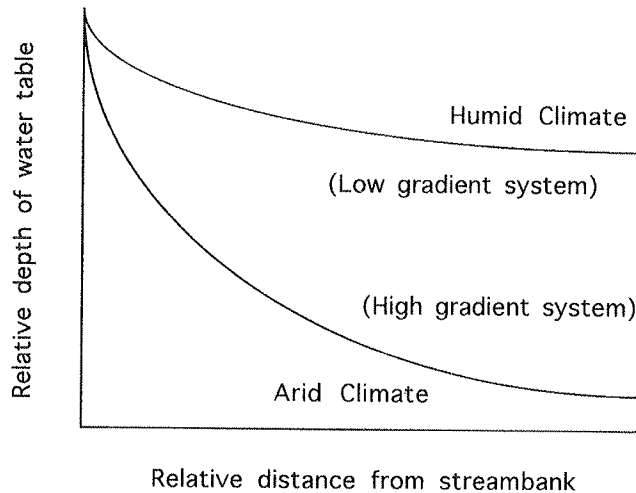


microsites are also vulnerable to subsequent scouring and depositional processes during flooding.

Regional variation in climatic patterns modifies fluvial geomorphic processes. For example, many arid and semi-arid regions of the western U.S. are dominated by higher levels of precipitation in winter relative to summer months, while humid regions of the Midwest have a more uniform distribution of precipitation throughout the year. Major mountain systems, such as the Cascades and the Rocky Mountains, further modify these regional precipitation patterns. This climatic variation affects many of the fluvial processes that control river channel morphology (Leopold et al. 1964; Dunne and Leopold 1978; Leopold 1994). For example, sporadic heavy rains are more prevalent in arid regions. Such sporadic, yet intense storms accelerate terrace erosion (i.e., channel widening) and/or valley evacuation (i.e., channel downcutting) (Huckleberry 1994). In humid regions, small, light rainstorms are more prevalent and promote valley deposition (i.e., alluviation). In the arid Southwest, geologic evidence shows that the relative dominance of these geomorphic processes shifted as periods dominated by arid conditions (1880–1920) evolved towards more humid climatic conditions (1950–1980) (Leopold 1994).

Climate and watershed position strongly influence alluvial water table characteristics. As shown in Fig. 3, alluvial water tables occur at shallower depths

Fig. 3. Generalized relationship between water table depth and distance from streambank for different climatic regimes and fluvial geomorphic settings. (Modified from Reichenbacher 1984.)



under humid than arid conditions. Water table characteristics also differ within a watershed, as valley and channel slope vary from steep, narrow floodplains at high elevations (i.e., high riverine gradients of montane floodplains) to relatively flat and wide alluvial floodplains at low elevations (i.e., lower riverine gradients of mature piedmont valley floodplains). In steep gradient reaches, water tables may fluctuate rapidly, whereas water levels remain more constant in broad, flat floodplains. Large, alluvial floodplains are also closely-linked with regional aquifers that tend to moderate water table fluctuations (Leopold 1994; Leopold et al. 1964). As a result of these linkages, larger floodplains are relatively complex hydrogeomorphic systems in which interactions between fluvial processes and alluvial groundwater systems (i.e., hyporheic zones) may have profound effects upon riparian cottonwood forests (Stanford and Ward 1993); they warrant further investigation.

The environmental features of riverine systems provide a variable water supply and periodic, yet repeated, disturbances to which riparian cottonwoods have adapted. But there is variability in fluvial processes from year to year, and it has significant effects on the long-term health and vigor of riparian cottonwood forests.

Life history and ecological properties of riparian cottonwoods

Comprehensive life history and demographic studies of riparian cottonwoods are limited, yet general patterns emerge that link the nature and timing of fluvial

processes with the expression of life history traits in these species (Rood and Mahoney 1990; Johnson 1992, 1994; Stromberg 1993; Stromberg et al. 1991, 1993, 1996a; Scott et al. 1996a, b). Key life history and ecological properties of riparian cottonwoods are summarized in Tables 1 and 2, while relationships between the expression of these traits and stream discharge are shown in Fig. 4.

Table 1. Life history traits and ecological properties of *Populus angustifolia*, *P. balsamifera*, and *P. trichocarpa* (*Tacamahaca* section).

Life history traits/ecological properties	Species characteristics
Reproduction:	
Flowering time	Apr.–May (<i>P. balsamifera</i>) ⁶ Mar.–May (<i>P. trichocarpa</i>) ⁵
Seed dispersal time	May–July (<i>P. balsamifera</i>) ⁶ May–June (<i>P. trichocarpa</i>) ⁵
Seed weight	0.3 mg (<i>P. balsamifera</i>) ⁶
Dispersal agents/distance	Air and water/several km (All spp.)
Asexual traits	Cladogenesis (<i>P. trichocarpa</i>) ⁵ Root suckering and crown breakage
Germination/establishment:	
Seed viability (natural conditions)	1–2 wk (<i>P. balsamifera</i>) ⁶ 1–2 wk (<i>P. trichocarpa</i>) ⁵
Seed germination	24 h/moist, bare soil (All spp.)
Seedling root growth rates	6–8 mm/d (<i>P. balsamifera</i>) ¹ 4–12+ mm/d (<i>P. trichocarpa</i>) ^{4,8}
Soil pH	6–8 (<i>P. balsamifera</i>) ⁶ 5–7 (<i>P. trichocarpa</i>) ⁵
Growth/maturation:	
Age at reproductive maturity	8–10 yr (<i>P. balsamifera</i>) ⁶ 7–10 yr (<i>P. trichocarpa</i>) ⁵
Lifespan	100–200 yr (<i>P. angustifolia</i>) ⁷ 100–200 yr (<i>P. balsamifera</i>) ^{1,6} 100–200+ yr (<i>P. trichocarpa</i>) ⁵
Plant height at reprod. maturity	8–13.5 m (<i>P. balsamifera</i>) ¹ 10–16.8 m (<i>P. trichocarpa</i>) ⁵
Plant dbh at reprod. maturity	8–11.7 cm (<i>P. balsamifera</i>) ¹ 12–20 cm (<i>P. trichocarpa</i>) ⁵
Mature stand density (trees/ha)	38.3–91.5/ha (<i>P. angustifolia</i>) ^{2,3} 88.9–120/ha (<i>P. balsamifera</i>) ^{1,3} 110–294/ha (<i>P. trichocarpa</i>) ⁵
Rooting depths of mature stands	3–5+ m (All spp.)

Sources: ¹Peterson and Peterson (1992); ²Szaro (1990); ³Shaw (1991); ⁴Reed (1995);

⁵DeBell (1990); Dewit and Reid (1992); ⁶Zasada and Phipps (1990); ⁷Baker (1990);

⁸Mahoney and Rood (1991, 1992).

