RIPARIAN TREE RESPONSE TO VARIATION IN CLIMATE AND ALTERED STREAMFLOW ALONG THE DOLORES RIVER, COLORADO

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ABSTRACT

RIPARIAN TREE RESPONSE TO VARIATION IN CLIMATE AND ALTERED STREAMFLOW ALONG THE DOLORES RIVER, COLORADO

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This study investigated the recruitment and growth of three riparian tree species (*Populus angustifolia*, *Populus deltoides* subsp. *wislizenii*, and *Acer negundo*) in response to variation in streamflow and climate at multiple reaches at the unregulated Upper Dolores and San Miguel Rivers and the canal diverted (pre-dam) and dam regulated (post-dam) Lower Dolores River. We used a dendrochronological approach to determine tree age and develop standardized growth indices during the time period of 1961 through 2008. We developed 20 climate and streamflow variables to test hypotheses about relationships between establishment and growth of native riparian trees. Our results show that stream diversion through irrigation canals during the pre-dam period (1961-1984) reduced mean flow during the summer months of July through September, while river damming (1985-2008) reduced flows the most in May and June. Compared to the unregulated rivers, we observed an apparent lack of recruitment along the Lower Dolores River for *P. angustifolia* during the post-dam period at Reaches 1 and 3 and for *P. deltoides* subsp. *wislizenii* during the pre-dam period at Reach 6. The establishment of *P. angustifolia* at three reaches along the Dolores River was consistently associated with winter mean temperature and not streamflow, suggesting that the lack of recruitment during the post-dam period at Reaches 1 and 3 was not due to river damming. In contrast, the establishment of *P. deltoides* subsp. *wislizenii* was positively correlated with summer minimum flow along the Lower Dolores River. These results suggest that diversion of water through irrigation canals can have an equal, or greater, impact than damming on the regeneration of riparian tree species due to reductions in summer base flows. Furthermore, spring maximum flow was weakly associated with the establishment of *Populus* spp. along the Dolores and San Miguel Rivers, but more strongly related to *A. negundo* establishment. Overall, the establishment of *A. negundo* was associated with higher streamflow for both spring and summer seasons and negatively associated with higher temperatures for all seasons. For *P. angustifolia*, growth was most strongly associated with spring mean flow during the pre-dam period at Reaches 1 and 3 of the Dolores River and at the Canyon Preserve of the San Miguel River. In contrast, growth of *P. angustifolia* was most strongly associated with summer mean flow during the post-dam period at Reaches 1 and 3. Growth of *P. deltoides* subsp. *wislizenii* was rarely correlated with seasonal streamflow, while correlations were strongest for *A. negundo*. The growth of *A. negundo* was correlated with spring and summer mean flows along the Lower Dolores River for both pre- and post-dam periods at Reaches 3 and 4, as well as winter mean flow during the post-dam period at Reach 4. Palmer Drought Severity Index was strongly correlated with the growth of *Populus* spp. under canal diverted and regulated flows. In contrast, we observed no correlations between Palmer Drought Severity Index and the growth of *Populus* spp. at unregulated comparison sites. This result suggests that river regulation and water diversion through irrigation canals increased the sensitivity of tree growth to drought.

We recommend that releases into the Dolores River from McPhee Dam maintain seasonal variation in streamflow and that summer base flows are maintained at or above the long-term average in order to sustain regeneration of *P. deltoides* subsp. *wislizenii*. We also recommend higher streamflow releases from McPhee Dam during the spring and summer seasons if managers want to bolster the recruitment of *A. negundo*.

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PREFACE

My thesis contains an introduction (Chapter 1), literature review (Chapter 2), one manuscript chapter (Chapter 3), and management implications (Chapter 4). Chapter 3 is written in manuscript format so that it may be submitted for publication in a scientific journal. Literature cited is placed at the end of each chapter. Please excuse any redundancy among chapters due to the manuscript format.

Chapter 1

Introduction

Following the large increase of dams constructed along rivers in the western U.S. from the 1950s through the 1970s, numerous investigations relating riparian forest conditions to alterations in streamflow have provided land and water managers with a rich source of information. An understanding of the effects of river damming on establishment and growth of native riparian trees is important for land and water managers, particularly in the western United States where river damming has the potential to greatly impact the downstream hydrology of rivers. Chapter 2 provides a comprehensive literature review of hydrologic, geomorphic, and native riparian tree studies of impacts of damming in the western United States. This chapter was intended to synthesize the influences of climate and river regulation on the hydrology of rivers, impacts of river regulation on geomorphology, streamflow requirements for establishment of native riparian trees, riparian tree water sources, and tree physiological response to flooding.

Chapter 3 specifically addresses the following objectives: (1) compare the effects of stream diversion via irrigation canals and flow regulation via the construction of McPhee Dam on the downstream hydrology of the Lower Dolores River, Colorado; (2) compare the number of establishment years of native riparian trees (*P. angustifolia*, *P. deltoides* subsp. *wislizenii*, and *A. negundo*) between regulated and unregulated rivers; (3) determine whether tree establishment was related to streamflow and climatic variables; and (4) examine the relationship between tree growth and streamflow and climate variables. Chapter 3 provides information on the number of establishment events along the unregulated Upper Dolores and San Miguel Rivers, the water-diverted Lower Dolores River during the pre-dam period (1961-1984), and the regulated Lower Dolores River during the post-dam period (1985-2008). Logistic regression models were developed to explore factors associated with native tree establishment. Furthermore, linear regression models developed for native tree growth provided information about tree growth response to climate and altered streamflow.

Finally, Chapter 4 offers general streamflow recommendations for water and land managers who want to increase the number of establishment events and sustain appropriate growth for the native riparian trees, *P. angustifolia*, *P. deltoides* subsp. *wislizenii*, and *A. negundo*, along the Dolores River.

Chapter 2

Literature Review

Natural Streamflow of Perennial Rivers in the Western U.S.

Seasonal Variation of Streamflow by Region

The source of water for streams in the western U.S. is precipitation, which can vary in magnitude and timing among regions (Cayan and Peterson, 1989). The timing of precipitation influences the predictability and variability of stream hydrology, resulting in regional differences among streams based on hydrological characteristics (Poff, 1996). For example, many rivers in the Rocky Mountain Region receive large inputs of water from snowmelt with a concurrent increase in late spring to early summer temperatures at mid to high elevations, providing higher flows at lower elevations, while streamflow during the remainder of the season is more stable at low flows. Thus, the highly predictable seasonal flow patterns in the Rocky Mountain Region are largely controlled by precipitation, primarily falling as snow during the winter season. The predictability of streamflow is also high along the coastal region where the timing of maximum precipitation is in the early winter (Cayan and Peterson, 1989; Poff, 1996). In contrast, streamflow in the Southwestern U.S. is more variable and unpredictable with flood pulses occurring throughout the winter and late-summer seasons (Poff, 1996; Stromberg, 2001).

Effect of Climate on Streamflow

In the western United States, winter snowpack is a major influence on streamflow, which has been associated with winter atmospheric circulation patterns and the Southern

Oscillation in the southeast Pacific Ocean. The Pacific/North American (PNA) pattern typically displays a low pressure system over the North Pacific Ocean and high pressures over the Pacific Northwest that diverts severe winter storms northward (Cayan, 1996). Thus, for most regions, snow water equivalent (SWE) anomalies have been negatively associated with the PNA pattern (Cayan, 1996).

In contrast, years of above average SWE and subsequent above average streamflow occur when a low pressure system occupies an area within the vicinity of the region; however, this climate pattern associated with greater SWE is more variable compared to the PNA pattern that produces less SWE (Cayan, 1996). Along the coastal region from Alaska to southern California, above average streamflow conditions are associated with low pressure systems that develop in the north Pacific during the winter months and are dependent upon the relative location of the high pressure system in the Pacific Ocean (Cayan and Peterson, 1989; McCabe, 1996). In contrast, streams further inland (Interior Alaska, Utah, Montana) generally experience greater flows when high pressure systems develop over the central North Pacific, except for streams in the Southwest where the response is similar to the coastal region (Cayan and Peterson, 1989).

The El Niño/Southern Oscillation that is associated with warming surface waters of the Eastern Pacific Ocean also influences precipitation and streamflow differently for regions of the western U.S (Kahya and Dracup, 1993; Dracup and Kahya, 1994). In general, during El Niño years (negative SOI values), days with above average precipitation and streamflow are more frequent throughout the Southwest, and less frequent in the Northwest (Cayan et al., 1999). More specifically, El Niño enhances precipitation in Arizona and western New Mexico through the spring (March-May) and in the fall (September-November), while the Great Basin Desert receives above average precipitation through the months of April-October. (Ropelewski and Halpert, 1986; Andrade and Sellers, 1988). In the Northwest, La Niña enhances streamflow from October to August of the subsequent year (Dracup and Kahya, 1994).

Alterations of Streamflow by Regulation

Within the past century, the number of large-structure dams in the U.S. has increased, particularly in the 1960s, while the greatest increase in total reservoir storage capacity occurred from the 1950s to the 1980s (Graf, 1999). While the greatest density of dams occur in eastern and southeastern states, the ratio of reservoir storage to runoff is greatest in the Great Plains, Rocky Mountain, and Southwest regions (Graf, 1999; Graf 2006). Extreme cases of this exist in the Rio Grande and Upper Colorado River Basins where dams are capable of storing 3.8 and 3.0 times the mean annual run-off, respectively, which is an order of magnitude greater than river basins in the Mid-Atlantic and New England regions, where storage capacity ranges from 25-26% of mean annual flow (Graf, 1999). As a result, dams in western regions have a greater potential to impact downstream hydrology (Williams and Wolman, 1984; Poff et al., 1997; Graf, 2006).

The primary operational purposes of dams, such as irrigation supply, flood control, hydropower, and municipal, varies by region; however, river damming appears to have similar effects on downstream hydrology for numerous rivers across the Great Plains, Rocky Mountain, and Southwest Regions (Poff and Hart, 2002; Graf, 2006). Variation in streamflow under regulated flows has declined relative to the highly variable pre-dam flow conditions that were characterized by pulses of high flows during snowmelt or winter precipitation events. Prolonged releases from short-term storage reservoirs during the summer season have generally increased base flows. The combination of attenuated spring flows and increased base flows has contributed to regional homogenization of river flow (Poff et al., 2007).

Two common effects of river regulation on downstream flow regimes include a reduction in high spring flows and an increase in summer base flows (Fenner et al., 1985; Rood and Mahoney, 1995; Shafroth et al., 2002; Poff et al., 2007). For example, the reduction in mean annual peak flow after the onset of river regulation for five rivers in the Upper Colorado River Basin ranged from 24-54%, while reduction during the same time periods ranged from 0-10% for two nearby unregulated rivers (DeWine and Cooper, 2007). Similar to these findings, Williams and Wolman (1984) reported an average reduction of 39% in mean annual peak flow for 29 regulated rivers in the western and Great Plains regions; however, reductions of mean annual peak flow were highly variable among rivers, ranging from 3 to 91%. Summer base flows have been reported to increase 200 to 300% of pre-dam values (Cooper et al., 2003; Braatne et al., 2007). Despite large decreases in maximum annual flow, a few rivers have not experienced any changes in annual average flow after regulation, in large part due to increases in base flow and reductions in peak flows as a result of river regulation (Rood and Mahoney, 1995; Dykaar and Wigington, Jr., 2000; Grams and Schmidt, 2002).

Impacts of River Regulation on Geomorphology

Sediment Transport

One major impact of dams on sediment transport is alteration of sediment trapping (Williams and Wolman, 1984). The lack of suspended sediment is greatest in reaches just below the dam, and river sediment load generally increases as distance from the dam increases, as a result of local tributaries providing sediment to the river (Williams and Wolman, 1984; Andrews, 1986; Rood and Mahoney, 1995). Thus, the majority of sediment provided to the floodplain of regulated rivers is a result of erosive processes within the floodplain and local tributaries entering the channel downstream of the dam. As sediment becomes displaced from the river, additional downcutting of the river bed lowers the bed elevation, a phenomenon known as degradation. The length of the degradation zone downstream from dams generally increases through time, and can range from 4-120 km, depending on flow releases, bed-material sizes, and topography (Williams and Wolman, 1984). As sediment sources become increasingly depleted, the rate of degradation decreases as sediment capable of being eroded is diminished and larger rocks that become exposed through degradation act as a shield against further erosion. Since reservoirs are effective sediment traps, material for bar formation is reduced under regulated flows. In a national study of geomorphic effects of large dams, Graf (2006) found that low and high bars were 68 and 52% less frequent, respectively, in regulated reaches compared to unregulated reaches.

River Channel Process and Form

In addition to the sediment transport regime, alterations in flow regime and dominant geomorphic processes as a result of river regulation can disrupt natural processes involved in the structuring of floodplain topology (Church, 2002; Grams and Schmidt, 2002). In the interior western U.S., altered flow regimes through river regulation, such as attenuated peak flows, have resulted in a large reduction of geomorphic complexity and active floodplain area, more commonly referred to as channel narrowing (Grams and Schmidt, 2002; Shafroth et al., 2002; Graf, 2006). The reduction of the active floodplain reduces the area of the active channel which includes functional surfaces such as lateral, point, and mid-channel bars and islands. In the interior western U.S., geomorphic complexity, or total number of functional surfaces associated with the reach per unit length of reach, has declined (Graf, 2006). In extreme cases, total bar and island area decreased by as much as 80% as a result of river damming in combination with bank stabilization through boulder revetments, logging, and gravel mining (Dykaar and Wigington, Jr., 2000).

