Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration†

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Summary  Cottonwoods (Populus spp.) are adapted to riparian or floodplain zones throughout the Northern Hemisphere; they are also used as parents for fast-growing hybrid poplars. We review recent ecophysiological studies of the native cottonwoods Populus angustifolia James, P. balsamifera L., P. deltoides Marsh., P. fremontii S. Watson and P. trichocarpa T. & G. in North America, and P. nigra L. in Europe. Variation exists within and across species and hybrids; however, all riparian cottonwoods are dependent on shallow alluvial groundwater that is linked to stream water, particularly in semi-arid regions. This conclusion is based on studies of their natural occurrence, decline following river damming and dewatering (water removal), water relations, isotopic composition of xylem water, and by the establishment of cottonwoods along formerly barren natural channels after flow augmentation in response to the conveyance of irrigation water. When alluvial groundwater is depleted as a result of river dewatering or groundwater pumping, riparian cottonwoods exhibit drought-stress responses including stomatal closure and reduced transpiration and photosynthesis, altered 13C composition, reduced predawn and midday water potentials, and xylem cavitation. These physiological responses are accompanied by morphological responses including branch sacrifice and crown die-back. In severe cases, mortality occurs. For example, severe dewatering of channels of the braided Big Lost River in Idaho led to mortality of the narrowleaf cottonwood, P. angustifolia, and adjacent sandbar willows, Salix exigua Nutt., within 5 years, whereas riparian woodlands thrived along flowing channels nearby. The conservation and restoration of cottonwoods will rely on the provision of river flow regimes that satisfy these ecophysiological requirements for survival, growth and reproduction.

Keywords: Populus.

Introduction

Cottonwoods (Populus spp.) occur in riparian zones (river valleys) throughout the Northern Hemisphere (Johnson et al. 1994, Braatne et al. 1996, Naiman and Décamps 1997). Along with willows (Salix spp.), cottonwoods are ecological pioneers that colonize barren riparian sites, and in semi-arid environments they are the dominant and often exclusive riparian tree species (Rood and Mahoney 1995, Scott et al. 1997, Patten 1998). In wetter regions, such as eastern North America and central Europe, cottonwoods are followed in succession by other hardwoods, and in the Pacific region of North America and boreal regions of North America and Europe, they are followed by conifers (Johnson 1994, Polzin and Rood 2000).

Riparian cottonwoods provide stream-bank stabilization and wildlife habitat, contribute to aquatic ecosystems, and provide the parental genotypes for natural and artificial interspecific hybrids (Eckenwalder 1996). Natural hybrids are important for ecosystem biodiversity (Schweitzer et al. 2002, McIntyre and Whitham 2003), and artificial intersectional hybrids often grow vigorously and provide fiber, fuel and wood products. However, cottonwood forests are particularly vulnerable to degradation of riparian zones as a result of livestock production, tree harvesting for fiber and fuel, and clearing for agriculture, human settlement and transportation corridors (Rood and Mahoney 1990, Patten 1998, Muller et al. 2002).

River damming and water diversion have further contributed to the collapse of cottonwood populations along many rivers (Rood and Mahoney 1990, Braatne et al. 1996). The decline of cottonwoods downstream from dams prompted us to review the dependency of riparian cottonwoods on stream flow and the consequences of dewatering (removal of water) on cottonwood water relations. We focus on studies conducted after 1990, thereby complementing previous reviews of cottonwood water relations (Blake et al. 1996, Smith et al. 1998), impacts of damming (Rood and Mahoney 1990, Friedman et al. 1998, Nilsson and Bergren 2000), and life history and conservation (Braatne et al. 1996, Karenberg et al. 2002). We have adopted the taxonomic treatment of Populus described by Eckenwalder (1996).

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Stream flow dependency

The determination of a causal relationship between river damming and dewatering and cottonwood decline is based on evidence that cottonwoods are dependent on water originating from stream flow. There are five lines of evidence supporting this association (Table 1).