Sexual reproduction and establishment

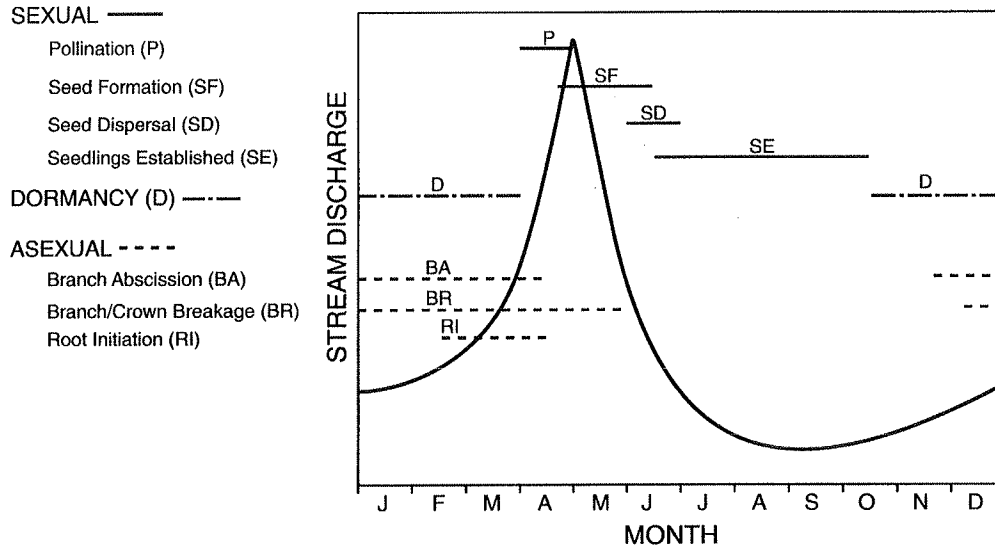
Being dioecious, cottonwood trees are either male or female. In both sexes, the flowers are clustered in catkins, which tend to be borne in the upper tree crown. Male and female catkins are readily distinguished from one another, as male catkins are typically smaller and reddish-purple, whereas female flowers and catkins are significantly larger and greenish in appearance. Males commonly initiate flowering before females and both sexes flower approximately 1–2 wk

Table 2. Life history traits and ecological properties of *Populus deltoides* and *Populus fremontii* (*Aigeiros* section).

Life history traits/ecological properties	Species characteristics
Reproduction:	
Flowering time	Mar.–Apr. (<i>P. deltoides</i>) ^{8–10} Feb.–Mar. (<i>P. fremontii</i>) ^{6,12,13}
Seed dispersal time	May–Aug. (<i>P. deltoides</i>) ^{8–10} Mar.–Apr. (<i>P. fremontii</i>) ⁶
Seed weight	0.3–0.6 mg (<i>P. deltoides</i>) ^{4,9,10}
Seeds/tree/yr	25+ million (<i>P. deltoides</i>) ^{5,9,10}
Dispersal agents/distance	Air and water/several km (All spp.)
Asexual traits	Limited to crown breakage and flood-related disturbance
Germination/establishment:	
Seed viability (natural conditions)	1–2 wk (<i>P. deltoides</i>) ^{9,10} 1–3 wk (<i>P. fremontii</i>) ⁷
Seed germination	24 h/bare
Seedling root growth rates	4–6 mm/d (<i>P. deltoides</i>) ¹⁶ 4–12 mm/d (<i>P. fremontii</i>) ^{6,7,15}
Soil pH	5.5–8 (<i>P. deltoides</i> var. <i>delt.</i>) ⁹
Soil salinity	0–1500 mg/L (<i>P. fremontii</i>) ¹⁷
Growth/maturation:	
Age at reproductive maturity	5–10 yr (<i>P. d.</i> var. <i>delt.</i>) ^{5,9} 10 yr (<i>P. d.</i> var. <i>occ.</i>) ^{5,10} 5–10 yr (<i>P. fremontii</i>) ⁶
Lifespan	130+ yr (<i>P. fremontii</i>) ^{3,19} 100–150+ yr (<i>P. deltoides</i>) ^{9,10}
Plant height at reprod. maturity	10–15 m (<i>P. deltoides</i>) ^{9,10}
Plant dbh at reprod. maturity	12–20 cm (<i>P. deltoides</i>) ^{9,10}
Mature stand density (trees/ha)	192/ha (<i>P. deltoides</i>) ¹¹ 50–400+/ha (<i>P. fremontii</i>) ^{1,6,19}
Rooting depths of mature stands	3–5+ m (All spp.) ^{14,18}

Sources: ¹Strahan (1983); ²Szaro (1990); ³Shanfield (1983); Howe and Knopf (1991); ⁴Bessey (1904); ⁵Schreiner (1974); ⁶Reichenbacher (1984); ⁷Horton et al. (1960) and Fenner et al. (1984); ⁸Farmer (1966); ⁹Cooper (1990); ¹⁰Van Haverbeke (1990); ¹¹Johnson et al. (1976); ¹²Asplund and Gooch (1988); ¹³Stromberg et al. (1991); ¹⁴Jackson et al. (1987); ¹⁵McBride et al. (1988); ¹⁶Segelquist et al. (1993) and Stromberg et al. (1993, 1996a); ¹⁷Jackson et al. (1990) and Shafroth et al. (1995b); ¹⁸Stromberg et al. (1996b); ¹⁹Hunter et al. (1987) and Szaro (1989).

Fig. 4. Generalized timing and duration of reproductive events for riparian cottonwoods in relation to the annual pattern of stream discharge.



prior to leaf initiation in the early spring (March–April). Flowering and pollination thus coincide with springtime peaks in riverine flow (Fig. 4), though significant variation in the timing and duration of flowering exists within and between species (Table 2). In part, phenological variation within and between species reflects environmental differences between plants growing at different elevations and latitudes (Dunlap 1991; Farmer 1993). Under the cool, shortgrowing season of high latitudes and elevations, flowering may not begin until late May, while at lower elevations and latitudes flowering will have ceased in most populations by mid-April. In the arid Southwest, flowering by *P. fremontii* is over by late February to early March (Reichenbacher 1984; Asplund and Gooch 1988; Stromberg et al. 1991). Significant phenological variation in flowering period has also been reported within populations (Dunlap 1991; Farmer 1993), occasionally spanning a range of more than 2 months. Such intrapopulation variance in flowering appears greater in *P. deltoides* than in other species (Farmer 1966; Brian Stanton, personal communication). Additional studies are needed to clarify genetic-environmental interactions controlling the timing of flowering and pollination (see Stanton and Villar in Chapter 5).