Channel narrowing can occur due to a number of reasons. Along the Green River, Grams and Schmidt (2002) found that channel narrowing, as a result of river regulation, occurred throughout a diverse assemblage of reach types, and in all channel types, channel narrowing was attributed to vertical aggradation of depositional surfaces that formed after the onset of river regulation. However, Grams and Schmidt (2002) observed distinct differences in channel narrowing between canyon and meandering reaches. In the canyon reaches, active, mid-channel gravel bars composed of bed load sediment were transformed to aggrading islands of fine-grained suspended sediment, which did not exist during the pre-dam period but were more common under regulated flows. In the meandering reaches, vertical aggradation occurred at low to intermediate elevation benches, which are adjacent to higher elevation benches that formed prior to river regulation and are rarely inundated. Allred and Schmidt (1999) also observed channel narrowing as a result of vertical aggradation of low to intermediate benches along the active channel, and provided further evidence that channel narrowing occurs through continual inundation of bars and subsequent deposition of the bar. Furthermore, they found that channel bars increased in elevation through vertical accretion to the point that they could no longer be inundated, disconnecting bars from the active channel and subsequently narrowing the channel.

In both studies (Allred and Schmidt, 1999; Grams and Schmidt, 2002), geomorphic processes involved in channel narrowing were primarily attributed to the reduction in flood magnitude and power as a result of river regulation except for meandering reaches where significant changes in flood power did not occur. Shafroth et al. (2002) found that flood power, intermittency, and summer flow explained 57% of the variation in stream channel width, and flood power and intermittency were positively correlated and summer flow was negatively correlated with stream channel width. During regulated flows and periods when channel width did not change, summer flows were extremely low, which suggests that low base flows may also play a role in preventing channel narrowing.

Along the Green River, Merritt and Cooper (2000) describe a complex series of morphologic changes that occurred following regulation, where channel adjustment corresponded with changes in vegetation. Initially following regulation, channel narrowing occurred as reductions in flow magnitude facilitated establishment of vegetation along surfaces that were once active during the pre-dam period (Merritt and Cooper, 2000). More recently, bars formed from sediment generated by bank erosion became stabilized through vegetation colonization, leading to the development of fluvial marshes within the channel as islands and channel margins. The formation of fluvial marshes has been attributed to the lack of high, scouring flows that remove sediment accumulation in the channel. Finally, in combination with lateral degradation through bank erosion, the islands and multiple flow paths through reaches deflect flow toward high banks resulting in continued bank erosion and fluvial marsh development (Merritt and Cooper, 2000). Similar to these findings, Stevens et al. (1995) observed a wide-spread increase in marsh development in the Grand Canyon, Arizona, which was attributed to the reduction in flooding associated with the construction of Glen Canyon Dam. In both studies, fluvial marshes were characterized as patches of wetland vegetation such as *Typha domingensis*, *Phragmites australis*, *Juncus* spp., *Salix* spp., and *Eleocharis* spp. Similar to the pioneer tree species, *Populus fremontii* and *Populus deltoides*, these wetland obligate species may also serve as indicator species of fluvial adjustments that have occurred since the onset of river regulation.

Establishment of Native Riparian Trees

Mechanisms of Establishment

Establishment of native riparian trees can occur through either seedling recruitment or clonal reproduction which includes branch propagation following stem breakage, shoot regrowth of toppled saplings (flood training) as a result of flooding, coppice regrowth of main stems after decapitation due to herbivory or ice-scouring, rooting of excised shoot fragments (cladoptosis), and root suckering. Riparian trees in the genus *Populus* can regenerate through all of these mechanisms (Rood et al., 1994; Rood et al., 2003). Clonal reproduction through root and stump sprouts is also common for *Acer negundo*, particularly for young, vigorous trees (USDA Forest Service, 1990).

In an extensive study along four rivers in southern Alberta, Rood et al. (1994) found that 52% of excavated saplings originated as seedlings while 30 and 18% of *Populus* saplings originated through clonal mechanisms of root and shoot suckering, respectively. Root suckering was restricted to species in the Tacamahaca section of *Populus* such as balsam poplar (*Populus balsamifera*), narrowleaf cottonwood (*Populus angustifolia*), and interspecific hybrids (Baker, 1990; Rood et al., 1994; Gom and Rood, 1999). For *Populus deltoides*, clonal reproduction accounted for 72% of stems in southern Alberta, which was generally restricted to flood training. Through exacavation of branch fragments, Rood et al. (2003) found that the role of branch propagation after physical disturbances such as flooding and ice-scouring that topples saplings, subsequently shearing branches, plays a major role in facilitating clonal reproduction of *Populus* species in the Tacamahaca section, while cladoptosis was a rare occurrence. However, for *Populus deltoides* and *Populus fremontii* in the Aigeiros section, reproduction through sheared branches during flooding or ice-scouring was a rare occurrence.

With respect to seedling recruitment of native riparian trees, *Populus* species in the Aigeiros section, such as *Populus fremontii* and *Populus deltoides*, have received a lot of investigation. The process of seedling recruitment begins when seed dispersal occurs throughout the spring to early summer, which generally coincides with high streamflow, and large quantities of seeds are wind or water-dispersed throughout the floodplain resulting in large numbers of germinants (Fenner et al., 1985; Stella et al., 2006). In order for germination to occur, *Populus* seeds require bare, moist mineral soil (Stromberg, 1993; Stromberg, 1997; Cooper et al., 1999). In contrast, *Acer negundo* seed dispersal begins in the fall, where seeds are wind-dispersed until spring; germination occurs in spring in a variety of sites (USDA Forest Service, 1990).

Flow Requirements

In the two years following germination, mortality of seedlings ranges from about 96-100% due to desiccation or soil erosion. The topographic elevation of seedling germination and flow conditions is important in maintaining appropriate soil moisture to sustain growth or prevent scour of seedlings (McBride and Strahan, 1984; Stromberg, 1997; Cooper et al., 1999; Mahoney and Rood, 1998; Polzin and Rood, 2006). After reviewing a number of studies along western U.S. Rivers, Mahoney and Rood (1998) proposed that seedling germination 0.6 to 2 meters in elevation above base flow, along with an appropriate decline in stream flow, allows for seedling roots to maintain contact with the receding zone of moisture and subsequent survival through the first season. Seedlings that germinate at elevations below this range are susceptible to mortality through deposition, scour, or inundation while seedlings that germinate above this range are susceptible to dessication (Mahoney and Rood, 1998; Polzin and Rood, 2006).

Similar to these findings, Cooper et al. (1999) found that seedlings germinating at relatively low positions along the Yampa River were scoured by subsequent spring flooding, and the surviving seedlings were restricted to an elevation of 1.25 to 2.5 m above base flow. However, through isotopic analysis and excavation of seedlings in experimental plots, Cooper et al. (1999) showed that seedlings did not become phreatophytic until their third or fourth growing season, and drought induced mortality occurred for seedlings despite the relative elevation to base flow. In addition to factors such as a relatively high river stage during seed dispersal and precipitation following germination as a means of providing soil moisture, fine-textured sediment was found to be an important factor in allowing seedlings to survive at high elevations along the Yampa River, due to a greater water holding capacity (Cooper et al., 1999).

Throughout many regions of the western U.S., major flooding events have been associated with the establishment of *Populus* either during the year of the flood or years following flooding (Baker, 1990; Scott et al., 1997; Cooper et al., 2003; Polzin and Rood, 2006). In one extreme case, continual *Populus* recruitment lasting up to two decades was attributed to major flooding that occurred in 1935 and 1965 along ephemeral streams on the Colorado Piedmont (Friedman and Lee, 2002). Region-wide pulses of native tree regeneration after major floods have been reported in the Southwest. For example, regional river flooding in the winter and spring of 1993 and spring of 1995 yielded a pulse of recruitment events for *Alnus*, *Fraxinus*, *Platanus*, *Populus*, and *Salix* along West Clear Creek, Arizona (Galuszka and Kolb, 2002), for *Populus* and *Salix* along the Hassayampa River, Arizona (Stromberg, 1997), for *Populus* and *Salix* along the Verde River, Arizona (Beauchamp and Stromberg, 2007), and for *Populus* along canyon reaches of the Yampa River, Colorado (Cooper et al., 2003). While little regeneration occurred for *Acer negundo* along West Clear Creek, Arizona, following the 1993 flood (Galuszka and Kolb, 2002), establishment of *Acer negundo* was correlated with unusually high peak flows, including the 1993 flood, along four major rivers of the upper Colorado River Basin (DeWine and Cooper, 2007).

The association of native tree regeneration with annual peak flows has mainly been attributed to the role of high flows in scouring established vegetation and depositing sediment that provide extensive nursery sites at relatively high elevations, subsequently allowing seedlings to survive through winter ice jams or high flows following germination (Scott et al., 1997; Stromberg, 1997; Polzin and Rood, 2006). Along ephemeral streams in eastern Colorado, regeneration of *Populus* was associated with extended periods of channel narrowing following intense flooding, allowing for pioneer species such as *Populus* to colonize former channel beds (Friedman and Lee, 2002).

Establishment of *Populus* has also been positively associated with channel narrowing along the Bill Williams, North Platte, South Platte, and Platte Rivers. However, reductions in flow due to river regulation were the primary cause of channel narrowing (Johnson, 1994; Shafroth et al., 2002). Along the regulated Bill Williams River in the Southwest, reductions in flow magnitude exposed portions of the riverbed further facilitating establishment of *Populus* in former active channels (Shafroth et al. 2002). Shafroth et al. (2002) suggested that seedling survival rates were higher during the post-dam period due to increased summer average flows and lack of subsequent high flows that were common during the pre-dam monsoon seasons. Similarly, Johnson (1994) reported reduced flow magnitude along the regulated North Platte, South Platte and Platte Rivers, which exposed much of the riverbed, particularly in the month of June.

Johnson (1994) suggested that *Populus* seed dispersal in combination with low flows during June allowed extensive seedling colonization of exposed portions of the riverbed.

Limitations to Establishment

Despite the few cases where flow alteration through river regulation has facilitated establishment of native riparian trees, flow regulation has been reported as a major limitation to native tree regeneration along numerous rivers of the western U.S (Rood and Mahoney, 1990). In addition to the trapping of sediment, reduction of flow magnitude and frequency through river regulation can alter the meander rate, meander migration, and amount of scouring and deposition occurring in the floodplain, subsequently reducing the potential for recruitment of *Populus* (Johnson et al., 1976; Bradley and Smith, 1986; Howe and Knopf, 1991). The reduction of flooding also permits encroachment of grasses, sedges, and shrubs at the river's edge blocking potential sites for *Populus* seedlings (Rood and Mahoney, 1995).

One of the most extensively studied rivers in the western U.S., the regulated Green River, has experienced major shifts in geomorphic characteristics that restrict *Populus* germination to islands and cut banks, unlike the unregulated Yampa River where germinants were found to inhabit vertically accreting bars and backwaters with fine-texture soils (Cooper et al., 1999). Cooper et al. (1999) further suggests that these topographic locations along the regulated Green River could not sustain long-term survival of *Populus* germinants due to long periods of inundation on islands and instability of soil along cut banks. Through a dendrochronological approach of estimating tree age, Cooper et al. (2003) found that *Populus* establishment was primarily linked to flow releases that reached or exceeded power plant capacity of the dam operations. In contrast, *Populus* establishment along the nearby, unregulated Yampa River occurred every year from 1974 to 1994. During this time, *Populus* established on both bare and vegetated vertically accreting bars and within vertically accreting intermittent channels, both under a wide range of flow magnitudes, as well as high floodplain surfaces during intense flooding events (Cooper et al., 2003). Thus, the number of *Populus* recruitment events along the unregulated Yampa River greatly exceeded those along the regulated Green River where the ongoing geomorphic adjustment of the channel, combined with reduced flow variability, has nearly eliminated *Populus* establishment.

At a broader spatial scale across numerous rivers, the effects of river regulation on native tree establishment become more apparent. Across eight ecoregional provinces of the Southwest, Merritt and Poff (2010) reported a reduction in the probability, abundance, and dominance of *Populus* recruitment with increasing flow modification at 13 perennial rivers that varied in flow alteration, which corroborates studies that utilized data collected from only one regulated river. A similar approach was used by DeWine and Cooper (2007) where *Acer negundo* trees were studied to determine the effects of river regulation on establishment along six rivers of the Upper Colorado River Basin. In this region, the areal extent of post-regulation *Acer negundo* cohorts was significantly less than cohorts that established during the pre-regulation period and recent cohorts that established along an unregulated river (DeWine and Cooper, 2007). While establishment occurred at lower topographic positions along regulated reaches relative to elevations along unregulated reaches, establishment of *A. negundo* was positively correlated with high peak flows.

The long-held notion that cattle grazing limits the establishment of *Populus* is partially supported in the literature. Samuelson and Rood (2004) found that cattle grazing can affect the age structure of *P. trichocarpa* by reducing the frequency of recruitment pulses. Compared to grazed plots, density was greater for seedlings, saplings and mature trees in the ungrazed plots, however, differences in density were significant for sapling and trees and not for seedlings. Auble and Scott (1998) also found that ungrazed exclosures had higher overall *P. deltoides* seedling density. Further evidence of grazing pressures on *Populus* species have been reported by numerous researchers based on informal observations (Brotherson et al., 1983; Rucks, 1984; Shanfield, 1984). These observations included noticeable regeneration in areas where cattle grazing was low, or a lack of recruitment in areas of heavy cattle grazing.