Natural occurrence

In semi-arid regions where low precipitation limits woody vegetation, cottonwoods are restricted to riparian zones where supplemental water is provided by a stream or river (Braatne et al. 1996). The extent of cottonwoods away from the river is related to elevation rather than distance. Trees are restricted to streamside bands up to 3 to 4 m above the base stage of the river in late summer (Stromberg et al. 1996, Horton et al. 2001b).

Damming and dewatering

Studies along dammed rivers further indicate cottonwood dependency on stream flow (Table 1; Rood and Mahoney 1990, Friedman et al. 1998, Patten 1998). Cottonwood populations downstream from many dams have declined, especially in response to dewatering as a result of irrigation during the hot, dry period of mid- to late summer.

The Big Lost River provides a vivid demonstration of the negative impacts of dewatering on riparian woodlands (Figure 1). This river flows in braided alluvial channels in Idaho (latitude 43.6° N, longitude 113.5° W): some of the channels are used to convey irrigation water (R.M. Lundy, Big Lost River Irrigation District, unpublished report, 1993), whereas other channels are entirely dewatered during the irrigation period. Narrowleaf cottonwoods (P. angustifolia James) and sandbar willows (Salix exigua Nutt.) died along the diverted channels but continued to thrive along the flowing channels (Figure 1). Mortality occurred over about 5 years of summer dewatering, with complete mortality by 1993. The period from 1987 through 1991 included a sequence of dry years that prompted increased dewatering, which contributed to drought stress (R.M. Lundy, unpublished report, 1993). Lundy concluded that alluvial groundwater is reliant on stream flow and that mortality of cottonwood and willow occurs within 5 years of stream dewatering.

There are several other reports of cottonwood decline following damming, confirming dewatering as a cause of cottonwood decline (Braatne et al. 1996, Mahoney and Rood 1998, Patten 1998). Additional factors contributing to cottonwood decline include livestock grazing and trampling, invasion by exotic weeds, an excess of beaver or large ungulates (elk), and herbicide application and drift (Braatne et al. 1996, Patten 1998).

Supplemental flows

Dewatering can result in cottonwood decline, whereas the provision of supplemental water can promote cottonwood forests. Irrigation canals are often unlined, permitting water to infiltrate adjacent riparian zones. Additional vegetation, often including cottonwoods and willows, frequently follows along these canals. Natural channels are also used to convey irrigation flows. Such channels may be intermittent (irregular flows).

Table 1. Evidence that riparian cottonwoods are dependent on stream flow.

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<tr>
<th>Evidence</th>
<th>Description</th>
<th>References</th>
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<tr>
<td>Natural occurrence</td>
<td>In semi-arid regions such as prairies, cottonwoods are restricted to riparian zones, and upland areas are naturally treeless.</td>
<td>Widespread observation</td>
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<tr>
<td>Dewatering</td>
<td>Depletion of alluvial groundwater as a result of reduced stream flow following damming or diversion, groundwater pumping or interruption of the stream to groundwater transfer has resulted in cottonwood decline.</td>
<td>Figure 1. Rood and Mahoney 1990, Smith et al. 1991, Stromberg and Patten 1992, Busch and Smith 1995, Rood et al. 1995, Pautou et al. 1997, Scott et al. 1999, 2000, Somogyi et al. 1999, Horton et al. 2001b, Amlin and Rood 2003</td>
</tr>
<tr>
<td>Supplemental water</td>
<td>Cottonwoods colonize banks along irrigation canals and become established following flow augmentation of natural channels that were previously treeless as a result of intermittent flows.</td>
<td>Figure 2; widespread observation</td>
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and consequently may not support phreatophytic cottonwoods and willows. Cottonwoods become established when the channel flow is augmented, further demonstrating the reliance of cottonwoods on stream water (Figure 2).