Wind-dispersed pollen fertilizes the ovule within 24 h of landing upon the receptive stigma (see Stettler et al. in Chapter 4 and Stanton and Villar in Chapter 5). The process of ovule ripening and seed maturation is temperature-dependent, with seed formation and dispersal occurring within 3–6 wk following fertilization (Fig. 4, Tables 1 and 2; see also Stettler et al. in Chapter 4). Upon maturation, cottonwood seeds are extremely small, weighing approximately 0.3–0.6 mg

per seed (Schreiner 1974; Hardin 1984; Zasada and Phipps 1990), and contain little or no endosperm. Females produce a large and dependable crop of seed, more or less annually. Estimates of annual seed production by large, mature individuals of *P. deltoides* have been reported to exceed 25 million seeds per tree (Bessey 1904; Schreiner 1974). Yet age- and size-specific studies of seed production have been limited (Hardin 1984) and merit further investigation.

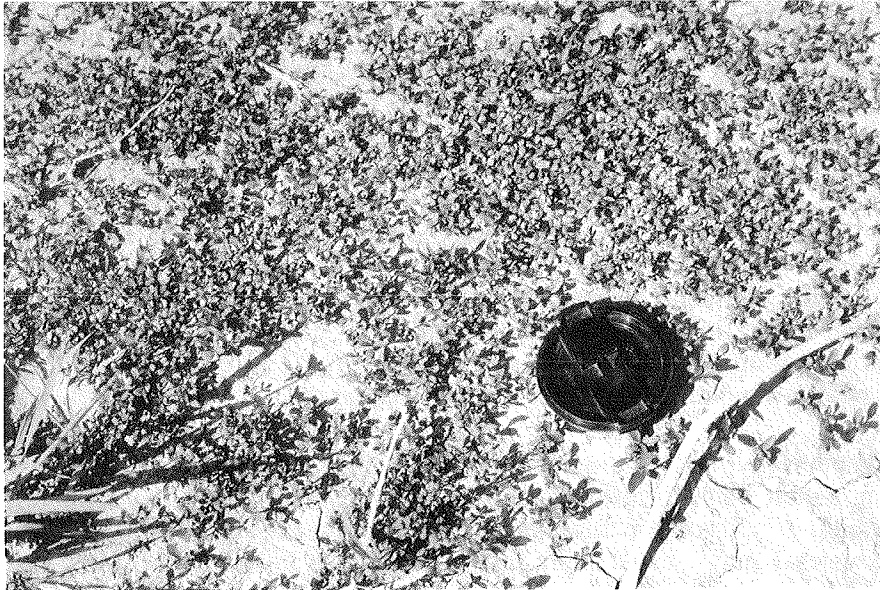
Cottonwood seeds, borne by numerous fluffy, cotton-like hairs, are dispersed long distances by wind and water. Although no studies have specifically documented dispersal distance, general observations suggest that most of the seed is deposited within a few hundred metres of the mother plant. The potential for long-range dispersal (several km or more) via convective wind currents clearly exists. However, methodological constraints associated with the large, air-borne seed crop of these species have prevented quantitative studies on the nature and timing of long-distance dispersal. The best evidence for effective dispersal (and associated gene flow) is the common lack of genetic differentiation among populations, with the bulk of genetic variation (e.g., in isozymes >90%) being found within populations (see Farmer in Chapter 2).

Seed dispersal typically coincides with declining river flows following spring-time snowmelt and stormflows (Fig. 4), thereby increasing the probability of seeds landing in favorable microsites along the river channel. In some instances, seed dispersal may persist well into the summer months. For example, seed dispersal has been observed in mid-July among populations of *P. deltoides* along the upper Missouri River (Johnson et al. 1976) and Central Platte River (Johnson 1994) and late-August in the lower Mississippi Valley (Farmer 1966; Brian Stanton, personal communication). This late shedding of seed by *P. deltoides* may reflect an adaptation to summer rainfall and periodic summer flooding on rivers within its natural range.

Seed viability is very short, generally lasting only 1–2 wk under natural conditions (Tables 1 and 2; Horton et al. 1960; Fenner et al. 1984; Cooper 1990; Debell 1990; VanHaverbeke 1990; Zasada and Phipps 1990). Once a seed becomes wet, viability will be lost in 2–3 d if a favorable microsite is not encountered. Low seed viability has also been reported in relation to high levels of air humidity. The short-term viability of seeds is clearly a limiting factor in the life cycle of cottonwoods, as germination must occur within a relatively short time period. In some cases, seeds may not be fully viable when dispersed from the mother plant (*P. fremontii*, Fenner et al. 1984). These seeds typically become viable within a few days following dispersal; however, the pattern and mechanism of post-dispersal seed viability requires additional study.

On appropriate microsites, germination is rapid. The root radicle emerges from the seed, enters the soil, and cotyledons begin to expand within 24 h (Reed 1995). Young roots are noted for their development of “collet hairs” at the base

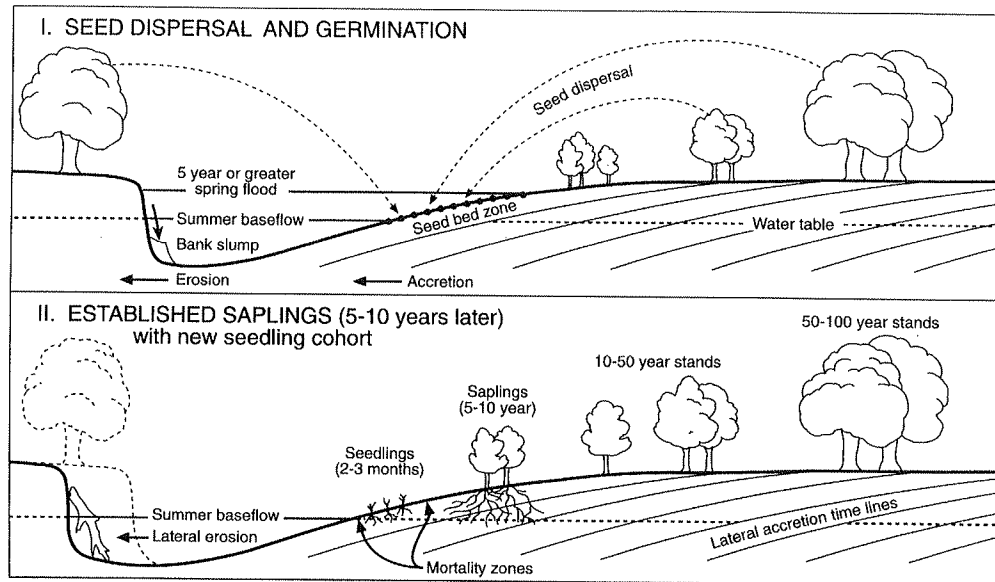
Fig. 5. All cottonwoods are prolific seed producers and initial viability is almost complete. Consequently, if seeds land on moist, mineral soils, extensive mats of seedlings result. However, almost all of these seedlings die due to drought stress and complete mortality often follows dewatering when stream flows are diverted for irrigation or other uses. (Photo by S.B. Rood.)



of the hypocotyl (Moss 1938; Noble 1979). These hairs are anatomically distinct from root hairs and attach quickly to sand and silt particles to provide anchorage and absorption (Noble 1979; Johnson 1994).