In contrast to these studies, Green and Kauffman (1995) found that the only woody species included in their study, *Populus trichocarpa*, failed to show a significant increase in stem density over a ten year period of cattle exclusion at Catherine Creek in Northeastern Oregon. Furthermore, a few researchers have speculated that mortality through high flows is similar to or outweighs pressures of grazing, and that grazing may have a larger effect on recruitment in years where seedling establishment occurs during years of high flows (Szaro and Pase, 1983; Auble and Scott, 1998). Mortality through subsequent flooding events would likely diminish after a year of high flow, thereby increasing seedling susceptibility to grazing.

Riparian Tree Growth Response to Variation in Flow and Climate Factors

Riparian Tree Water Sources

Stream and groundwater are an important source of water for native riparian trees along western rivers and streams; however, the importance of stream water as a source can vary among streams. In some cases, riparian trees have exemplified phreatophytic behavior where groundwater in alluvial aquifers was the primary source with little to no variation in the source of water (Busch et al., 1992; Horton et al., 2003). In other cases, water in surface unsaturated soils supplied directly from precipitation can serve as important water sources (Kolb et al., 1997; Snyder and Williams, 2000).

Water source for riparian trees can vary by site, species, season, tree size, or a combination of these factors. For example, Snyder and Williams (2000) observed differences among three species across a gradient of ground water depth and by season. Throughout the entire growing season, *Salix goodingii* primarily utilized groundwater despite fluctuations in the depth to groundwater across three sites, while *Populus fremontii* utilized 26 to 33% of its water from upper soil layers at ephemeral reaches and 8-16% at perennial reaches during the monsoon season along the San Pedro, Arizona. Thus, for *Populus fremontii*, the percent of shallow soil water used increased as the depth to groundwater increased. Seasonal shifts in water use among soil, stream, and groundwater were also observed along Bishop Creek, California, where the hydrogen isotope ratio increased through the months of May to September for three riparian tree species (Smith et al., 1991). Kolb et al. (1997) reported seasonal shifts in water sources between tree sizes for *Acer negundo*. Large *Acer negundo* trees along a perennial reach of Oak Creek Arizona, primarily used groundwater until the fall when shallow soil water derived from precipitation accounted for up to 20% of water uptake, while small trees used a higher proportion of shallow soil water in both early summer and fall.

Water sources can vary among trees of different sizes (Dawson and Ehleringer, 1991; Philips and Ehleringer, 1994). Dawson and Ehleringer (1991) found that hydrogen isotope ratio was significantly different among small and large diameter *Acer negundo* and *Acer grandidentatum* trees. They suggested that smaller trees utilized water from an adjacent stream while larger trees utilized a more reliable water source, such as deep subsurface flows. Thus, large diameter trees were not directly responsive to precipitation. This finding was confirmed by another study at the same study site where xylem water from larger trees contained zero per cent of precipitation, while xylem water from smaller trees contained 19% precipitation (Philips and Ehleringer, 1994).

There is evidence of corresponding physiological responses to adjustments in water source in cases where precipitation provides a substantial water source. Snyder and Williams (2000) observed a positive significant relationship between predawn water potential and oxygen isotope ratios for *Populus fremontii* and *Prosopis velutina* along the San Pedro River, Arizona. From these results, Snyder and Williams (2000) suggest that monsoon precipitation may reduce water stress for these species. In contrast, Kolb et al. (1997) reported little variation in predawn and mid-day water potential for *A. negundo* along Oak Creek, Arizona, despite changes in water sources.

Response to Climatic Factors

High vapor pressure deficit (VPD), the difference between atmospheric vapor pressure and saturated vapor pressure in the leaf mesophyll, is generally negatively correlated with leaf gas exchange measurements such as net photosynthetic rate and stomatal conductance (Smith et al., 1991; Kolb et al., 1997; Horton et al., 2001a). In the Southwest, VPD was found to be the most important factor limiting net photosynthesis and stomatal conductance for *Populus fremontii*, *Salix goodingii*, and *Acer negundo* (Kolb et al., 1997; Horton et al., 2001b). In eastern California, VPD appeared to have its largest effect for *Populus trichocarpa* during hot days of the summer along diverted reaches that received a low supply of water (Smith et al., 1991).

At a larger temporal scale, annual growth of native riparian species has been correlated with seasonal and annual temperature variables, and this relationship can vary among species, tree age, and site based on hydrologic characteristics (Stromberg and Patten, 1991; Stromberg, 2001; Galuszka and Kolb, 2002). At West Clear Creek, Arizona, tree growth response to temperature varied by site where temperature partially explained variation in growth for four of the five species studied along constrained reaches, while temperature was not a significant variable for any of the species along unconstrained reaches (Galuszka and Kolb, 2002). Within the bedrock-constrained reach, differences in climate response among species also occurred. For example, monsoon mean maximum temperatures were positively and negatively correlated with growth of *Alnus oblongifolia* and *Acer negundo*, respectively. At Sycamore Creek, Arizona, growth of younger *Platanus wrightii* trees was negatively correlated with annual temperature, while middle-age trees were not responsive to temperature (Stromberg, 2001). An interesting case for differences in response to temperature occurred for *Populus* stands growing along regulated and unregulated reaches of the Missouri River, North Dakota. Prior to river regulation, streamflow and precipitation parameters were positively correlated with annual patterns of growth followed by a shift in response following the onset of river regulation, where growth was correlated with temperature and evapotranspiration rates (Reily and Johnson, 1982). Thus, sensitivity to temperature can vary among riparian trees based on geomorphic constraints, species, tree age, and alterations in streamflow.

Response to Flooding

Since the water source for riparian trees has been associated with stream water, tree growth has also been associated with surface flow (Stromberg and Patten, 1991; Stromberg and Patten, 1996; Willms et al., 1998). Depending on the species, growth has been negatively and positively correlated with streamflow measures that were related to specific flooding events such as annual and seasonal maximum flows. For example, within the same reach, annual radial growth of *Acer negundo* and *Platanus wrightii* was negatively correlated with maximum summer and spring surface flow, respectively, while growth of *Fraxinus velutina* was positively correlated with maximum spring surface flow (Galuszka and Kolb, 2002).

Another approach to identifying important streamflow variables, used by Stromberg (2001), involves the number of flooding events in a given year or season, referred to as flood frequency, which, compared to other regions of the U.S., may be more useful in arid environments where flooding events provide most of the annual surface flows and are capable of occurring numerous times within a year. Flood frequency was found to explain most of the variation in mean annual radial growth of young *Platanus wrightii* cohorts, particularly along summer-dry and intermittent reaches where growth increased as flood frequency increased (Stromberg, 2001).

Since flooding in the western U.S. can potentially provide a substantial contribution to seasonal and annual surface flows, a close association of flood frequency and annual maximum flows can exist between annual average flows (Johnson, 1994; Stromberg, 2001). Under natural flows, annual average flows are indicative of high surface flows that have occurred during a brief portion of the hydrologic year. However, due to flooding attenuation of regulated and water-diverted rivers, the close relationship between annual maximum flows and annual average flows could potentially become decoupled as a result of river regulation. Thus, correlative relationships between tree growth and mean annual flow may vary among regulated and unregulated rivers. For example, Stromberg and Patten (1990) found that mean annual flow was positively correlated with annual radial growth of *Populus trichocarpa* during both prediversion and diversion periods at Rush Creek, California. However, further investigation of the relationship between growth and seasonal flow parameters revealed an interesting finding. During the pre-diversion period, growth was only correlated with flow conditions during the spring season (April through June), which coincided with months that maintained high flows. In contrast, growth during the diversion period was correlated with flow conditions for every month of the year and both seasons, spring and summer (July through September).

The shift in tree response to flow conditions has also occurred as a result of differences in geomorphic setting, as well as differences in stand basal area. Across nine streams in the eastern Sierra Nevada of California, flow-growth coefficients for *P.*

trichocarpa increased as valley floor width increased, which suggests that growth is more responsive to fluctuations in streamflow conditions in wide, unconfined valleys (Stromberg and Patten, 1996). In contrast, flow-growth coefficients were negatively correlated with stand basal area which suggests that competition from other trees potentially has a greater influence over growth, relative to flow conditions, in stands with a high density of trees.

Restoration of Native Riparian Forests

Restoration of native riparian forests generally includes specific approaches that promote the establishment of tree seedlings, particularly in degraded ecosystems along regulated rivers. From these approaches, tree planting, mechanical disturbance of the floodplain, removal of exotic plants, supplemental irrigation, and combinations of these methods have emerged as potentially successful strategies of promoting native tree establishment (Friedman et al., 1995; Briggs and Cornelius, 1998). A more holistic approach, such as restoring natural flow regimes during years of high flows, can also serve as a successful strategy in riparian tree restoration (Rood et al., 2005). Following the large flood of 1995 in southern Alberta, ramping flow releases from the Oldman and St. Mary dams were implemented, which facilitated the establishment of billions of cottonwood and willow seedlings (Rood et al., 2005).

The approach of restoring natural flow regimes was rooted in the broader concept of using reference conditions as a baseline for determining success of restoration efforts, where natural flow was considered a reference condition (Poff et al., 1997). Development of reference conditions to determine restoration success has been used in other ecosystems, such as southwestern ponderosa pine forests (Moore et al., 1999). The criteria for establishing baseline conditions generally included an understanding of key variables involved in natural disturbance regimes, forest structure and tree patterns prior to anthropogenic influences to the ecosystem (Moore et al., 1999). Similarly, success of restoration efforts in riparian forests in the western U.S. can be defined based on similar criteria; however, due to the relatively short life span of most riparian trees and external pressures such as logging and cattle grazing, it is difficult to understand pre-settlement conditions of western riparian forests. Thus, the question arises: What defines a naturally occurring riparian forest in the western U.S.?

This is an important question that could potentially structure our measure of success in restoring riparian forests. Historical accounts and photographs of forest conditions may be our best window into the past. For example, General Land Office (GLO) survey notes of the Platte River indicated that scattered woodlands occurred along the banks, islands were densely inhabited by riparian forests, and forests gradually declined moving upstream and westward from western Nebraska into Colorado (Johnson, 1994; Johnson, 2000). In contrast, Webb and Leake (2000) present a strong case through the use of repeat photography that spans 140 years that riparian woody vegetation, native and non-native, has increased on many regulated rivers of the Southwest. Due to the uncertainty of natural conditions of riparian forests, we currently rely on unregulated rivers as a reference condition for regulated rivers (Rood and Mahoney, 1995; Cooper et al., 1999; Merritt and Cooper, 2000). Thus, the importance of conserving the few remaining unregulated rivers in the western U.S. is equally as important as restoring the ecological functions of highly regulated rivers.

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Chapter 3

Riparian Tree Response to Variation in Climate and Altered Streamflow along the Dolores River, Colorado

Abstract

This study investigated the recruitment and growth of three riparian tree species (*Populus angustifolia*, *Populus deltoides* subsp. *wislizenii*, and *Acer negundo*) in response to variation in streamflow and climate at multiple reaches at the unregulated Upper Dolores and San Miguel Rivers and the canal diverted (pre-dam) and dam regulated (post-dam) Lower Dolores River. We used a dendrochronological approach to determine tree age and develop standardized growth indices during the time period of 1961 through 2008. We developed 20 climate and streamflow variables to test hypotheses about relationships between establishment and growth of native riparian trees. Our results show that water diversion through irrigation canals during the pre-dam period (1961-1984) reduced mean flow during the summer months of July through September, while river damming (1985-2008) reduced flows the most in May and June. Compared to the unregulated rivers, we observed an apparent lack of recruitment along the Lower Dolores River for *P. angustifolia* during the post-dam period at Reaches 1 and 3 and for *P. deltoides* subsp. *wislizenii* during the pre-dam period at Reach 6. The establishment of *P. angustifolia* at three reaches along the Dolores River was consistently associated with winter mean temperature and not streamflow, suggesting that the lack of recruitment during the post-dam period at Reaches 1 and 3 was not due to river damming. In contrast, the establishment of *P. deltoides* subsp. *wislizenii* was positively correlated with

summer minimum flow along the Lower Dolores River. These results suggest that diversion of water through irrigation canals can have an equal, or greater, impact than damming on the regeneration of riparian tree species due to reductions in summer base flows. Furthermore, spring maximum flow was weakly associated with the establishment of *Populus* spp. along the Dolores and San Miguel Rivers, but more strongly related to *A. negundo* establishment. Overall, the establishment of *A. negundo* was associated with higher streamflow for both spring and summer seasons and negatively associated with higher temperatures for all seasons. For *P. angustifolia*, growth was most strongly associated with spring mean flow during the pre-dam period at Reaches 1 and 3 of the Dolores River and at the Canyon Preserve of the San Miguel River. In contrast, growth of *P. angustifolia* was most strongly associated with summer mean flow during the post-dam period at Reaches 1 and 3. Growth of *P. deltoides* subsp. *wislizenii* was rarely correlated with seasonal streamflow, while correlations were strongest for *A. negundo*. The growth of *A. negundo* was correlated with spring and summer mean flow along the Lower Dolores River for both pre- and post-dam periods at Reaches 3 and 4, as well as winter mean flow during the post-dam period at Reach 4. Palmer Drought Severity Index was strongly correlated with the growth of *Populus* spp. under canal diverted and dam regulated flows. In contrast, we observed no correlations between Palmer Drought Severity Index and the growth of *Populus* spp. at unregulated comparison sites. This result suggests that river regulation and diversion through irrigation canals increased the sensitivity of tree growth to drought.