Isotopic analyses

Stable isotopes of oxygen and hydrogen occur naturally and, because of fractionation accompanying evaporation and other physical processes, specific water sources have particular isotopic compositions. Generally, there is minimal fractionation in stem tissues, and thus xylem water reflects the isotopic composition of the source water taken up by roots (Dawson and Ehleringer 1991).

Busch et al. (1992) used isotopic analyses to confirm the reliance of riparian cottonwoods on alluvial groundwater originating from river water. For both the Bill Williams and the lower Colorado rivers in Arizona, $^2$H and $^{18}$O ratios consistently showed that P. fremontii S. Watson xylem water was similar to alluvial groundwater, which was in turn similar to river water (although evaporative enrichment of $^2$H occurred over the summer). Other researchers have conducted isotopic analyses that further demonstrate the reliance of riparian cottonwoods on water originating from stream flow (Table 1).

However, there are several complications associated with isotopic analyses (Dawson and Ehleringer 1991). For example, along the Red Butte Creek near Salt Lake, Utah, groundwater from hill-slope aquifers flows into the streamside zone and supplements the water originating from the stream. A study by Kolb et al. (1997) with box elder (Acer negundo L.), another riparian phreatophyte, revealed seasonal differences. The $^{18}$O composition of xylem water indicated that large and small trees along a stream in Arizona were solely reliant on groundwater with an $^{18}$O composition similar to that of the adjacent stream throughout the dry summer period, whereas, at other times, these trees obtained up to one-half of their water from shallow surface water that originated as recent, local pre-
cipitation. Riparian trees were thus reliant on groundwater that originated from stream water during dry periods but were opportunistic and would take up water from local precipitation when available, a pattern consistent with conclusions by Snyder and Williams (2000).

Why cottonwoods are dependent on stream flow

These observations collectively demonstrate that riparian cottonwoods are dependent on stream flows. The trees are especially dependent along streams in semi-arid regions where the riparian groundwater is recharged by stream water. However, rivers influence several other conditions that contribute to the suitability of riparian zones for cottonwoods and that are impacted by damming and flow regulation (Table 2).

Flowing water has the capacity to erode alluvial sediments, which are transported downstream and redeposited. Both the scour and deposition zones provide barren areas suitable for seedling recruitment. With damming and diversion, the sediment patterns are altered (Table 2), and when dams are operated to attenuate flood peaks there can be a reduction in sediment movement downstream. Furthermore, suspended sediments settle out in reservoirs and this can produce a downstream zone of sediment degradation and down-cutting. Both reduced sediment movement and sediment depletion can degrade the suitability of the riparian area for cottonwood establishment.

Reservoirs also trap floating materials including woody debris and seeds or vegetative fragments suitable for clonal reproduction. Hydrochory, i.e., water-based propagule dispersal, can be diminished by alterations to stream flow and the imposition of reservoirs (Nilsson et al. 1991, Nilsson and Bergren 2000).

Table 2. Ecological processes associated with stream flow that influence riparian cottonwoods.

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<tr>
<th>Process</th>
<th>Description</th>
<th>References</th>
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<td>Vegetation exclusion</td>
<td>High flows retard encroachment of inundation-intolerant upland vegetation into riparian zones.</td>
<td>Rood and Mahoney 1995, Rood et al. 1999, Polzin and Rood 2000</td>
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</table>
Stream flow alterations can indirectly influence cottonwoods by altering inundation patterns that impact other plant species (Table 2). Upland plants are naturally excluded from floodplain zones because of their intolerance to flooding. With changes in flood patterns, upland plants can encroach on riparian zones and compete with cottonwoods and willows.

**Water relations**

Water relations relevant to the ecophysiology of riparian cottonwoods include the traditional soil (substrate)—plant—atmosphere continuum (Braatne et al. 1992, Kozlowski and Pallardy 1997). Analyses of water relations must also consider the origins of shallow alluvial groundwater from precipitation, stream flow and regional groundwater.