In late spring and early summer, germinating seeds and seedlings are commonly found in large numbers along point bars as well as other moist, exposed substrates within alluvial floodplains (Figs. 5 and 6). Seedling densities have been reported to range from as few as 20 to more than 4000 per square metre (Strahan 1983; McBride and Strahan 1984; Lee et al. 1991; Virginillo et al. 1991; Johnson 1994; Reed 1995; Stromberg et al. 1991, 1993). Temporal and spatial variation in favorable microsites appears to be the primary determinant of seedling recruitment (see mortality zones in Fig. 6). The growth and development of seedlings is closely correlated with the relative abundance of light and soil moisture (Rood and Mahoney 1990; Mahoney and Rood 1991, 1992). Given the lack of endosperm, full sunlight is critical as seedlings are highly dependent upon photosynthate derived from cotyledons and juvenile leaves for sustained growth and development. As a result, cottonwood seedlings are poor competitors in vegetated sites (Johnson et al. 1976; Fenner et al. 1984; Johnson 1994). The soil must also be moist throughout the early stages of seedling establishment (1–2 wk), and seasonal declines in water tables regulate patterns of seedling recruitment

Fig. 6. Patterns of seed dispersal, germination, and establishment in relation to microtopographic position and river stage of a meandering river. (Modified from Bradley and Smith 1986.)



throughout the first growing season (Mahoney and Rood 1991, 1992; Segelquist et al. 1993; Johnson 1994). If the rate of water table decline exceeds the rate of root growth (4–6 mm/d for most species, but up to 12 mm/d in *P. trichocarpa*, Tables 1 and 2), water deficits lead to seedling mortality. Early germinating seedlings can tap groundwater at depths of 75 cm by the end of the growing season, and in some instances reach depths greater than 150 cm (Johnson 1994; Reed 1995). Rates of root growth and seedling establishment are also higher in fine, silty sands than coarse, gravelly soils (Kocsis et al. 1991). The impact of high surface temperatures is partially moderated by narrow juvenile leaves, yet periods of high evaporative demand accentuate seedling water deficits and drought-induced mortality (Johnson 1994). Vulnerability to drought persists until sapling roots reach alluvial water tables at depths of two metres or more (Fig. 6).

While cottonwood seedlings and saplings are intolerant of drought, they are tolerant of inundation and siltation (Fig. 7, Smit 1988; Rood and Mahoney 1990; Mahoney and Rood 1992). This tolerance helps cottonwoods survive extended periods of inundation (3–4 wk or more) during establishment and in subsequent years. Inundation and siltation eliminate many competitors, thus aiding seedling/sapling growth by keeping recruitment zones relatively open. While seedlings are tolerant of inundation, springtime flooding also eliminates many seedlings adjacent to the main channel by physical scouring (Figs. 6 and 7, Bradley and Smith 1986; Rood and Mahoney 1990). The lack of cottonwoods

Fig. 7. Cottonwood saplings in the flooded Oldman River at Lethbridge, Alberta. The diversity of sapling form reflects the occurrence and hybridization of three species, the Plains Cottonwood, *Populus deltoides* var. *occidentalis*, the narrowleaf cottonwood, *P. angustifolia*, and the black cottonwood, *P. trichocarpa*, or balsam poplar, *P. balsamifera*, that are difficult to distinguish without female flowers. All riparian cottonwoods are very flood-tolerant, capable of surviving weeks or even months of inundation. (Photo by S.B. Rood)



along some steep-gradient reaches and small watersheds may be due to post-dispersal scouring. In some instances, scouring by winter ice also leads to extensive seedling and sapling mortality (Johnson 1994).

The complexity of interactions between fluvial processes and seedling recruitment reveals a critical “bottleneck” in the life history of riparian cottonwoods. Low flows during seed dispersal are necessary to expose open, moist microsites for germination and recruitment. In contrast, higher “peak” flows during the dispersal phase may prevent exposure of microsites for recruitment until after the seeds have been dispersed or lost their viability. Higher flows following the dispersal phase may also bury or scour newly germinated seedlings. As a result, the location of germinating seedlings relative to the main channel influences subsequent patterns of seedling recruitment and mortality (see mortality zones in Figs. 6 and 8, Bradley and Smith 1986; Segelquist et al. 1993; Johnson 1994; Stromberg et al. 1991, 1993, 1996a). Under conditions of low riverine flows and seasonal drought, proximity to the main channel would be advantageous as seedlings not established in moist soils would likely succumb to drought. Yet, these seedlings would be vulnerable to physical scouring in subsequent years. A

reversal in recruitment success may occur in years dominated by higher riverine flows and cool, moist growing conditions that enable recruitment above the scour zone of the main channel. However, these seedlings would remain vulnerable to drought-induced mortality. Given the nature of these interactions, it is apparent that the conditions essential for seedling recruitment are not met on an annual basis (Baker 1990; Rood and Mahoney 1990; Johnson 1994). In fact, suitable conditions occur irregularly (Barnes 1985; Johnson 1994), on intervals of 5–10 yr or longer (Figs. 6 and 8, Bradley and Smith 1986; Baker 1990; Stromberg et al. 1991, 1993; Hughes 1994; Johnson 1994; Scott et al. 1996*a, b*).