Introduction

In western North America, river damming threatens native riparian forests (Johnson et al., 1976). Studies of regulated rivers have shown that a lack of seedling recruitment, reduced forest abundance and areal extent, and reduced tree growth can often be attributed to river regulation (Reily and Johnson, 1982; Rood and Mahoney, 1990; Merritt and Cooper, 2000; DeWine and Cooper, 2007). More recently, the abundance and probability of native tree recruitment along western rivers have been shown to be negatively affected by flow modification (Merritt and Poff, 2010).

Due to the large ratio of reservoir storage to runoff, dams in the western regions of the U.S. have a greater potential to impact the downstream hydrology of rivers than dams in other regions (Graf, 1999; Graf, 2006). Natural flow conditions that were once characterized by high flows during snowmelt or winter precipitation events have been greatly altered as a result of river regulation (Poff et al., 1997). Despite regional differences of streamflow patterns of rivers and operational purposes of dams, river damming often has similar effects on downstream flows for numerous rivers across the western U.S. (Poff, 1996; Poff and Hart, 2002; Graf, 2006). River regulation has been associated with the reduction of maximum flow and increases in summer base flow (Fenner et al., 1985; Rood and Mahoney, 1995; Shafroth et al., 2002). The combination of these effects has resulted in reduced seasonal variation in streamflow and has contributed to regional homogenization of river flow (Poff et al., 2007).

Streamflow alteration can influence the survival of riparian tree seedlings for numerous reasons. First, germination of riparian trees in the genera *Populus* primarily occurs on bare, moist sediment, which is supplied and created by high flows that deposit soil and scour away vegetation (Stromberg, 1993). Attenuated flows, an outcome of river regulation, reduce the geomorphic complexity and active floodplain area, subsequently diminishing potential germination sites for pioneer riparian species such as *Populus fremontii* and *Populus deltoides* (Grams and Schmidt, 2002; Graf, 2006). Second, flow conditions during the time of seed dispersal dictate the topographic elevation of the germination site (Mahoney and Rood, 1998). Following germination, both the topographic elevation of seedlings and flow conditions are important factors in maintaining appropriate soil moisture to sustain growth or to prevent scour of seedlings (McBride and Strahan, 1984; Stromberg, 1997; Mahoney and Rood, 1998; Cooper et al., 1999; Polzin and Rood, 2006). During years of low flow, seeds deposited at low elevations may be susceptible to high flows or ice scour in subsequent months or years (Auble and Scott, 1998). Thus, high flows scour established vegetation and deposit sediment, and thus contribute to the creation of nursery sites at topographic elevations suitable for seedling survival (Scott et al., 1997; Stromberg, 1997; Galuszka and Kolb, 2002; Cooper et al., 2003).

A few studies, however, have shown that river regulation has no effect on tree recruitment and sapling density (Beauchamp and Stromberg, 2007), or can even facilitate recruitment (Johnson, 1994; Shafroth et al., 2002). Establishment of *Populus* has been associated with channel narrowing through reductions in peak flow. As the channel narrows, portions of the riverbed are exposed, further facilitating establishment in former active channels and increasing seedling survival due to availability of suitable habitat and lack of scouring flows (Johnson, 1994; Shafroth et al., 2002). Higher seedling survival under regulated flows has also been attributed to higher summer flows as a result of extended releases of stored water from reservoirs during the drier summer months (Shafroth et al., 2002).

Much attention has been focused on establishment of *Populus* spp. within the Aigeiros section, prairie cottonwood (*P. deltoides*) and Fremont cottonwood (*P. fremontii*), but less is known about establishment of the widespread riparian species, *Populus angustifolia* and *Acer negundo*, which can reproduce through seedling recruitment and clonal processes (USDA Forest Service, 1990; Rood et al., 1994). For *P. angustifolia*, climatic conditions such as cool and wet falls were important for recruitment (Baker, 1990), while recruitment of *A. negundo* has been found to be associated with unusually high peak flows of regulated rivers (DeWine and Cooper, 2007). In contrast, peak flow and recruitment of *A. negundo* were not associated along an unregulated stream in Arizona (Galuszka and Kolb, 2002).

Growth of western riparian trees has been both positively and negatively associated with streamflow, depending on the species (Stromberg and Patten, 1990; Stromberg and Patten, 1991; Galuszka and Kolb, 2002). In combination with streamflow, seasonal or annual variation in temperature has been associated with riparian tree growth. Sensitivity to temperature can vary among riparian trees based on reach geological characteristics, species, and tree age (Stromberg, 2001; Galuszka and Kolb, 2002). The growth response of native riparian trees to climate and streamflow can change as a result of alterations in streamflow as well as differences in geomorphology among river reaches. With the onset of river regulation, environmental variables that influence tree growth of *P. deltoides* have been found to shift from flow and precipitation during pre-dam periods to evapotranspiration and temperature during post-dam periods

(Reily and Johnson, 1982). Similarly, shifts in growth response to streamflow have occurred along diverted reaches where growth during a pre-diversion period was responsive to flow during high flow months, while growth during a post-diversion period was responsive to flow for all months of the growing season (Stromberg and Patten, 1990). Geomorphic constraints, such as bedrock confined channels and steep-gradient, narrow canyons, can also influence the growth response of riparian trees to climate and flow. Riparian trees growing in constrained reaches were more sensitive to temperature and less sensitive to fluctuations in streamflow compared with trees at unconstrained reaches (Stromberg and Patten, 1996; Galuszka and Kolb, 2002).

Here we report the results of the influences of river diversion and dam regulation on riparian tree regeneration and growth response to variation in climate and streamflow along the Dolores and San Miguel Rivers in southwestern Colorado. The objectives of our study were to: (1) compare the effects of stream diversion via irrigation canals and flow regulation via the construction of McPhee Dam on the downstream hydrology of the Lower Dolores River; (2) compare the number of establishment years of native riparian trees (*P. angustifolia*, *P. deltoides* subsp. *wislizenii*, and *A. negundo*) between regulated and unregulated reaches and rivers; (3) determine whether tree establishment was related to streamflow and climatic variables; and (4) examine the relationship between tree growth and streamflow and climate variables. We specifically tested the following hypotheses at regulated and unregulated reaches and rivers: (1) river regulation reduced the number of tree establishment events along the regulated Lower Dolores River; (2) tree establishment was positively correlated with spring maximum flow; (3) the relationship between growth and seasonal mean flow differed between regulated and unregulated reaches; and (4) the relationship between growth and Palmer Drought Severity Index (PDSI) differed between regulated and unregulated reaches.

Methods

Study Area

The study location was in southwestern Colorado on the floodplains of the Lower and Upper Dolores Rivers below and above McPhee Dam, respectively, as well as the floodplains of the San Miguel River. The Dolores River begins in the San Juan Mountains in Colorado and flows northwest into the Colorado River in southeast Utah (Figure 1). The Dolores River is regulated by McPhee Dam which was constructed in 1984. McPhee Dam impounds 381,000 Acre-Feet of water for irrigation, municipal, and industrial purposes (Dolores River Dialogue, 2005). The San Miguel River originates in the San Juan Mountains southeast of Telluride, CO and flows northwest into the Dolores River (Figure 1). The nearly unregulated San Miguel River contains a few diversion dams, but flow is largely controlled by snowmelt and precipitation.

Eight reaches on the lower Dolores River have been defined by the Dolores River Dialogue based on gradient, sinuosity, vegetative characteristics, and limiting factors on channel movement and formation (Dolores River Dialogue, 2005). The study sites on the lower Dolores River included reaches one through six, over approximately 213 kilometers (km) of river length, and an elevation difference of 539 meters (m). Reach 1 is located just below McPhee Dam. Reach 6 is located at Saucer Basin just above the confluence of the Dolores and San Miguel Rivers (Figure 1). Reach 2 was not included in the study due to limited access.

Reach 1 of the Lower Dolores River is 17.7 km long with an approximate gradient of 2.37 m/km and a valley floor width of 0.4 to 0.8 km (Dolores River Dialogue, 2005). Reach 3 is 14.5 km long with an approximate gradient of 6.31 m/km and is in a narrow, confined canyon. Reach 4 alternates between confined canyons and wide alluvial valleys. The average gradient across Reach 4 is 2.29 m/km with the largest gradients at the first three segments and a low gradient at Segment 5. Reach 5 flows through Slickrock Canyon, a narrow canyon containing highly sinuous, entrenched meanders below steep sandstone cliffs. The gradient of this reach is 2.08 m/km. Finally, at Reach 6, Slickrock Canyon opens into Paradox Valley, a wide alluvial valley with a gradient of 1.89 m/km.

Less is known about the sites located along the San Miguel and Upper Dolores Rivers included in this study. We selected these unregulated comparison sites based on similar elevation and geomorphic characteristics to specific reaches of the Lower Dolores River. For example, the Tabeguache Preserve of the San Miguel River and Reaches 4 and 6 of the Lower Dolores River have similar elevations (~1620 m at Reach 4, ~1520 m at Reach 6, and ~1550 m at the Tabeguache Preserve), were unconstrained by bedrock, and supported riparian forests. The Dolores River sites above McPhee Dam and Reach 1 of the Lower Dolores River have similar relatively wide floodplains with at least one bench above the active channel. We also made comparisons among Reach 3 of the Lower Dolores River and the Canyon Preserve of the San Miguel River because both segments are characterized as high gradient, narrow canyon reaches.

The study site above McPhee Dam included three segments located on the western bank of the river just past mile marker 17 along Highway 145, on the eastern bank of the river across from the Dolores Public Library, and on the eastern bank of the river across from Joe Rowell Park in the town of Dolores. Two study sites on the San Miguel River were located at the Tabeguache and Lower Canyon Preserves, managed and owned by The Nature Conservancy. The Tabeguache Preserve is located along Highway 141 between mile markers 67.2 to 74 just above the confluence of the San Miguel River and Tabeguache Creek. The Canyon Preserve is located along Highway 145 6.4 km north of Placerville, CO.

Delineation of Segments

Field sampling was conducted in the spring and summer of 2009 and 2010. At the lower Dolores River study area, each reach was divided into two, three, or five equal-length segments depending on the reach length (Figure 1). Reach 2 and Reach 4, Segment 4 were not included in the field sampling due to difficult access. Prior to selecting sites within each segment, we scouted the entire segment. Sites were selected that contained a broad range of tree size classes. If the segment did not contain stands with a broad range of size classes, we started at the beginning of the segment, and worked downstream, collecting samples from trees within the entire segment. At the San Miguel River study site, the 11.2 km stretch of river at the Tabeguache Preserve was divided into two equal-length segments, while the 3.2 km stretch of river at the Canyon Preserve only included one segment. At the Upper Dolores River study site, above McPhee Dam, three segments of river were selected.

Tree Sampling and Measurement

Our main objective for the tree sampling was to determine the year of establishment for the population of trees at each reach segment. Three trees per size class per topographic position were cored using an increment borer at each reach segment. We assigned trees to 5.0 cm diameter at breast height classes and a topographic position which included: active channel, gravel/boulder bar, ephemeral/abandoned channel, and first bench (Galuszka and Kolb, 2002). Saplings that originated as seedlings or root sprouts were not separated in this study because we were interested in all forms of regeneration (Baker, 1990; Galuszka and Kolb, 2002). We excavated the soil around each tree to expose the root collar. We cored trees 6-10 cm above the root collar using an increment borer. For mature trees 10 to 100 cm diameter at breast height (dbh), we extracted two increment cores spaced 90° apart per tree, and for saplings 0 to 10 cm dbh, we extracted only one core per tree. For trees with a diameter at coring height <3 cm, we either collected a cross-section where seedlings were abundant or estimated ages by bud scale scars where seedlings were present but not abundant. For each cored tree, we measured stem diameter at coring height (dch), 6 to 10 cm above the root collar, and also at breast height. We acquired the location of each cored tree, and the center-point of each sampled topographic position using a GPS unit. We visually estimated the elevation of the center of each topographic position above base flows. We estimated tree basal area of surrounding trees by establishing variable-radius plots at each cored tree using a BAF prism (BAF = 2 m^2/ha).

We prepared the cores for analysis in the laboratory by gluing them into wood mounts and sanding them using a series of sandpaper grades (Stokes and Smiley, 1968).

For cores that included the pith, tree age was determined by counting annual rings using a dissecting scope. For cores that did not contain the pith, two methods of age estimation for *P. deltoides* subsp. *wislizenii* and *P. angustifolia* were compared among two sites that contained a high sample size of trees, Reach 4/Segment 5 and Reach 1/Segment 1. The first method was the prediction of tree age based on tree age and diameter at coring height regressions for trees with cores that contained the pith at each site. The second method involved selecting sampled trees at the same sites (Reach 4/Segment 5 and Reach 1/Segment 1) that contained two cores, one with the pith and one without the pith. For the core without the pith, the template method was used to estimate tree age (Applequist, 1958). Thus, for these trees, we obtained both estimated and observed ages. Correlations between observed and predicted ages were compared between methods at both sites. Tree age for problematic cores (e.g., contained false rings or rings that were very difficult to see near the pith) was verified by three experienced people.