**Gaining versus losing streams**

Streams commonly obtain water from the adjacent groundwater and thus groundwater flow is from the riparian zone into the stream. This hydraulic pattern is typical for forested regions that comprise most of North America and Europe. Such rivers are referred to as “gaining” streams because they gain water from adjacent alluvial and hill-slope aquifers.

In arid and semi-arid regions, the hydraulic linkage is often reversed. Local precipitation is lower than potential evapotranspiration and makes a limited contribution to groundwater. Consequently, during dry periods, water often flows from the stream into the riparian groundwater. Such streams are referred to as “losing” streams because they lose water to the alluvial aquifer.

There are several approaches to discriminating between gaining and losing streams. Upland forests have a positive balance between precipitation and evapotranspiration and are generally associated with gaining streams. The hydraulic linkage can also be verified through direct measurement of groundwater elevations. For gaining streams, the adjacent riparian groundwater occurs above the stream surface. In contrast, along losing streams, the alluvial groundwater table tends to slope downward away from the stream. For example, in a sediment mixture of sand, gravel and cobble, the water table was determined to recede with a slope of about 0.5% (i.e., 0.5 m per 100 m distance) through cottonwood zones away from the St. Mary River and Willow Creek in southwestern Alberta, indicating that these are losing streams (Rood and Mahoney 1995, Amlin and Rood 2003).

Isotopic analyses of water can also be used to determine groundwater hydrology (Busch et al. 1992, Kolb et al. 1997). For a losing stream, the riparian groundwater is similar in isotopic composition to the stream water, whereas along a gaining stream, the isotopic composition of riparian groundwater resembles groundwater from adjacent upland regions and, in turn, local precipitation. However, seasonal mixing of water sources and seasonal reversal of water fluxes, in addition to physical fractionation, can complicate interpretation of the isotopic composition of water.

In semi-arid regions, riparian cottonwoods are the principal natural trees (Braatne et al. 1996, Patten 1998). In such areas, the streams are typically losing streams and the cottonwoods are thus reliant on the water that infiltrates from the stream into the riparian groundwater (Rood and Mahoney 1995). Consequently, these systems are particularly vulnerable to de-watering as a result of damming and diversion (Rood and Mahoney 1990, Friedman et al. 1998).

**Physiological water relations**

Many independent studies have demonstrated that cottonwood mortality downstream from dams is largely caused by drought stress (Rood and Mahoney 1990, Braatne et al. 1996, Patten 1998). Symptoms of drought stress include reduced growth and altered water relations within a sequence of physiological and morphological changes (Table 3).

Studies of the physiological consequences of groundwater depletion can be grouped into four categories. The first study type involves the use of artificial systems for deliberate water table manipulation in partially controlled environments, usually greenhouses or garden plots (Mahoney and Rood 1991, 1992, Segelquist et al. 1993, Hughes et al. 1997, Horton and Clark 2001). For example, rhizopods are experimental devices that contain vertical growth tubes (cylinders with substrate) linked to a water reservoir (Mahoney and Rood 1991). The water level in the reservoir is manipulated, leading to corresponding changes in the water table level in the growth tubes. Multiple growth tubes and multiple rhizopods permit comparative study of the effects of different water table regimes, as well as other factors such as substrate texture (sediment particle size), on different riparian species and genotypes.

The second type of study involves field comparisons, typically with groundwater depletion caused by damming, diversion, groundwater pumping or sediment excavation (Smith et al. 1991, Busch et al. 1992, Scott et al. 1999, 2000, Horton et al. 2001a, 2001b, 2001c, Amlin and Rood 2003, Cooper et al. 2003). Compared with the first approach, these field comparisons are generally less controlled in terms of the extent of groundwater depletion and typically suffer from pseudo-replication. Multiple plants are monitored, but all are typically within a particular grove associated with the groundwater modification. However, the collective results of different field studies and controlled environment studies provide confidence in these analyses (Table 3).