Major differences in river channel morphology may also influence spatial and temporal patterns of seedling recruitment, as the distribution of suitable microsites change in relation to the dominant fluvial processes of a given river system (Johnson 1994; Scott et al. 1996*a, b*). For example, along low-gradient meandering streams in the arid Southwest, small floods allow for frequent (≤ 5 yr) episodes of seedling establishment on point bars in what has been described as an incremental-replenishment model (Hughes 1994). On less sinuous arid-region rivers, such as the Hassayampa River, cottonwoods establish in large numbers at infrequent intervals, after large, erosional floods that scour sediment from terraces (Stromberg et al. 1993). This pattern has been referred to as a

Fig. 8. Successful seedlings and some clonal saplings originate in arcuate bands that track specific elevations along meandering rivers and especially, at point bars at the end of meander lobes. The curving bands of even-aged saplings or trees originated from specific flood events and provide a hydrological history of the river. Here, sapling bands of narrowleaf cottonwoods and plains cottonwoods occur at a meander lobe along the Oldman River near Lethbridge, Alberta. (Photo by S.B. Rood.)



general-replenishment model, characterized by infrequent (ca. 30–50 yr recurrence intervals), large floods that set up recruitment conditions over large areas of the floodplain (Stromberg et al. 1993; Hughes 1994). In effect, temporal and spatial variation in fluvial processes result in a highly variable environmental regime for riparian cottonwoods, yet life history traits associated with reproduction and establishment converge upon the sequence of fluvial events following springtime snowmelt and stormflows. Future studies should explore the dynamic nature of these events and seek to quantify the physiological and genetic components of life-history variation relative to the timing and duration of fluvial geomorphic processes.

Asexual reproduction

Asexual reproduction is widespread among riparian cottonwoods (Tables 1 and 2). The most common mode of asexual reproduction is crown breakage and tree fall during wind storms and flooding events (Fig. 4). Broken branches can become buried in sediment, where they subsequently sprout and develop vigorous shoots. Crown damage and disturbance of shallow roots may also promote root suckering in some species, though this form of suckering is less common among *Aigeiros* species (Rood et al. 1994). Cladogenesis, the shedding of branchlets via formation of an abscission layer during winter months or following pollen release in the spring (Fig. 4), is a unique form of asexual reproduction common to *Tacamahaca* species but absent in *Aigeiros* species (Galloway and Worrall 1979; Dewit and Reid 1992).

Within native stands, the proportion of trees established from sexual vs. asexual propagules will vary with species, climatic condition, and drainage basin. In some instances, asexual propagules may outcompete seedlings, though few studies have sought to document the relative role of sexual vs. asexual propagules in native stands (Rood et al. 1994; Stromberg et al. 1996a). In either case, asexual propagation offers an alternative pathway to establishment in a highly variable riverine environment and, as a result, significantly influences the genetic structure of riparian cottonwood populations (Rood et al. 1994; Reed 1995; Stromberg et al. 1996a).

Establishment of riparian cottonwoods in nonalluvial habitats

Many of the ecological and life history properties associated with the establishment of cottonwoods in riparian habitats can result in their colonization of nonalluvial environments. During early spring and summer, the bare, moist mineral soils required for germination and establishment are readily found in adjacent agricultural fields and forest clearings. Given sufficient precipitation during the growing season, cottonwood seedlings can establish in great numbers in these disturbed environments. As a result, the establishment of *P. trichocarpa*

and *P. deltoides* in agricultural fields and forest clearings is common in moister regions of North America, such as the Pacific northwest and midwest, especially lands cleared along upper floodplain terraces (J.H. Braatne and P.E. Heilman, personal observations). In the Great Lakes region, seedlings and young stands of *P. deltoides* and *P. balsamifera* are also commonly observed along the margins of lakes and wetlands. In general, these isolated individuals and/or small stands of riparian cottonwood represent an opportunistic event as they are invaded and eventually dominated by secondary successional forest species.

Growth and maturation

Similar as in other plants, the nature and timing of environmental stress determine relative rates of growth and development in riparian cottonwoods. Early stages of sapling growth and stand development are influenced by seasonal flooding, drought, grazing, fire, and other site-specific conditions. Vulnerability to drought persists until sapling roots reach the moist soil associated with late-season alluvial water tables at depths of two metres or more (Fig. 6). Major flooding events (10- to 50-yr floods) eliminate young saplings as well as mature trees, though losses associated with these floods are often compensated by additional seedling recruitment on newly, exposed microsites. In general, *Aigeiros* species are more drought-tolerant than *Tacamahaca* species (see Blake et al. in Chapter 17). In fact, morphological and physiological adaptations to a warmer, drier climatic regime may account for the relative dominance of *Aigeiros* species at lower elevations and latitudes relative to the *Tacamahaca* species (Braatne et al. 1992; Hinckley et al. 1992, see Eckenwalder in Chapter 1). For example, stomata of *Aigeiros* species close rapidly in response to increasing air and soil-water deficits, while leaf orientation (ca. perpendicular to the sun) minimizes heat loads (Hinckley et al. 1992; see also Ceulemans and Isebrands in Chapter 16 and Blake et al. in Chapter 17). Differences in frost tolerance and susceptibility to xylem embolism may also account for major differences in species distributional patterns (Tyree et al. 1994; also see Chapters 16–18). Additional ecophysiological studies are needed to assess relationships between physiological adaptation to environmental stress and species distributional patterns.

Height growth during the early stages of sapling development may be limited, as energy is preferentially allocated to rapidly-growing roots. Two- to three-year-old cohorts of *P. fremontii* ranged from 5 to 50 cm tall (Stromberg et al. 1991, 1996a), while similar age classes of other species typically range from 25 to more than 60 cm tall (Cordes 1991; Stobbs et al. 1991; Peterson and Peterson 1992; Reed 1995). Once their root systems have become established, height growth is rapid and may reach 10–15 m upon the attainment of reproductive maturity (Tables 1 and 2).

Age of reproductive maturity and the lifespan of riparian cottonwoods vary among species, though quantitative studies of these demographic parameters are generally lacking for natural populations. The age at which reproductive maturity is attained ranges from 5 to 10 yr for most cottonwoods (Tables 1 and 2), though *Aigeiros* species typically reach reproductive maturity earlier than *Tacamahaca* species (Reichenbacher 1984; DeBell 1990; Cooper 1990). On average, *Aigeiros* poplars also appear to be shorter-lived than *Tacamahaca* poplars. Ages of older trees from 100 to 150 yr have been observed for *Aigeiros* species, while *Tacamahaca* species may live more than 200 yr (Cooper 1990; DeBell 1990; VanHaverbeke 1990; Zasada and Phipps 1990; Stromberg 1993). Although these data provide a general background on patterns of reproductive maturity and longevity, these life history and demographic parameters require more extensive study in natural populations.