The template method was superior to the age-diameter model in predicting tree age (Figures 2 and 3). At Reach 1/Segment 1, the relationship of observed and predicted values was significant for the template and age-diameter methods ($p < 0.0001$); however, the correlation between observed and predicted values was lower for the age-diameter method ($r^2 = 0.877$) than the template method ($r^2 = 0.926$) (Figure 2). Similarly, at Reach 4/Segment 5, the correlation between observed and predicted age was lower for the age-diameter method ($r^2 = 0.681$) than the template method ($r^2 = 0.908$) (Figure 3). Consequently, the template method was used to predict ages of trees with increment cores not containing the pith.

Using an image analysis software program, WinDENDRO (Regent Instruments Inc., Quebec, 2009), we measured the width of annual growth rings for mature trees that established prior to the construction of McPhee Dam in 1984. All cores used in the growth analysis were cross-dated using the software program, COFECHA, which allowed us to detect and correct for missing or false rings (Grissino-Mayer, 2001). After all cores were cross-dated, we fit a negative exponential or linear regression to each individual tree series data using ARSTAN (Cook and Holmes, 1986). Annual radial growth of each tree was standardized by dividing radial growth in each year by the predicted value from the regression. Annual radial growth indices for all trees within each reach, by species, were averaged in order to develop annual standardized indices. Series that contained at least 10 cores for most of the time period of analysis were used in statistical analysis described below (Figure 4).

Hydrologic and Climatic Variables

Dolores River flow data were obtained from the Dolores (09166500) and Bedrock (09169500) Gauge Stations from the U.S. Geological Survey, and the Dolores River Below McPhee Reservoir (DOLBMCCO) Gauge Station from the Colorado Division of Water Resources. These data included daily flow records from October 1961 through October 2008 at the Dolores Gauge, October 1984 through October 2008 for the McPhee Gauge, and October 1971 through October 2008 for the Bedrock Gauge. At Bedrock, missing data from 1961 to 1971 were predicted by linear regression of seasonal flow variables between the Bedrock and Cisco Gauge Stations for years 1972 to 1984 (Figure 5). The Cisco Gauge Station (09180000) was located further downstream from the

Bedrock Gauge, and was used to predict seasonal flow variables at Bedrock. The correlation (r^2) of seasonal flow variables between the Bedrock and Cisco Gauge Stations ranged from 0.715 to 0.948, and all *p*-values were less than 0.001 (Figure 5).

At the McPhee Gauge Station, pre-dam hydrologic data were not available because the gauge was installed after the construction of McPhee Dam in 1984. Prior to the construction of McPhee Dam, water was diverted from the Dolores River at a location downstream from the Dolores Gauge Station and upstream from the present location of the dam. Canal diversion flow data for Main Canals Number 1 (Structure ID: 4673) and Number 2 (Structure ID: 4674) were obtained from the Colorado Water Conservation Board and Colorado Division of Water Resources. Total daily diversion was calculated by adding flow values from the Main Canals No. 1 and 2. Missing flow data were calculated by subtracting total daily canal diversion from mean daily flow at the Dolores Gauge for the time period of 1974 to 1984. Negative values were set to zero. Of the 3,987 daily calculated values during this period, approximately 18% of values were negative, particularly during low flow periods of dry years (e.g., 1974 and 1977), which were most likely due to errors in the daily diversion data or local tributary inputs between the Upper Dolores Gauge Station and the canal diversion that were unaccounted for. However, 86% per cent of the negative values did not fall below -1 m^3/s, and the lowest calculated value was -4.36 m^3/s. Furthermore, our observations of near-zero values of flows in summers of dry years further downstream at the Bedrock Gauge generally support the calculation approach. The remaining 14 years of missing data (1961-1973) at the McPhee Gauge were predicted through linear regression of seasonal flow variables (1974-1984) from the Dolores Gauge and calculated pre-dam data at the McPhee Gauge

(Figure 6). The correlation (r^2) between seasonal mean and maximum flow from the calculated values and Dolores Gauge ranged from 0.744 to 0.997, *p*-values were generally less than 0.0001, and the relationship was generally non-linear (Figure 6). For seasonal mimimum flows, there were no significant relationships because the calculated values at the McPhee Gauge were often zero. Thus, seasonal minimum flow was not used as an independent variable during the pre-dam period at the McPhee Gauge.

Flow data for the San Miguel River were obtained from the Uravan (09177000) and Placerville (09172500) Gauge Stations from the U.S. Geological Survey. These data include daily flow records from October 1974 through October 2008 for the Uravan Gauge and from October 1961 through October 2008 at the Placerville Gauge. At Uravan, missing data from 1961 to 1973 were predicted through linear regression of seasonal flow variables at the Uravan and Placerville Gauge Stations (Figure 7). The correlation (r^2) of seasonal flow parameters between the two gauge stations ranged from 0.318 to 0.924, and with one exception, all *p*-values were less than 0.0001 (Figure 7).

Climate data were obtained from the Cortez (51866), Uravan (058560), and Telluride Climate Stations from the National Climatic Data Center. Climate data included daily precipitation and temperature summaries from 1961 through 2008. Missing temperature data at the Uravan Climate Station were predicted using linear regression of mean daily temperature at Uravan on data obtained from the Paradox (56318) and LaSal (424946) Climate Stations. Monthly Palmer Drought Severity Index (PDSI) values from Division 2 of Colorado were also obtained from the National Climatic Data Center. Palmer Drought Severity Index is interpreted as the departure of monthly precipitation values from normal, which is weighted by a soil water balance, but also accounts for meteorological conditions in the preceding month (Palmer, 1965). More negative values of PDSI indicate drought years, more positive values indicate wet years, and values near zero are normal years.

Data Analysis

All statistical analyses were conducted using SAS® statistical software (SAS Institute, Inc., 2009). We developed 20 environmental variables to describe variations in seasonal temperature, precipitation, and stream flow for the Dolores and San Miguel Rivers (Table 1). Environmental variables developed at each gauge and weather station were used for sampled reaches based on elevation (Table 2). For example, precipitation and temperature variables from the Uravan Weather Station were used for Reaches 4 through 6 of the Dolores River because the elevational midpoint between the Cortez and Uravan Weather Stations was 1705 meters, and was most similar to elevation along the upper portion of Reach 4. Thus, for Reaches 4 through 6, we pooled data for the analysis of *A. negundo* establishment to obtain a more robust sample size while maintaining a consistent association with a single climate (Uravan) and gauge (Bedrock) station across these reaches. Furthermore, we also pooled data for *P. angustifolia* establishment analysis at Reaches 1 through 3 to obtain a more robust sample size that more closely matched our sample size for our unregulated comparison reach, the Upper Dolores River, as well as maintaining a consistent association with a single climate (Cortez) and gauge (McPhee) station across reaches.

Multiple logistic regressions were used to model riparian tree establishment (establishment vs. non-establishment years) as a function of independent predictor variables of streamflow, precipitation, and temperature. An establishment year was defined as a year of well-documented establishment when two or more trees were established in a reach. Both estimated (template method) and observed years were pooled for common years within each reach. The process of variable selection for the models began with a two-sample t-test that compared means of independent variables between establishment and non-establishment years. Variables whose t-test had a p-value < 0.25 were included in a forward stepwise selection process where selection was based on the chi-square test statistic, and probability to enter and remove was: $p_{\text{entry}} = 0.20$ and $p_{\text{remove}} = 0.25$ (Hosmer and Lemeshow, 2000).

This approach to developing models to predict tree establishment yielded unstable parameter estimates at three sites. In particular, analysis of pre-dam (1961-1984) and post-dam (1985-2008) periods along the lower Dolores River only provided 24 observations per period, which led to unstable coefficients and standard errors. Thus, the two time periods were pooled across all sites at the lower Dolores River in order to increase the number of observations and maintain a consistent number of observations across all sites. This pooling eliminated numerical problems (unstable parameter estimates) that were encountered at these particular reaches.

Relationships between standardized growth indices for *Populus angustifolia, Populus deltoides* subsp. *wislizenii,* and *Acer negundo* and seasonal mean flows and PDSI were examined for all reaches using regression. Unlike our tree establishment analysis, we did not pool data across reaches due to inconsistencies among growth chronologies. We removed extreme drought years 2002 and 2003 (PDSI of -5.26 and -5.96), respectively for regression analysis of tree growth and PDSI for the winter season in order to maintain a consistent range of PDSI values for both pre- and post-dam time periods, while spring and summer PDSI (-8.17 and -9.07), respectively for year 2002 was removed for the same reason. Linear or quadratic fits were selected based on the highest coefficient of determination (r^2) values. In addition, multivariate models of tree growth were developed using the “evaluate all models” function of SAS JMP. Models were selected for each tree species and reach based on lowest AIC (Akaike’s Information Criterion) value (Anderson, 2008).

Results

Hydrologic Alteration

In order to understand the effects of diversion on streamflow of the Lower Dolores River (Reaches 1 through 6) we compared mean daily streamflow at the Dolores Gauge with calculated streamflow values after subtraction of flow that was diverted for irrigation from 1974 to 1984 (Figure 8). Relative to mean daily streamflow at the Dolores Gauge (Upper Dolores River) during the pre-dam period, we observed a 1.8 % reduction during the spring season (April – June) and a 72.6% reduction during the summer season (July - September) in streamflow at the Lower Dolores River. No major effects of water diversion were evident through the winter months (Figure 8).

We further estimated the effects of river regulation from McPhee Dam on streamflow of the Lower Dolores River by comparing mean daily streamflow at the Dolores Gauge above McPhee Dam and releases from McPhee Dam from 1984 to 2008 (Figure 9). Relative to mean daily streamflow at the Dolores Gauge (Upper Dolores River) during the post-dam period, we observed a 41.5% reduction during the spring season and a 63.4% reduction during the summer season at the Lower Dolores River (Figure 9). Furthermore, relative to the pre-dam period at the Lower Dolores River, we observed a 35.7% reduction during the spring season and less than 1% reduction during the summer season at the Lower Dolores River during the post-dam period. Thus, streamflow conditions of the Lower Dolores River can be classified into three time periods: 1) the unregulated period at the Upper Dolores Reach from 1961 to 2008, 2) the pre-dam period along the Lower Dolores River (Reach 1 through Reach 6) from 1961 to 1984, and 3) the post-dam period along the Lower Dolores River (Reach 1 through Reach 6) from 1985 to 2008.

Tree Establishment

The number of well-documented establishment events of *P. angustifolia* was similar for both the Upper Dolores Reach (4) and Reaches 1 and 3 (4) during the pre-dam period of 1961 to 1984 (Figure 10a, b). However, the number of establishment events during the post-dam period of 1985 to 2008 at Reaches 1 and 3 (8) was less than at the Upper Dolores Reach (18) (Figure 10a, b). During this same time period, a low number of establishment events occurred for *P. angustifolia* at the Tabeguache (5) and Canyon Preserves (3) along the unregulated San Miguel River; however, the sample sizes at these sites were particularly low (Figure 10c, d). In contrast, the number of establishment events along the Lower Dolores River for both *A. negundo* (4) and *P. deltoides* subsp. *wislizenii* (8 at Reach 4, 10 at Reach 6) were slightly greater compared to unregulated comparison sites such as the Upper Dolores (2) for *A. negundo* and the San Miguel River (7) for *P. deltoides* subsp. *wislizenii* (Figures 11 and 12). At the Upper Dolores Reach, however, the sample size for *A. negundo* was smaller (n=20) compared to Reaches 1 and 3 (n=40). The most apparent lack of establishment events for *P. deltoides* subsp. *wislizenii* (3) occurred during the pre-dam period at Reach 6 of the Dolores River (Figure 11b). The number of pre-dam establishment events for *P. deltoides* subsp. *wislizenii* (11) was greater at the San Miguel River (Figure 11c) than the Lower Dolores River (9 at Reach 4, 3 at Reach 6; Figure 11a, b). The number of establishment events for *P. deltoides* subsp. *wislizenii* was high at Reach 6 in the late 1980s and early 1990s compared with the San Miguel River (Figure 11b, c).

We tested the hypothesis that spring maximum flow would be positively correlated with the establishment of all tree species. Spring maximum flow explained little variation in tree establishment; r^2 values ranged from 0.001 to 0.281 over all species and reaches (Table 3). However, spring maximum flow was positively correlated with tree establishment at two sites for *A. negundo*, Upper Dolores and Reaches 4 through 6 (pooled) (Table 3). In contrast, spring maximum flow was negatively correlated with tree establishment at two sites for *P. angustifolia*, Reaches 1 and 3 and Canyon Preserve (Table 3).

Multivariate models of the probability of well-documented establishment events had R^2 values that ranged from 0.106 to 0.598, and 60% of the models had R^2 values less than 0.300 (Tables 4 through 6). With one exception, models with R^2 values greater than 0.300 also had relatively high ROC (Receiver Operating Characteristic) values (> 0.800) (Tables 4 through 6).

Models with high R^2 and ROC values were developed for *P. angustifolia* at Reaches 1 and 3 and Canyon Preserve. At Reaches 1 and 3 for the pooled pre- and post-dam period (1961-2008), winter mean temperature and spring precipitation were positively and negatively correlated with establishment, respectively (Table 4). *Populus angustifolia* establishment at the Canyon Preserve was negatively correlated with summer maximum flow and positively correlated with subsequent year maximum flow, spring mean temperature, and spring mean flow. All establishment models for *P. deltoides* subsp. *wislizenii* had R^2 values below 0.200 (Table 5).