The third line of study involves comparisons of eco-physiological characteristics of cottonwoods collected from different environments and brought to a particular study site, typically a common garden or greenhouse. The different genotypes are often members of a particular species that originate from natural riparian zones with different climates (Sparks and Black 1999, Dunlap and Stettler 2001, Rowland 2001), although some studies consider different cottonwood species (Kranjcec et al. 1998).

The fourth approach involves studies of the physiology of water relations of hybrid poplars in silvicultural plantings (Bassman and Zwier 1991, Braatne et al. 1992, Tschaplinski and Tuskan 1994, Tschaplinski et al. 1994, 1998). These studies often consider different genotypes and particularly hybrid families consisting of clones of two (or more) parental species.
Aspects of the water relations of cottonwoods that have been extensively investigated by one or more of these approaches are summarized in Table 3. The physiological responses of native cottonwoods to groundwater depletion have been fairly confidently established, and can be summarized as follows.

As the balance between groundwater availability and transpirational demand becomes unfavorable, xylem water potential declines (Table 3). Usually, this leads to rapid stomatal closure, although there are substantial differences across cottonwood species and genotypes (Bassman and Zwier 1991, Tschaplinski et al. 1994, Sparks and Black 1999, Dunlap and Stettler 2001), and preconditioning may be required, particularly in *P. trichocarpa* T. & G. (Schulte et al. 1987). Stomatal closure, as indicated by reduced stomatal conductance, is the primary mechanism by which most plants reduce transpiration to conserve water during drought cycles. With stomatal closure, CO₂ uptake is also reduced, which can reduce photosynthesis and subsequent growth.

In severe or sustained drought conditions, stomatal closure is insufficient to maintain a favorable water balance. Subse-