Studies of sex ratios in natural populations of riparian cottonwoods have been limited. Balanced sex ratios (1:1) have been reported for populations of *P. deltoides* growing along the lower Mississippi River (Farmer 1964) and the Hocking River in Ohio (Hardin 1983). In contrast, Comtois et al. (1986) documented skewed sex ratios among *P. balsamifera* populations in northern Quebec. In this study, males were more common in extreme environments, whereas females typically dominated more protected and nutrient-rich environments. Other researchers have also observed skewed sex ratios in riparian cottonwoods in western North America. In some populations of *P. trichocarpa*, males dominate warmer and drier habitats, whereas other populations are either completely male or female and seemingly independent of environmental conditions (J.H. Braatne, unpublished data and personal observations). Given the widespread habitat partitioning between genders in *Salix* spp. (Dawson and Bliss 1989, 1993) and *Acer negundo* (Dawson and Ehleringer 1993), the possibility for habitat partitioning between male and female cottonwoods deserves more attention. Further research is needed to determine the cause and consequences of skewed sex ratios in riparian cottonwood populations.

Mature stand densities are highly variable within and among species (Tables 1 and 2); reported values range from 40 to 192+/ha for *Aigeiros* species (Johnson et al. 1976; Strahan 1983; Reichenbacher 1984; Szaro 1989; Stromberg et al. 1991, 1993) to 82–294+/ha for *Tacamahaca* species (DeBell 1990; Zasada and Phipps 1990; Peterson and Peterson 1992). Given seedling and sapling requirements for light, no regeneration by seed occurs within cottonwood stands. Any small shoots observed within mature stands are due to asexual propagation (root suckering and/or rooting of broken branches). As a result, riparian cottonwood forests often appear as linear strips of even-age/size stands; each stand representing a discrete period of propagule establishment and growth (Figs. 6 and 8). In places where the river channel has moved systematically in a uniform direction, an age/size gradient develops with young stands of small trees nearest the river and older stands of larger trees found farther from the channel (Figs. 6 and

Fig. 9. In very dry areas of the American Southwest, riparian cottonwoods provide a sharp contrast to the adjacent xeric landscapes. Here, a few Fremont cottonwoods, *Populus fremontii*, persist along the lower Truckee River near Reno, Nevada, after a century of river damming, water diversion, and tree harvesting. Although only a half dozen cottonwoods exist in this view, they still provide many woodland attributes. (Photo by S.B. Rood.)

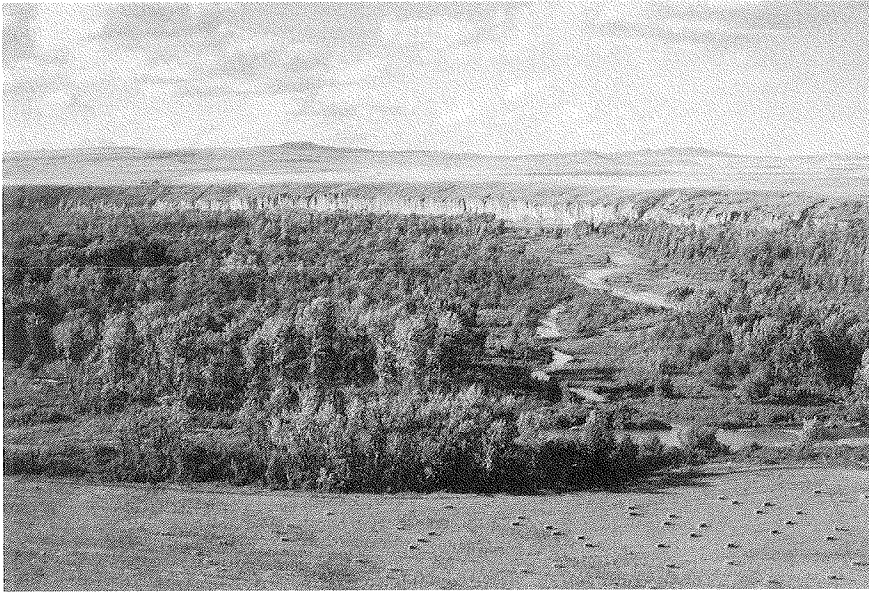


8). Mature stands of cottonwood may remain within the active floodplain or occur at slightly higher elevations on secondary terraces. As stands mature and become increasingly isolated from active fluvial processes, sex ratios may become skewed (J.H. Braatne, unpublished data), and stands are invaded by secondary successional forest species (Johnson et al. 1976). Of increasing concern is the relative dominance of older, relictual cottonwoods and lack of younger stands of riparian cottonwood throughout western North America (Fig. 9). The causes and consequences of these recent declines in riparian cottonwoods are discussed in the following section.

Conservation and restoration of riparian cottonwood forests

As noted in previous sections, cottonwoods are often the dominant forest species in many of the riparian habitats in western North America. These riparian forests have special importance for humans and are extremely rich wildlife habitats (Fig. 10, Finch and Ruggiero 1993). For example, although riparian vegetation occurs on less than 1% of the western North American landscape, it provides habitat for more bird species than all other vegetation types combined (Knopf et al. 1988).

Fig. 10. A riparian woodland with narrowleaf, *Populus angustifolia*, and black cottonwoods, *P. trichocarpa*, along the Oldman River in southwestern Alberta. In semi-arid regions, the riparian cottonwoods provide welcome aesthetic, recreational, and environmental relief from the otherwise treeless regions; these riparian woodlands harbor the region's richest wildlife habitats, providing environmental value much beyond that of the wood resource. (Photo by S.B. Rood.)



Due to their rapid growth and sometimes ragged appearance (due to cavitation-induced branch and crown dieback, Tyree et al. 1994), riparian cottonwoods have sometimes been considered as undesirable weeds ('cottonweeds'). However, these trees often serve as the foundation for the riparian forest ecosystem and are especially valued in the otherwise treeless semi-arid regions of western North America. Unlike wetter areas to the east (Wilson 1970) and west (Szaro 1990), a loss of riparian cottonwoods in many semiarid riparian areas is not compensated by enrichment from other tree species. If these cottonwoods die, so does the riparian forest ecosystem.

Causes of decline in riparian cottonwood populations

Only small remnants of once abundant riparian cottonwood forests survive in most regions of the southwestern United States (Fig. 9). Estimates of the magnitude of riparian vegetation loss and degradation range from 70 to 95% for the Southwest (Johnson and Haight 1984; National Research Council 1992). Even more severe declines have been experienced in the heavily developed areas of California, such as the Sacramento Valley, which has lost about 98.5% of the riparian forests that existed in 1850 (Sands and Howe 1977). Losses in the more

Table 3. Negative impacts on riparian cottonwood forests across western North America.