For *A. negundo*, summer mean flow was positively correlated with establishment at the Upper Dolores River. At Reaches 1 and 3 for the pooled pre- and post-dam periods (1961-2008), winter mean and spring maximum temperature were both negatively correlated with establishment, while spring minimum flow was positively correlated with establishment (Table 6). At reaches 4, 5, and 6 for the pooled pre- and post-dam periods (1961-2008), spring maximum and summer minimum flows were positively correlated with *A. negundo* establishment, while summer mean temperature was negatively correlated with tree establishment (Table 6).

Tree Growth

Standardized values of radial tree growth were compared to values calculated by a first order autoregressive model. The correlation between lag_{-1} year and the year of interest was moderately low and ranged from 0.282 to 0.566 over all species and reaches. The correlation between standardized and autoregressive standardized values was generally high and ranged from 0.753 to 0.927 over all species and reaches. Thus, the standardized values without autoregression were used in the growth analysis.

Regressions between growth and seasonal mean flows generally had a positive quadratic fit, and in a few cases, regressions displayed a bell shaped curve. With a few exceptions, the relationship between streamflow and growth was low for *P. angustifolia*; streamflow explained less than 30% of the variation in growth (Table 7). An exception was that growth of *P. angustifolia* was significantly related to summer mean flow during the post-dam period but not during the pre-dam period at Reaches 1 and 3 (Table 7). The relationship between streamflow and growth was stronger for *A. negundo* than other species (Table 7). More specifically, relationships were strongest for *A. negundo* during the spring and summer seasons for both pre- and post-dam periods, except for Reach 4 where the relationship was strongest during the post-dam winter season (Table 7). For *P. deltoides* subsp. w*islizenii*, streamflow explained little variation in growth and r^2 values never exceeded 0.300 (Table 7).

Similarly, regressions between growth and Palmer Drought Severity Index (PDSI) generally had a positive quadratic fit, and in a few cases, regressions had a bell shaped curve. Palmer Drought Severity Index was correlated with annual growth of *P. angustifolia* during the post-dam period (1985-2008) at Reach 1 for all seasons, while no correlation was observed at the pre-dam (1961-1984) Reach 1 and at the unregulated Upper Dolores River (Table 8). A similar pattern emerged for both *A. negundo* during the winter season and *P. deltoides* subsp. *wislizenii* during the spring and summer seasons at Reach 4 (Table 8; Figures 13 and 14). At Reach 3, we also observed a higher correlation between *A. negundo* growth and winter PDSI during the post-dam period compared to the pre-dam period (Table 8, Figure 15). In contrast, growth of *P.*

angustifolia at Reach 3 was more strongly correlated with both spring and summer PDSI for the pre-dam period compared to the post-dam period (Table 8).

The correlations between *P. angustifolia* growth and PDSI for pooled pre- and post-dam periods at Reach 1 were significant for all seasons and consistently greater than correlations observed at the unregulated Upper Dolores River (Table 9, Figure 16). A similar pattern emerged for *P. angustifolia* at Reach 3 and its comparison site at the unregulated San Miguel River, Canyon Preserve, where correlations between growth and PDSI were greater at Reach 3, especially for spring and summer seasons (Table 9, Figure 17). For *P. deltoides* subsp. *wislizenii,* correlations between growth and PDSI were greater for all seasons at Reach 4 compared to the Tabeguache Preserve at the unregulated San Miguel River (Table 9, Figure 18).

Our development of multivariate, best-fit models of tree growth that included climate and flow variables further substantiated results related to seasonal PDSI. At Reaches 1 and 4, best-fit models included seasonal PDSI during the post-dam period for all species (Tables 10, 11, and 12). For *P. angustifolia,* seasonal PDSI was not included in the best-fit model at the unregulated reaches such as the Upper Dolores and Reach 1 during the pre-dam period, and models explained little variation in annual growth ($R^2 < 0.250$) (Table 10). Similarly, at Reach 4 for the pre-dam period, PDSI was not included in the model, and flow and climate variables explained 55 and 76% of the variation in growth of *P. deltoides* subsp. *wislizenii* and *A. negundo*, respectively (Tables 11 and 12). At this reach, variables included in the model were consistent for both species and included spring mean flow, spring minimum flow, spring precipitation, and summer precipitation. At Reach 3, however, seasonal PDSI was also included in the best-fit model for both *P. angustifolia* and *A. negundo* during the pre-dam, post-dam, and pooled time periods (Tables 10 and 12). Similarly, winter PDSI was included in the best-fit model for growth of *P. angustifolia* at the Canyon Preserve of the unregulated San Miguel River (Table 10).

Discussion

Tree Establishment

River diversion via irrigation canals and dam regulation from McPhee Dam both altered the downstream hydrology of the Dolores River, and major influences of each form of diversion occurred during different seasons. Our hydrologic analysis of pre-dam flow conditions at the McPhee gauge shows that irrigation diversion reduced streamflow primarily during the summer season, while dam regulation from McPhee Dam reduced streamflow during the spring and summer seasons. Dam regulation clearly resulted in a greater reduction of spring flows (April – June) than canal diversion. During the summer season (July – September) of the pre-dam period, reductions due to canal diversion were slightly greater compared to dam regulation. Streamflow comparisons of the pre- and post-dam periods at the Lower Dolores River further show that dam regulation reduced spring streamflow, while summer streamflow did not change, compared with canal diversion in the pre-dam period.

We tested the hypothesis that spring maximum flow was correlated with establishment of native riparian trees. Establishment years were defined as well-documented establishment events when two or more trees were established in a reach. We found that spring maximum flow explained little variation in establishment of *P.*

deltoides subsp. *wislizenii* and *P. angustifolia*. This result was further substantiated with logistic regression models developed to describe the probability of tree establishment for these species; spring maximum flow was included in only one model for *P. deltoides* subsp. *wislizenii* and *P. angustifolia* across all reaches. Furthermore, another supporting result is the large number of establishment events observed for these species during the post-dam periods, despite streamflow reductions during the months of May and June. Cooper et al. (2003) found that peak flow was rarely included in tree establishment models for *P. deltoides* subsp. *wislizenii* at the unregulated Yampa River; however, peak flow was often included in models for reaches along the regulated Green River.

We found moderate support for a positive role of spring maximum flow on *A. negundo* establishment. Our results are similar to those of DeWine and Cooper (2007), who observed positive influences of spring maximum flow on *A. negundo* establishment. However, they reported a higher correlation (Pseudo-r^2 of 0.41 to 0.91) between *A. negundo* establishment and annual peak flow along the unregulated Yampa and regulated Green Rivers in Colorado, compared with our study (r^2 of 0.145 to 0.281). In our study, the sample sizes for *A. negundo* were similar to those of DeWine and Cooper (2007) (n of 20 to 40).

Winter mean temperature consistently explained variation in the establishment of *P. angustifolia* along three reaches of the Upper and Lower Dolores Rivers, which suggests that dam regulation was not an important factor in establishment events of *P. angustifolia* along the Lower Dolores River because dam regulation did not change regional temperature. For *P. angustifolia*, we observed a greater number of establishment events along the unregulated Upper Dolores River (18) compared to the regulated Lower

Dolores River (8) at Reaches 1 and 3 during the post-dam period (1985-2008). However, winter mean temperature was positively correlated with establishment at both the Upper Dolores and Reaches 1 and 3. At the Canyon Preserve of the unregulated San Miguel River, we found that an entirely different set of variables were important in explaining the establishment of *P. angustifolia*. The negative and positive correlations between summer maximum flow and subsequent year maximum flow, respectively, and establishment suggest that seedlings are susceptible to scouring by subsequent high flows during the summer months, and subsequent high flows the following year promote establishment.

In contrast to our results along the Dolores River, Baker (1990) found that climatic factors such as low fall temperature and high fall precipitation were important in establishment of *P. angustifolia* along the Animas River, Colorado, not far from the Dolores River. Baker's (1990) analysis was restricted to an 11 year period from 1975 to 1985, which, coincidentally was the same time period where we observed no establishment years for *P. angustifolia* along the regulated Lower Dolores and unregulated Upper Dolores Rivers. At a larger temporal scale (~130 yrs.), Baker (1990) also found that stand-origin years were positively associated with high spring and fall peak discharges which is consistent with our finding that spring mean flow was positively correlated with establishment of *P. angustifolia* at the Canyon Preserve at the San Miguel River.

The inconsistencies of results among the Dolores, San Miguel, and Animas Rivers suggest that either numerous factors promote establishment of *P. angustifolia* and they vary by site or river, or factors other than climate and streamflow, such as stand age, reach geomorphic characteristics, inter- or intra-competition, or genotypic variation, may influence establishment for *P. angustifolia. Populus angustifolia* is a highly clonal species that primarily reproduces through root suckers, but is also capable of producing seedlings (Rood et al., 1994). In the same genera, *Populus tremuloides* also primarily reproduces through root suckers in the western U.S., where a clone is formed following a disturbance event such as logging or fire (Barnes, 1966). Thus, we expected flooding to be the primary cause of clonal reproduction for *P. angustifolia*. This hypothesis is partially supported by our results and by Baker (1990).

The lack of establishment for *P. deltoides* subsp. *wislizenii* at Reach 6 during the pre-dam period may be attributed to low flows throughout the summer months following high spring flows. At this reach, the positive relationship between establishment and summer minimum flow suggests that low flows during the summer season could have prevented seedlings from establishing due to water stress during the pre-dam period, although this relationship was fairly weak (R^2 = 0.158, ROC = 0.755). This suggestion is further supported by another line of evidence through our hydrologic analyses of pre- and post-dam periods along the Lower Dolores River and comparison of pre- and post-dam summer minimum flows at Reach 6, which showed that summer minimum flow was significantly lower during the pre-dam period. Furthermore, there was evidence of a consistent abrupt decline of flows during the receding portion of the hydrograph in early summer. Streamflow declines that reached near-zero values in July may have contributed to water stress of seedlings at this site. This finding supports the hypothesis that *Populus* utilizes groundwater provided by surface stream water following germination (Mahoney and Rood, 1998). Cooper et al. (1999) found that *Populus* seedlings do not utilize this source of water until the third or fourth growing season.

During the post-dam period, well-documented establishment events of *Populus deltoides* subsp. *wislizenii* were common at Reaches 4 and 6, which suggests healthy conditions for establishment of that species along the Lower Dolores River at these reaches. In contrast to our results, establishment was fairly uncommon for *Populus deltoides* subsp. *wislizenii* along the regulated Green River (Merritt and Cooper, 2000; Cooper et al., 2003). Compared to releases from McPhee Dam along the Lower Dolores River, releases from the Flaming Gorge Dam appeared to have a greater impact on streamflow during the months of May and June (Merritt and Cooper, 2000). Seasonal variation in streamflow is much more apparent along the Lower Dolores River compared to the regulated Green River, which has generally experienced greater reductions in streamflow during snowmelt run-off and increases in base flow for the remainder of the year.

Across all reaches of the Dolores River, high streamflow throughout the growing season appeared to facilitate establishment of *A. negundo*, while high temperatures appeared to negatively impact establishment. At the unregulated Upper Dolores River, low base flow in summer months likely prevented seedling survival due to water stress. Along Reaches 4 through 6, spring maximum flow was selected as a variable in the establishment model. This finding partially supports the results of DeWine and Cooper (2007), where annual peak flow was positively correlated with establishment of *A. negundo* along the Green River. DeWine and Cooper (2007) suggests that large floods in narrow canyon reaches facilitate recruitment by creating moist soil conditions conducive to seedling germination. In our study, low summer minimum flows at Reaches 4 through 6 also appear to have prevented *A. negundo* establishment, similar to the Upper Dolores Reach for *A. negundo* and for *P. deltoides* subsp. *wislizenii* establishment along Reach 6.

This result supports the findings of Dawson and Ehleringer (1991) that stream water was an important source of water for small *A. negundo* trees along Red Butte Creek, Utah. In combination with low summer minimum flows of the Dolores River, high summer temperatures appear to have limited establishment along Reaches 4 through 6. At Oak Creek, Arizona, Kolb et al. (1997) found that net photosynthetic rates of both small and large *A. negundo* trees were negatively affected by greater minimum temperatures. At our study site *A. negundo* seedlings may have been particularly sensitive to high temperature when water was a limiting factor especially during low summer flows.

Our finding that *A. negundo* establishment was more sensitive to streamflow compared to *Populus* spp. could be attributed to establishment of *A. negundo* at relatively high elevation locations of the floodplain. At our study sites, young *A. negundo* trees established at transition zones between the active channel and first bench, while most young *Populus* spp. established within active or ephemeral channels. Mature *A. negundo* trees were growing at higher elevations on benches (1.2 to 2.4 meters) compared to *Populus* spp. (0.8 to 1.2 meters in wide, alluvial valleys and 1.7 meters in narrow canyon reaches). Our observations of *A. negundo* establishing at higher topographic positions supports the results of Johnson (1976) who observed *A. negundo* inhabiting high terraces near the edge of the floodplain along the Missouri River, North Dakota. We speculate that *Acer negundo* establishment was more sensitive to variation in streamflow than *Populus* spp. because it established at higher topographic positions where groundwater was deeper, and thus, high stream flows supplied most water to *A. negundo*.