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<th>Response</th>
<th>Duration</th>
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<tr>
<td>Altered shoot growth</td>
<td>Weeks to season(s)</td>
<td>Mahoney and Rood 1991, 1992, Braatne et al. 1992, Segelquist et al. 1993,</td>
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<td></td>
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<td>Shafroth et al. 1994, Barsoum and Hughes 1998, Somogyi et al. 1999,</td>
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<td>Hughes et al. 2000, Rood et al. 2000b, Amlin and Rood 2002</td>
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<tr>
<td>Reduced shoot elongation</td>
<td>Days to weeks</td>
<td>Mahoney and Rood 1991, 1992, Busch et al. 1992, Willms et al. 1998,</td>
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<td></td>
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<td>Scott et al. 1999, Hughes et al. 2000, Rood et al. 2000b, Horton et al. 2001c,</td>
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<td></td>
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<td>Amlin and Rood 2002</td>
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<td>Reduced leaf area</td>
<td>Days to weeks</td>
<td>Smith et al. 1991, Braatne et al. 1992, Mahoney and Rood 1992,</td>
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<td>Busch and Smith 1995, Van Splunder et al. 1996, Scott et al. 1999,</td>
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<td>Rood et al. 2000b</td>
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<tr>
<td>Reduced trunk expansion</td>
<td>Weeks to season(s)</td>
<td>Stromberg and Patten 1990, 1991, 1992, Willms et al. 1998,</td>
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<td>Scott et al. 1999, 2000</td>
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<tr>
<td>Leaf senescence and mortality</td>
<td>Weeks</td>
<td>Mahoney and Rood 1992, Scott et al. 1999, Somogyi et al. 1999,</td>
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<td>Amlin and Rood 2003, Cooper et al. 2003</td>
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<tr>
<td>Branch sacrifice</td>
<td>Weeks to season(s)</td>
<td>Scott et al. 1999, Rood et al. 2000a, Horton et al. 2001b, Cooper et al. 2003</td>
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<td>Crown die-back</td>
<td>Multiple seasons</td>
<td>Stromberg and Patten 1991, 1992, Scott et al. 1999, Shafroth et al. 2000,</td>
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<td></td>
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<td>Horton et al. 2001b, 2001c, Cooper et al. 2003</td>
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<tr>
<td>Altered root growth</td>
<td>Days or longer</td>
<td>Mahoney and Rood 1992, Shafroth et al. 1995, 2000, Van Splunder et al. 1996,</td>
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<td>Hughes et al. 2000, Rood et al. 2000b</td>
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<tr>
<td>Mortality</td>
<td>Weeks to season(s)</td>
<td>Mahoney and Rood 1991, Segelquist et al. 1993, Shafroth et al. 1998, 2000,</td>
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<td>Sprenger et al. 2002, Cooper et al. 2003</td>
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<td>Reduced photosynthesis</td>
<td>Minutes to hours</td>
<td>Horton et al. 2001a, 2001b, 2001c</td>
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<td>Reduced midday xylem water potential</td>
<td>Minutes to hours</td>
<td>Smith et al. 1991, Busch and Smith 1995, Sparks and Black 1999,</td>
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<td>Rood et al. 2000b, Horton 2001a, Amlin and Rood 2003, Cooper et al. 2003</td>
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<tr>
<td>Reduced predawn water potential</td>
<td>Hours to day(s)</td>
<td>Rood et al. 2000b, Horton et al. 2001a, 2001b, 2001c, Cooper et al. 2003</td>
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<td>Increased xylem cavitation</td>
<td>Days to weeks</td>
<td>Braatne et al. 1992, Tyree et al. 1994, Sparks and Black 1999, Rood et al. 2000a</td>
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<tr>
<td>Altered phytohormones</td>
<td>Hours to days</td>
<td>Loewenstein and Pallardy 1998, Rood et al. 2000b</td>
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<tr>
<td>Reduced ¹³C in tissues</td>
<td>Weeks to year(s)</td>
<td>Leffler and Evans 1999, Horton et al. 2001c</td>
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sequently, water potential continues to decline, either over a daily cycle or over a number of days in which the predawn water potential is unable to recover (Table 3). A distinctive characteristic of cottonwoods is their exceptional vulnerability to xylem cavitation (Tyree et al. 1994, Sparks and Black 1999), typically losing one-half of their hydraulic conductance at xylem water potentials of only about –1.5 MPa.

The exceptional vulnerability of cottonwoods to xylem cavitation may be an adaptive trait that contributes to drought avoidance (Rood et al. 2000a). Following xylem cavitation, affected branches die, thereby eliminating the transpirational demand of these branches and improving the water balance of the remaining parts of the tree (Sperry and Pockman 1993, Rood et al. 2000a). Such branch sacrifice explains the abundant dead branches typical of *P. deltoides* Marsh. and *P. fremontii*, the cottonwood species adapted to the driest environments. The vulnerability of cottonwoods to cavitation is consistent with the proposal by Tyree and Sperry (1988) that some trees naturally function near the catastrophic xylem cavitation threshold.

In addition to the direct and often short-term consequences of drought stress, cottonwoods also display subsequent physiological changes associated with drought hardening (Kozlowski and Pallardy 1997). These changes may confer improved tolerance or avoidance during subsequent drought cycles, assuming that abscisic acid accumulates and provides a translocatable signal between roots and leaves (Loewenstein and Pallardy 1998). Other changes are often morphological, such as changes in leaf characteristics including leaf size, stomatal size and number, epidermal wax characteristics and external leaf features such as epidermal hairs (Dunlap and Stettler 2001).

Other morphological responses to drought stress often include localized growth reduction (Table 3). Cell elongation is driven by turgor, which is highly responsive to water potential, and thus elongation abruptly ceases with drought stress. However, with partial drought, root elongation continues and is substantially promoted by the declining water table that accompanies the natural river stage recession throughout the summer (Table 3). There is thus some coordination of growth allocation accompanying the water relations experienced by riparian cottonwoods, although the endogenous signals responsible for such coordination are unclear. Reproductive status of cottonwoods also decreases with water stress and this could reduce seed production, leading to a diminishing population (Rowland and Johnson 2001).