Factor	Comment
1. Livestock grazing	Cattle graze and trample seedlings. Overgrazed regions are characterized by a deficiency of seedlings and saplings, and forests decline as older trees die out.
2. Water diversion	Following river damming or the construction of diversion weirs, water is diverted offstream for irrigation. Subsequent instream flows are often insufficient, creating drought stress and accelerating mortality.
3. Domestic settlement	Clearing for homes, roads, bridges, and various other uses. Pressure is generally proportional to human population density.
4. Exotic plants	Characterized by natural (and artificial) disturbance, riparian areas are especially vulnerable to encroachment of exotic plants. Introduced trees include the salt cedar (<i>Tamarix pentandra</i>) and Russian olive (<i>Elaeagnus angustifolia</i>), and aggressive noxious weeds such as leafy spurge (<i>Euphorbia esula</i>) also occur.
5. Onstream reservoirs	Many riparian areas have been flooded by reservoirs. The rate of dam construction in the United States has declined over the past two decades but some damming is likely to continue in Canada.
6. Channelization	In many areas, extensive programs have attempted to straighten rivers and armor banks. Such actions inhibit the dynamic meandering of rivers that is essential for cottonwood replenishment.
7. Agricultural clearing	Clearing for pasture or crop production occurs where the proximity of floodplains to river water provides inexpensive irrigation. Agricultural clearing was more extensive in the early 1900s, and little net change has occurred in many areas since 1950.
8. Gravel mining	River valleys are prime areas for sand and gravel extraction. In addition to the areas excavated, roads, buildings, and screening plants often involve forest clearing. Although aesthetically offensive, abandoned gravel pits are sometimes areas of cottonwood recruitment, particularly through root suckering.
9. Direct harvesting	During early white settlement of western North America, poplars were harvested to provide building materials for forts and homes as well as fuel wood for heating and riverboat engines. Such use is presently minor in most regions.
10. Beavers	Beavers are a natural component of many riparian ecosystems and contribute to various processes, including cottonwood rejuvenation after beaver harvesting. However, an imbalance between beavers and trees may result from the loss of natural predators of beavers and the loss of some trees. The present consumer preference away from natural furs has reduced trapping, an artificial measure that controlled beaver populations through the past century.

Note: Impacts are listed in likely descending order of importance. The ranking would vary across river systems (revised from Rood and Mahoney 1990).

northerly areas of Colorado, Idaho, Wyoming, Montana, and Alberta have lagged behind the decline in California, although similar patterns are emerging. The causes of declines in riparian cottonwoods are numerous; similar types of impacts occur across different areas, but their relative significance differs among regions (see Table 3).

In many areas in western North America the heaviest pressure on riparian cottonwoods is related to livestock grazing (Table 3). Cattle browse and trample seedlings and saplings, thereby preventing replenishment of the forest. Management efforts to control livestock grazing include rotational grazing and exclusion fencing. This limits cattle use of riparian areas for short periods of time (ca. 5 yr) to allow younger trees to outgrow their most vulnerable stage.

Another major cause of the decline of riparian cottonwoods is river damming and water diversion (Tables 3, 4, and 5). Declines of cottonwoods downstream from dams in semi-arid regions of North America are well documented (Tables 4 and 5). Fortunately, these impacts are site specific since it is largely the pattern of downstream flow regulation, rather than simply the presence or absence of dams that determines the effect on riparian ecosystems. Although cottonwood decline has been common, occasional increases of cottonwoods have occurred following damming and stream flow modification, thus confirming that river type and flow patterns are critical factors in influencing riparian cottonwood forests (Rood and Mahoney 1990; Johnson 1994; Scott et al. 1996a).

In many semi-arid areas, onstream reservoirs are managed to conserve spring snowmelt which will later be diverted offstream for irrigation during summer. Dam operation can result in abrupt reductions in flow and sedimentation in late spring and early summer as well as in insufficient flows through the hot, dry period of midsummer. Both the abrupt flow reduction (Mahoney and Rood 1991) and the low summer flows probably contribute to drought stress which results in cottonwood die-back and mortality. Cottonwood seedlings are particularly vulnerable since they have limited, shallow root systems. The retention of sediments by dams also decreases the potential availability of microsites for seedling establishment. Due to the vulnerability of seedlings, recruitment of replacement trees is significantly impacted by river damming and water diversion. Without periodic recruitment, the cottonwood forest will suffer gradual decline as previously established trees age and die. Older trees appear more vulnerable to drought stress as they are physiologically decrepit and generally located on higher terraces where their root systems become isolated from alluvial waters due to excessive surface water diversion and groundwater extraction.

Cottonwoods are especially vulnerable to drought-induced xylem cavitation (Tyree et al. 1994). In some instances, vulnerability to cavitation may contribute favorably to natural systems since it results in shoot pruning during drought periods to reduce transpirational water loss. However, in flow-reduced systems,

Table 4. Reports of negative impacts of river damming on downstream riparian cottonwood forests in western North America.

Author (date)	River	Region	<i>Populus</i>	Comments
Johnson et al. (1976)	Missouri	N. Dakota	<i>P. deltoides</i>	Reduced tree growth and fewer seedlings
Brown et al. (1977)	Various	Arizona	<i>P. fremontii</i> , <i>P. angustifolia</i>	Reduced abundance
Ohmart et al. (1977)	Colorado	California	<i>P. fremontii</i>	Reduced abundance, absence of seedlings
Crouch (1979)	South Platte	Colorado	<i>P. deltoides</i>	Reduced abundance
Behan (1981)	Missouri	Montana	<i>P. deltoides</i>	Reduced abundance, absence of seedlings
Reily and Johnson (1982)	Missouri	N. Dakota	<i>P. deltoides</i>	Reduced tree growth
Brothers (1984)	Owens	California	<i>P. fremontii</i>	Reduced abundance
Stine et al. (1984)	Rush Creek	California	<i>P. balsamifera</i>	Reduced abundance
Strahan (1984)	Sacramento	California	<i>P. fremontii</i>	Fewer seedlings
Fenner et al. (1985)	Salt	Arizona	<i>P. fremontii</i>	Conditions unsuitable for seeding establishment
Bradley and Smith (1986)	Milk	Alberta/ Montana	<i>P. deltoides</i>	Reduced abundance, fewer saplings
Akashi (1988)	Bighorn	Wyoming	<i>P. deltoides</i>	Reduced abundance
Rood and Heinze-Milne (1989)	St. Mary, Waterton, and Belly	Alberta	<i>P. deltoides</i> , <i>P. trichocarpa</i> ^a , <i>P. angustifolia</i>	Reduced abundance
Howe and Knopf (1991)	Rio Grande	New Mexico	<i>P. fremontii</i>	Absence of seedlings
Smith et al. (1991)	Bishop Creek	California	<i>P. fremontii</i> , <i>P. balsamifera</i>	Smaller leaves, lower transpiration, and H ₂ O potential
Snyder and Miller (1991)	Arkansas	Colorado	<i>P. deltoides</i>	Reduced abundance
Stromberg and Patten (1991)	Bishop Creek	California	<i>P. fremontii</i> , <i>P. balsamifera</i>	Reduced tree diameter growth, crown cover, and survival
Stromberg and Patten (1992)	Bishop and Pine Creeks	California	<i>P. trichocarpa</i>	Increased mortality, reduced growth
Johnson (1992)	Missouri	North Dakota	<i>P. deltoides</i>	Fewer saplings
Rood et al. (1995)	St. Mary	Alberta	<i>P. deltoides</i> , <i>P. trichocarpa</i> , <i>P. angustifolia</i>	Reduced abundance, absence of seedlings
Rood and Mahoney (1996)	Marias	Montana	<i>P. deltoides</i> , <i>P. trichocarpa</i> , <i>P. angustifolia</i>	Absence of seedlings

Note: This is a chronological listing based on a table in Rood and Mahoney (1990), revised and expanded here.