Tree Growth

We hypothesized that annual growth of riparian trees along the Dolores and San Miguel Rivers would be correlated with seasonal mean streamflow and regional drought. Along the unregulated Upper Dolores and San Miguel Rivers, growth of riparian trees was not related to mean flow and PDSI for any season, except for *P. angustifolia* at the Canyon Preserve of the San Miguel River. Under natural flow conditions, tree growth was rather complacent, even during drought years. One explanation for complacent growth is that water availability was consistently high in the tree rooting zone even during drought years.

The shift in growth response for *P. angustifolia* at the Lower Dolores River from spring and winter flow during the pre-dam period to summer flow during the post-dam period can be attributed to diverted streamflow between these two periods. During the pre-dam period, canal diversion largely impacted summer flows, with a slight reduction in high flows during the months of May and June. In contrast, during the post-dam period, river damming largely impacted streamflow during the spring season. During the pre-dam period, growth was likely sensitive to high flows during the spring because high flows provided an abundance of water, subsequently recharging deep soil water and groundwater supply to trees, while summer flows did not provide much of the annual supply of water. As a result of dam regulation, spring streamflow decreased and trees likely were more dependent upon summer flows in the post-dam period since the recharge of deep soil water and groundwater during high spring flows may have been less frequent.

Controls over tree growth by streamflow were stronger for *A. negundo* than *P. angustifolia* and *P. deltoides* subsp. *wislizenii*, particularly during spring and summer for both pre- and post-dam periods. As previously mentioned above, mature *A. negundo* trees were growing at higher elevations compared to *Populus* spp. during the time of our study, which may explain why mature tree growth of *A. negundo* was more sensitive to streamflow than *Populus* spp. We speculate that for the benches where mature *A. negundo* trees grew, the depth to ground water was generally higher compared to benches where *Populus* spp. grew, which likely caused *A. negundo* trees to be more responsive to variation in streamflow. Only one other study has investigated the relationship between growth of *A. negundo* and streamflow; annual surface flow at the unregulated West Clear Creek, Arizona, was negatively correlated with growth (Galuszka and Kolb, 2002). The inconsistencies between our results and Galuszka and Kolb (2002) may reflect differences in streamflow and geomorphic setting. The deep canyon of West Clear Creek in the central Arizona is subject to high velocity flows during heavy precipitation events, transporting debris that can physically damage trees (Galuszka and Kolb, 2002).

Water diversion through river damming and irrigation canals along the Dolores River has increased the influence of regional drought on tree growth. Our analysis of tree growth and PDSI revealed that for both *P. angustifolia* and *P. deltoides* subsp. *wislizenii*, seasonal PDSI was correlated with growth for all seasons at canal diverted and dam regulated Reaches 1 and 4, but no correlation was observed at unregulated comparison sites, Upper Dolores and Tabeguache Preserve at the San Miguel River. Furthermore, we observed greater correlations between tree growth and PDSI at canal diverted and dam regulated Reach 3 compared to the unregulated Canyon Preserve of the San Miguel River. At the unregulated San Pedro River, Arizona, Snyder and Williams (2000) observed greater use of precipitation for *P. fremontii* along ephemeral reaches, where monsoon rains appeared to reduce water stress for this species. In our hydrologic analysis of the Lower Dolores River, we observed reductions in streamflow as a result of both dam regulation and water diversion through irrigation canals. We speculate that reductions in streamflow could have forced trees to rely on soil water supplied by precipitation, which is mechanistically related to PDSI.

We found evidence that river regulation increased tree growth sensitivity to regional drought along the Lower Dolores River, particularly at Reach 4 for *A. negundo* during the winter season and *P. deltoides* subsp. *wislizenii* during the spring and summer seasons. This finding was further substantiated by variables included in best-fit models of tree growth at these reaches. At Reach 4 for *P. deltoides subsp. wislizenii* and *A. negundo*, an apparent shift from control of tree growth by streamflow variables during the pre-dam period to PDSI during the post-dam is similar to results of Reily and Johnson (1982). They observed a similar shift along the Missouri River, where *Populus deltoides* growth was positively correlated with streamflow during the pre-dam period and actual evapotranspiration and temperature in the post-dam period. Reily and Johnson (1982) suggested that water supplied to groundwater by the river was no longer important to the growth of cottonwood during the post-dam period. In our study, the evidence of a shift in growth response was likely a result of a change in water source. During the pre-dam period, water supplied by the river, particularly during high spring flows, was an important source of water, and supplemental sources such as precipitation were utilized in the summer. After the construction of McPhee Dam, spring flows were greatly reduced, likely reducing the amount of deep soil water and groundwater recharge. The supply of water during the post-dam period may not have been enough to sustain high growth of riparian trees at Reach 4, consequently forcing trees to utilize water in shallow soils.

In addition to reduced spring flows, elevational adjustments of the channel, such as channel downcutting, may have influenced the sensitivity of growth to PDSI during the post-dam period. Channel downcutting following river damming is a common occurrence along rivers of the western U.S. and Great Plains Region (Williams and Wolman, 1984). As sediment becomes displaced from the river, additional downcutting of the river bed lowers the bed elevation, which may potentially alter the depth to groundwater and reduce tree access to stream and ground waters.

At high gradient, narrow canyon reaches, tree growth of *P. angustifolia* and *A. negundo* was sensitive to regional drought during pre- and post-dam periods. The differences in behavior of the growth response for trees at Reaches 3 and 4 during the pre-dam period may be explained by different geomorphic settings among the two reaches. Compared to Reach 4, Reach 3 is characterized by a steeper gradient, and is generally a more confined reach. Deep soil water and groundwater recharge from the river may not be an important mechanism in supplying water to trees at Reach 3. Across nine streams in the Eastern Sierra Nevada of California, Stromberg and Pattern (1996) found that growth of *P. trichocarpa* was less sensitive to annual stream flow volume in high gradient, narrow canyons compared to trees growing along wide, alluvial valleys. Stromberg and Patten (1996) suggested that trees growing in narrow canyons relied on a source of water other than groundwater supplied by streamflow, such as shallow surface soil water.

Certain limitations of this study should be considered as potential sources of uncertainty that may have influenced results. Determining the germination year for riparian trees, for example, can be problematic. Near the pith of most trees, annual rings were difficult to identify due to rotting xylem cells. The xylem near the pith was often broken into multiple pieces, but we attempted to obtain all pieces within the sample. Assemblage of broken pieces near the pith was generally helpful to determine a better approximation of tree age; however, samples that contained multiple broken pieces near the pith were difficult to age. With respect to our growth analysis, sample depth was fairly low (< 10 cores) at a few reaches during the period of 1961 to 1984 (e.g., Reach 4 and Tabeguache Preserve for *P. deltoides* subsp. *wislizenii*), and error was most likely greatest during this time period.

Conclusions

In our study, a dendrochronological approach provided information about tree age and growth in pre- and post-dam periods along the Lower Dolores River. We incorporated reaches along the unregulated Upper Dolores and San Miguel Rivers that provided a reference to further understand the effects of diversion and regulation on the recruitment and growth response of native riparian trees growing along the Lower Dolores River.

We observed a large number of establishment years at all reaches during the post-dam period and no evidence of large differences in the number of events between regulated and unregulated river reaches. There was, however, evidence of a lack of *P. deltoides* subsp. *wislizenii* recruitment due to low summer minimum flows during the pre-dam period at Reach 6, which can be attributed to water diversion via irrigation canals. We found that spring maximum flow was not a strong driver of the establishment of native riparian trees along the Dolores and San Miguel Rivers under natural, canal diverted, and dam regulated streamflow conditions over the temporal period of our study (1961-2008). Spring maximum flow was weakly and positively correlated with *A. negundo* establishment at some sites, but not for *Populus* spp. Higher spring and summer flows generally promoted *A. negundo* establishment, while high temperature had a negative influence on establishment. For *P. angustifolia*, growth appeared to be more sensitive to summer streamflow during the post-dam period compared to the pre-dam period. Overall, *A. negundo* establishment and growth were more sensitive to streamflow compared to *Populus* spp., which may be due to recruitment of *A. negundo* at higher topographic elevations relative to *Populus* spp. Finally, our results suggest that river damming and water diversion through irrigation canals increased tree growth sensitivity to regional drought for all species included in our study.

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Table 1. Environmental variables used in logistic, simple, and multiple regression analyses. Chronologies for 1961 through 2008 were developed for each variable at all weather and hydrologic gauge stations. *Only used in logistic regression analysis for establishment. †Only used in regression analysis for growth.

Description of Variable
Winter Mean Flow (October 1 – March 30)
Spring Mean Flow (April 1 – June 30)
Summer Mean Flow (July 1 – September 30)
Winter Maximum Flow (October 1 – March 30)
Spring Maximum Flow (April 1 – June 30)
Summer Maximum Flow (July 1 – September 30)
Winter Minimum Flow (October 1 – March 30)
Spring Minimum Flow (April 1 – June 30)
Summer Minimum Flow (July 1 – September 30)
Previous Year Maximum Flow* (October 1- September 30)
Subsequent Year Maximum Flow* (October 1-September 30)
Winter Precipitation (October 1 – March 30)
Spring Precipitation (April 1 – June 30)
Summer Precipitation (July 1 – September 30)
Winter Mean Temperature (October 1 – March 30)
Spring Mean Temperature (April 1 – June 30)
Summer Mean Temperature (July 1 – September 30)
Winter PDSI† (October 1 – March 30)
Spring PDSI† (April 1 – June 30)
Summer PDSI† (July 1 – September 30)

Table 2. Elevation range of all reaches along the Dolores and San Miguel Rivers and associated weather and hydrologic gauging stations. The unregulated comparison site for Reaches 1 and 3 was the Upper Dolores Reach, while the unregulated comparison site for Reaches 4 through 6 was the Tabeguache Preserve; however, in our growth analysis, the unregulated comparison site for Reach 3 was the Canyon Preserve.

River	Reach	Elevation (m)	Weather Station	Elevation (m)	Gauging Station	Elevation (m)
Dolores	Upper Dolores	2110 - 2182	Cortez	1880	Dolores	2115
	Reach 1	1980 - 2020	Cortez	1880	McPhee	2021
	Reach 3	1820 - 1850	Cortez	1880	McPhee	2021
	Reach 4	1620 - 1770	Uravan	1530	Bedrock	1506
	Reach 6	1510 - 1530	Uravan	1530	Bedrock	1506
San Miguel	Tabeguache Preserve	1550 - 1570	Uravan	1530	Uravan	1524
	Canyon Preserve	2160	Telluride	2643	Placerville	2142

Table 3. Results from logistic regression of well-documented establishment events and spring maximum flow for regulated and unregulated reaches along the Dolores and San Miguel Rivers. Italicized *p*-values represent significant relationships ($p < 0.05$).

River	Reach	Species	Regulation Status	Slope Direction	ROC	r^2	*p*-value
Dolores	Upper Dolores	*P. angustifolia*	Unregulated	-	0.522	0.007	0.509
		A. negundo	Unregulated	+	0.828	0.145	*0.031*
	Reach 1 & 3	*P. angustifolia*	Pre-dam	-	0.688	0.069	0.223
			Post-dam	-	0.727	0.115	0.061
			Pooled	-	0.727	0.110	*0.015*
	Reach 1 & 3	*A. negundo*	Pre-dam	+	0.725	0.085	0.176
			Post-dam	+	0.519	0.002	0.837
			Pooled	+	0.609	0.024	0.306
	Reach 4, 5 & 6	*A. negundo*	Pre-dam	+	0.788	0.201	*0.037*
			Post-dam	+	0.850	0.281	*0.014*
			Pooled	+	0.806	0.183	*0.005*
	Reach 4	*P. deltoides* subsp. *wislizenii*	Pre-dam	+	0.704	0.153	*0.027*
			Post-dam	+	0.527	0.002	0.826
			Pooled	+	0.624	0.061	0.051
	Reach 6	*P. deltoides* subsp. *wislizenii*	Pre-dam	+	0.603	0.006	0.752
			Post-dam	+	0.564	0.011	0.558
			Pooled	-	0.480	0.001	0.870
San Miguel	Tabeguache Preserve	*P. deltoides* subsp. *wislizenii*	Unregulated	+	0.557	0.009	0.450
		P. angustifolia	Unregulated	+	0.550	0.043	0.146
	Canyon Preserve	*P. angustifolia*	Unregulated	-	0.819	0.175	*0.018*

Table 4. Results from forward stepwise selection of flow and climate variables used to predict probability of well-documented *Populus angustifolia* establishment events along reaches of the Dolores and San Miguel Rivers.

River	Reach	Regulation status (Time period)	Independent Variables	Slope direction	ROC	Model R^2	*p*-value
Dolores	Upper Dolores	Unregulated (1961-2008)	Winter Mean Temp	+	0.729	0.126	*0.0039*
	Reach 1 and 3	Pre- and Post-dam (1961-2008)	Winter Mean Temp Spring Precipitation	+ -	0.889	0.412	<*0.0001*
San Miguel	Tabeguache	Unregulated (1961-2008)	Summer MAX Flow Winter MAX Flow	+ -	0.761	0.170	*0.0154*
	Canyon	Unregulated (1961-2008)	Summer MAX Flow Subsequent Year MAX Flow Spring Mean Temp Spring Mean Flow	- + + +	0.953	0.598	*0.0007*

Table 5. Results from forward stepwise selection of flow and climate variables used to predict probability of well-documented *Populus deltoides* subsp. *wislizenii* establishment events along reaches of the Dolores and San Miguel Rivers.