**Yellow signals caution**

For widespread application, physiological monitoring of cottonwood drought stress should be simple and inexpensive and should not require specialized instrumentation. With respect to these criteria, precocious senescence and branch sacrifice provide conspicuous indicators of drought stress (Table 3). Although there are differences in senescence patterns and vulnerability to cavitation across species (Tyree et al. 1994), all riparian cottonwoods display precocious senescence that precedes branch sacrifice and crown die-back following drought stress. The extent of senescence is apparently quantitative and thus reflects the severity of drought stress (Table 3). Senescence associated with branch sacrifice and crown die-back occurs well before death of the whole tree and provides visible symptoms of drought stress before lethal damage. In addition to assessments of leaf and branch senescence, variations in branch growth provide sensitive measures of recent (past years) water conditions (Willms et al. 1998).

Analyses of leaf senescence and branch sacrifice are also suitable for remote sensing by color photographs or multispectral scanning from aircraft or satellites. These remote sensing approaches would be suitable for scaling up the area of monitoring. Water flux can also be evaluated through remote sensing to provide an indicator of riparian conditions (Cooper et al. 2000).

**Adaptations of different cottonwood species**

Although there are generally similar ecophysiological patterns across cottonwood species, there are also differences (Bassman and Zwier 1991, Braatne et al. 1992, Tschaplinski and Tuskan 1994, Tschaplinski et al. 1994, 1998, Dunlap et al. 1995, Kranjec et al. 1998, McCamant and Black 2000, Dunlap and Stettler 2001, Rowland 2001). General patterns of adaptation of the different species emerge based on their geographic distribution (Figure 3). These distributions are largely associated with climatic patterns related to precipitation and temperature. The two factors overlap because temperature influences water demand as well as other physiological processes (Kranjec et al. 1998, McCamant and Black 2000).

Climatic ranges are also related to river dependency and water relations of riparian cottonwoods. Thus, the *Algeiros* species *P. deltoides* and *P. fremontii* usually occur in semi-arid environments, often along losing rivers. In contrast, the *Tacamahaca* species, especially *P. balsamifera* and *P. trichocarpa*, often occur in zones with wetter climates where rivers are often gaining and thus the alluvial groundwater is less dependent on stream flow. Although river regulation is still important in these mesic zones, there are differences in the relative influence of the different river functions across ecoregions (Table 2).

Based on distribution, the narrowleaf cottonwood, *P. angustifolia*, is intermediate between the other *Tacamahaca* bald poplars and the *Algeiros* cottonwoods. The natural climatic adaptation of black poplar (*P. nigra*) is difficult to assess because European riparian zones have been altered for centuries. *Populus nigra* has been planted in native and non-native regions and there has been introgression of genes from foreign poplars, particularly the North American *P. deltoides* (Van Dam and Bordacs 2002).

**River regulation for riparian restoration**

The ecophysiology of cottonwood adaptation to riparian zones is now fairly well understood. There are some notable knowledge gaps, such as the flow requirements for clonal recruitment (Rood et al. 1994, Gom and Rood 1999, Barsoum 2001). An understanding of seedling (sexual) reproduction and cot-

Water management strategies involving flow regulation downstream of dams can be of widespread benefit for riparian cottonwoods (Stanford et al. 1996, Poff et al. 1997, Mahoney and Rood 1998, Rood et al. 1998, Richter and Richter 2000, Hughes and Rood 2001, Stromberg 2001). Localized benefits can also be derived from supplemental water through irrigation or other treatments (Friedman et al. 1995, Molles et al. 1998, Sprenger et al. 2002). Knowledge of cottonwood water relations is also relevant to applications intended to restrict cottonwood expansion, which can also follow river regulation (Johnson 1997, 2000), or to influence competition between cottonwoods and other plants, particularly invasive weeds (Shafroth et al. 1994, Stromberg 1997, Gladwin and Roelle 1998, Sher et al. 2002).