^aDiscrimination of *P. balsamifera* and *P. trichocarpa* is difficult, particularly in areas where both species co-occur and hybridize.

Table 5. Contributing factors to the decline of western riparian cottonwood forests following river damming or water pumping from wells (revised from Rood and Mahoney 1990).

Proposed cause	Comments	References
I. Hydrological changes:		
A. Reduced water availability	Diversion of water offstream or well pumping creates a water deficit, resulting in drought stress, slow growth, and increased mortality	Brown et al. (1977); Brothers (1984); Stine et al. (1984); Hardy BBT Ltd. (1988); Rood et al. (1989); Reily and Johnson (1982); Smith et al. (1991); Snyder and Miller (1991); Stromberg and Patten (1991); Stromberg and Patten (1992); Rood et al. (1995); Scott et al. (1996)
B. Reduced flooding	Spring flooding is essential to create moist seedbeds for seedling establishment	Brown et al. (1977); Ohmart et al. (1977); Johnson et al. (1976); Reily and Johnson (1982); Johnson (1992); Rood et al. (1995)
C. Stabilized flows	Dynamic flows are essential for seedling establishment	Strahan (1984); Fenner et al. (1985); Howe and Knopf (1991); Johnson (1992); Rood and Mahoney (1996)
II. Geomorphological changes resulting from hydrological alterations:		
A. Reduced meandering and channelization	With reduced flooding, channel migration and the creation of seedbeds are reduced	Ohmart et al. (1977); Johnson et al. (1976); Bradley and Smith (1986); Howe and Knopf (1991); Snyder and Miller (1991); Johnson (1992)

cavitation can result in significant shoot mortality and crown die-back, particularly if drought stress is prolonged (Albertson and Weaver 1945). These consequences are typical of problems along flow-reduced dammed rivers, although different patterns of flow regulation can also create other problems for riparian cottonwood forests (Table 5). Temporal and spatial patterns in cottonwood decline can be diagnostic in revealing the specific negative impact(s) of river damming and flow diversion.

Conservation and restoration strategies

An important prerequisite for the conservation of riparian cottonwoods is a greater recognition of both their value and their vulnerability. (See Whitham in Chapter 11, for a special reference on the need to protect natural cottonwood hybrids and riparian hybrid zones.) Back in the 1950s and 1960s, there were active programs to clear riparian woodlands in an effort to reduce transpirational water loss in semi-arid regions (National Research Council 1992; U.S. Department of Interior 1994). The ineffectiveness of such 'phreatophyte control' programs was soon revealed since the loss of the stabilizing streamside vegetation resulted in increased erosion, reduced retention of rainfall, and subsequently falling rather than rising alluvial water tables. Although phreatophyte control programs are seldom practiced anymore, other state and federal resource management programs often fail to promote conservation of riparian woodlands (National Research Council 1992; U.S. Department of Interior 1994; Shafroth et al. 1995a).

With greater appreciation of riparian cottonwoods, more attention should be directed to protect unregulated streams and rivers. Rather than allocating riparian lands to various purposes and later protecting selective reaches of a river system, conservation planning should begin by identifying valuable riparian zones and ensuring their protection prior to further regional development.

Along dammed streams and rivers, firmly legislated commitments are required to ensure the delivery of sufficient flows and sediment to allow the survival, growth, and reproduction of riparian cottonwoods and other riparian vegetation. The U.S. Department of Interior has recently sought to counteract damming effects along the Colorado River by mimicking natural flood and sedimentation regimes. Such efforts are essential for the development of new approaches to the restoration of vegetation along regulated streams and rivers. However, it will also be critical to guarantee sufficient instream flows during drought years. While it may be difficult to justify instream flows solely for riparian vegetation, maintenance of these flow regimes also improves water quality and fisheries as well as other aesthetic and recreational river resources, benefitting human as well as ecosystem health.

Riparian restoration programs have been promoted along various rivers in western North America (National Research Council 1992; Friedman et al. 1995; Scott et al. 1996a), yet the role of riparian cottonwoods in many of these revegetation programs remains unclear. Riparian restoration requires the integrated management of both the land and water, creating complexities in both biological and physical resources and complicating administration which invariably involves multiple private, regional, state or provincial, and federal participants (National Research Council 1992; U.S. Department of Interior 1994).

Restoration programs will involve a combination of approaches related to flow regulation, land-use policies, and intervention to promote stream channel restoration and revegetation (National Research Council 1992). Revegetation measures may include deliberate seeding of suitable riparian zones where a shallow water table would promote seedling survival. In some instances, plowing and sod removal in combination with limited irrigation may also be required to promote natural seedling establishment (Friedman et al. 1995). In areas lacking native seed sources, rooted seedlings, and saplings as well as unrooted cuttings, whips, and poles may be propagated and transplanted into suitable riparian habitats (Hoag 1993; Briggs 1994). In revegetation programs, native species should be used, and a range of genotypes should be propagated in a manner that encourages biodiversity. Site scarification, the mechanical disturbance of the substrate, may also be used to propagate cottonwoods that already exist on site. Scarification will promote root suckering and thus may be most effective for *Tacamahaca* species including *P. trichocarpa*, *P. balsamifera* and *P. angustifolia*. Although root suckering of the *P. deltoides* and *P. fremontii* (Sect. *Aigeiros*) is uncommon, even these species appear to respond to some mechanical disturbance.

In spite of active cottonwood restoration programs along various rivers and streams, only a limited number of published reports on these activities exist, particularly in refereed journals (see Friedman et al. 1995; Shafroth et al. 1995a). There is a serious information deficiency on these topics. Researchers and riparian resource managers who have experience in cottonwood restoration are encouraged to publish their findings as they will be of considerable interest for riparian cottonwood restoration not only in western North America, but also in other parts of the world.

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