Several recent studies have demonstrated historic correlations between cottonwood status and stream flow. Pulses of cottonwood reproduction have accompanied years with high flow or appropriate flow patterns (Scott et al. 1996, Poff et al. 1997, Mahoney and Rood 1998, Rood et al. 1998, Richter and Richter 2000, Hughes and Rood 2001, Stromberg 2001). Localized benefits can also be derived from supplemental water through irrigation or other treatments (Friedman et al. 1995, Molles et al. 1998, Sprenger et al. 2002). Knowledge of cottonwood water relations is also relevant to applications intended to restrict cottonwood expansion, which can also follow river regulation (Johnson 1997, 2000), or to influence competition between cottonwoods and other plants, particularly invasive weeds (Shafroth et al. 1994, Stromberg 1997, Gladwin and Roelle 1998, Sher et al. 2002).

Several recent studies have demonstrated historic correlations between cottonwood status and stream flow. Pulses of cottonwood reproduction have accompanied years with high flow or appropriate flow patterns (Scott et al. 1996, 1997, Mahoney and Rood 1998, Rood et al. 1999). The next step in cottonwood restoration is just commencing with the alteration of river regulation patterns. Hughes and Rood (2003) recently reviewed strategies for the restoration of floodplain woodlands, including two recent case studies documenting favorable cottonwood responses to deliberate changes in stream flow regulation.

In one case study, chronic dewatering of the lower St. Mary River in southern Alberta during the irrigation season led to the loss of more than 90% of the riparian black and narrowleaf cottonwoods ($P.\ trichocarpa$ and $P.\ angustifolia$) over the half-century following the 1951 completion of the St. Mary Dam (Rood and Mahoney 1995). Although flooding persisted downstream from that dam, flood flows were followed by abrupt flow decline that prevented successful cottonwood recruitment. In 1995, a natural flood flow occurred and the St. Mary Dam was managed to provide a relatively natural stage recession rate of 4 cm day$^{-1}$ (Rood and Mahoney 2000). Substantial cottonwood seedling establishment resulted, in contrast to the lack of recruitment following the previous flood years of 1964 and 1975.

The lower Truckee River in the high desert of western Nevada provides an even more dramatic case study (Rood et al. 2003). This river was progressively dammed and dewatered, leading to the collapse of the aquatic and riparian ecosystems. Increased instream flows commenced in the early 1980s as part of a program to restore an endangered endemic fish, the cui-ui sucker ($Chasmistes\ cujus$). The collateral recruitment of Fremont cottonwoods ($P.\ fremontii$) as well as sandbar and other willows followed during 2 years in which the river stage gradually receded at about 2.5 cm day$^{-1}$ following the period of seed release. The new cottonwoods continue to grow and are reestablishing habitat for birds and other wildlife that had been lost over the twentieth century.

**Conclusion**

Throughout the 1980s, several studies revealed the collapse of riparian cottonwood forests downstream from dams in western North America (Rood and Mahoney 1990). Investigations throughout the 1990s have partially clarified the ecophysiological dependency of riparian cottonwoods on stream flow and revealed aspects of the morphological and physiological adaptation of cottonwoods and willows to riparian floodplains.
Continuing studies throughout the late 1990s and into the new century have extended this research and attempted to integrate physiological studies with water management case studies. Commencing in the late 1990s, studies have reported successful applications of deliberate river regulation to satisfy the ecological and physiological needs of cottonwoods and thus effect the restoration of riparian cottonwoods. There have been considerable advances in the understanding of cottonwood ecophysiology and the continuing increase in this knowledge base should improve future prospects for cottonwood conservation and restoration.

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