River	Reach	Regulation status (Time period)	Independent Variables	Slope direction	ROC	Model R^2	*p*-value
Dolores	Reach 4	Pre- and Post-dam (1961-2008)	Winter MAX Flow Spring MAX Flow	- +	0.745	0.190	*0.0027*
	Reach 6	Pre- and Post-dam (1961-2008)	Summer MIN Flow	+	0.755	0.158	*0.0029*
San Miguel	Tabeguache	Unregulated (1961-2008)	Summer MAX Flow Winter MIN Flow	+ -	0.719	0.106	*0.0347*

Table 6. Results from forward stepwise selection of flow and climate variables used to predict probability of well-documented *Acer negundo* establishment events along reaches of the Dolores River.

River	Reach	Regulation status (Time period)	Independent Variables	Slope direction	ROC	Model R^2	*p*-value
Dolores	Upper Dolores	Unregulated (1961-2008)	Summer Mean Flow	+	0.823	0.312	*0.0016*
	Reach 1 & 3	Pre- and Post-dam (1961-2008)	Winter Mean Temp Spring MIN Flow Spring Mean Temp	- + -	0.841	0.288	*0.0060*
	Reach 4, 5 & 6	Pre- and Post-dam (1961-2008)	Spring MAX Flow Summer Mean Temp Summer MIN Flow	+ - +	0.881	0.352	*0.0016*

Table 7. Relationship (r^2) between standardized growth and seasonal mean flows for reaches along the Upper and Lower Dolores and San Miguel Rivers. A quadratic fit was the best fit for all species across all reaches. *p-value < 0.05; **p-value <0.001

River	**Reach**	**Species**	**Regulation Status**	**Mean Flow**	**r^2**
Dolores	Upper Dolores	*P. angustifolia*	Unregulated	Winter	0.066
				Spring	0.013
				Summer	0.011
	Reach 1	*P. angustifolia*	Pre-dam	Winter	0.055
				Spring	0.274*
				Summer	0.125
			Post-dam	Winter	0.003
				Spring	0.072
				Summer	0.323*
	Reach 3	*P. angustifolia*	Pre-dam	Winter	0.423*
				Spring	0.274*
				Summer	0.214
			Post-dam	Winter	0.019
				Spring	0.212
				Summer	0.407*
	Reach 3	*A. negundo*	Pre-dam	Winter	0.112
				Spring	0.441*
				Summer	0.438*
			Post-dam	Winter	0.143
				Spring	0.585**
				Summer	0.470*
	Reach 4	*A. negundo*	Pre-dam	Winter	0.032
				Spring	0.452*
				Summer	0.358*
			Post-dam	Winter	0.441*
				Spring	0.323*
				Summer	0.409*
	Reach 4	*P. deltoides* subsp. *wislizenii*	Pre-dam	Winter	0.119
				Spring	0.232
				Summer	0.275*
			Post-dam	Winter	0.087
				Spring	0.145
				Summer	0.205
San Miguel	Tabeguache Preserve	*P. deltoides* subsp. *wislizenii*	Unregulated	Winter	0.101
				Spring	0.140*
				Summer	0.099
	Canyon Preserve	*P. angustifolia*	Unregulated	Winter	0.042
				Spring	0.219*
				Summer	0.065

Table 8. Relationship (r^2) between standardized growth and seasonal Palmer Drought Severity Index (PDSI) for reaches along the Lower Dolores River. A quadratic fit was the best fit for all species across all reaches. **p*-value < 0.05, ***p*-value < 0.001

River	Reach	Species	Regulation Status	PDSI	r^2
Dolores	Reach 1	*P. angustifolia*	Pre-dam	Winter	0.108
				Spring	0.227
				Summer	0.245
			Post-dam	Winter	0.353*
				Spring	0.369*
				Summer	0.297*
	Reach 3	*P. angustifolia*	Pre-dam	Winter	0.235
				Spring	0.417*
				Summer	0.499**
			Post-dam	Winter	0.235
				Spring	0.265*
				Summer	0.300*
	Reach 3	*A. negundo*	Pre-dam	Winter	0.266*
				Spring	0.644**
				Summer	0.537**
			Post-dam	Winter	0.660**
				Spring	0.651**
				Summer	0.526**
	Reach 4	*A. negundo*	Pre-dam	Winter	0.004
				Spring	0.233
				Summer	0.168
			Post-dam	Winter	0.300*
				Spring	0.166
				Summer	0.140
	Reach 4	*P. deltoides* subsp. *wislizenii*	Pre-dam	Winter	0.031
				Spring	0.076
				Summer	0.138
			Post-dam	Winter	0.209
				Spring	0.288*
				Summer	0.291*

Table 9. Relationship (r^2) between standardized growth and seasonal Palmer Drought Severity Index (PDSI) for reaches along the regulated Lower Dolores River (pre- and post-dam) and unregulated comparison reaches at the Upper Dolores and San Miguel Rivers (1961-2008). A quadratic fit was the best fit for all species across all reaches. **p*-value < 0.05, ***p*-value < 0.001

River	**Reach**	**Species**	**Regulation Status**	**PDSI**	**r^2**
Dolores	Upper Dolores	*P. angustifolia*	Unregulated	Winter	0.001
				Spring	0.005
				Summer	0.006
Dolores	Reach 1	*P. angustifolia*	Pre- and Post-dam	Winter	0.313**
				Spring	0.277**
				Summer	0.224*
Dolores	Reach 3	*P. angustifolia*	Pre- and Post-dam	Winter	0.355**
				Spring	0.411**
				Summer	0.454**
San Miguel	Canyon Preserve	*P. angustifolia*	Unregulated	Winter	0.326**
				Spring	0.136*
				Summer	0.111
Dolores	Reach 4	*P. deltoides* subsp. *wislizenii*	Pre- and Post-dam	Winter	0.260*
				Spring	0.236*
				Summer	0.235*
San Miguel	Tabeguache Preserve	*P. deltoides* subsp. *wislizenii*	Unregulated	Winter	0.075
				Spring	0.083
				Summer	0.113

Table 10. Results from multivariate model selection based on AICc values of flow and climate variables related to standardized growth of *Populus angustifolia* along unregulated and regulated reaches of the Dolores and San Miguel Rivers.

River	Reach	Regulation status (Time period)	Independent Variables	Slope direction	Model R^2	*p*-value	AICc
Dolores	Upper Dolores	Unregulated (1961-2008)	Spring MAX Flow	+	0.185	0.0618	-81.400
			Winter MIN Flow	-			
			Spring Mean Temp.	+			
			Summer Mean Temp.	-			
	Reach 1	Pre-dam (1961-1984)	Winter Precipitation	+	0.202	*0.0277*	-28.815
		Post-dam (1985-2008)	Summer PDSI	+	0.608	*0.0009*	-33.608
			Summer Mean Temp.	+			
			Winter Precipitation	-			
			Summer Precipitation	-			
		Pooled (1961-2008)	Summer PDSI	+	0.109	0.0750	-55.004
			Summer Precipitation	+			
	Reach 3	Pre-dam (1961-1984)	Winter PDSI	-	0.677	*0.0002*	-28.045
			Spring PDSI	+			
			Winter Mean Flow	+			
			Spring Precipitation	-			
		Post-dam (1961-2008)	Summer PDSI	+	0.546	*0.0003*	-21.948
			Winter Mean Temp	+			
		Pooled (1961-2008)	Summer PDSI	+	0.511	*<0.0001*	-50.732
			Winter Mean Flow	+			
			Summer MAX Flow	+			
			Winter Mean Temp.	+			
San Miguel	Canyon Preserve	Unregulated (1961-2008)	Winter PDSI	+	0.618	*<0.0001*	-58.740
			Spring MAX Flow	+			
			Spring Mean Temp.	+			
			Summer Mean Temp.	-			

Table 11. Results from multivariate model selection based on AICc values of flow and climate variables related to standardized growth of *P. deltoides* subsp. *wislizenii* along unregulated and regulated reaches of the Dolores and San Miguel Rivers.

River	Reach	Regulation status (Time period)	Independent Variables	Slope direction	Model R^2	*p*-value	AICc
Dolores	Reach 4	Pre-dam (1961-1984)	Spring Mean Flow Spring MIN Flow Spring Precipitation Summer Precipitation	+ - + +	0.552	*0.0030*	-14.241
		Post-dam (1985-2008)	Summer PDSI Summer MIN Flow	+ -	0.391	*0.0055*	20.906
		Pooled (1961-2008)	Summer PDSI Winter Mean Temp.	+ -	0.252	*0.0015*	17.643
San Miguel	Tabeguache Preserve	Unregulated (1961-1984)	Spring Mean Flow Summer MAX Flow Summer Precipitation	+ - +	0.233	*0.0080*	-4.955

Table 12. Results from multivariate model selection based on AICc values of flow and climate variables related to standardized growth of *A. negundo* along unregulated and regulated reaches of the Dolores and San Miguel Rivers.

River	Reach	Regulation status (Time period)	Independent Variables	Slope direction	Model R^2	*p*-value	AICc
Dolores	Reach 3	Pre-dam (1961-1984)	Winter PDSI	-	0.688	*<0.0001*	-23.168
			Spring PDSI	+			
			Spring Precipitation	-			
		Post-dam (1985-2008)	Summer PDSI	+	0.754	*<0.0001*	-4.589
			Winter MIN Flow	+			
			Summer Mean Temp	+			
		Pooled (1961-2008)	Spring PDSI	+	0.679	*<0.0001*	-24.525
			Spring Mean Flow	-			
			Spring MAX Flow	+			
			Winter MIN Flow	+			
			Summer Mean Temp.	+			
	Reach 4	Pre-dam (1961-1984)	Spring Mean Flow	+	0.758	*<0.0001*	-6.345
			Spring MIN Flow	-			
			Summer Mean Temp	+			
			Spring Precipitation	+			
			Summer Precipitation	+			
		Post-dam (1985-2008)	Winter PDSI	+	0.414	*0.0007*	-5.471
		Pooled (1961-2008)	Spring Mean Flow	+	0.500	*<0.0001*	-13.905
			Spring MIN Flow	-			
			Summer MIN Flow	+			

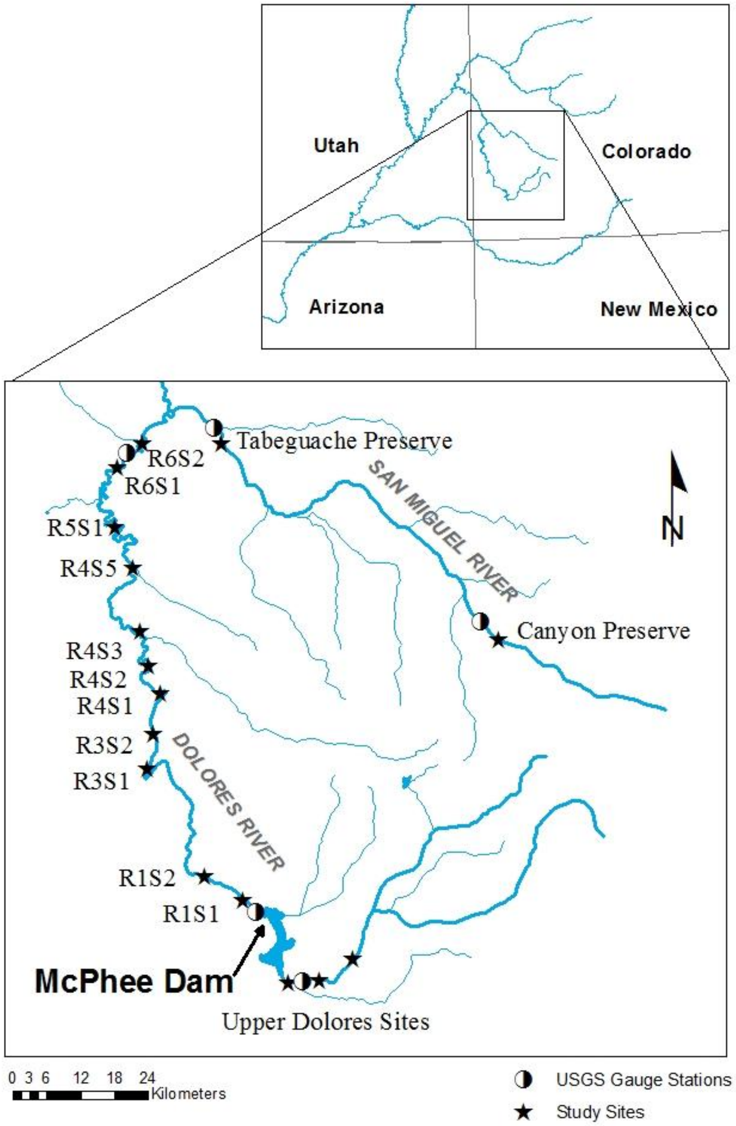

Figure 1. Map of study sites along Upper Dolores, Lower Dolores, and San Miguel Rivers. All regulated sites are designated by R (reach) and S (segment), while unregulated sites are designated by location (Upper Dolores Sites, Tabeguache and Canyon Preserves).

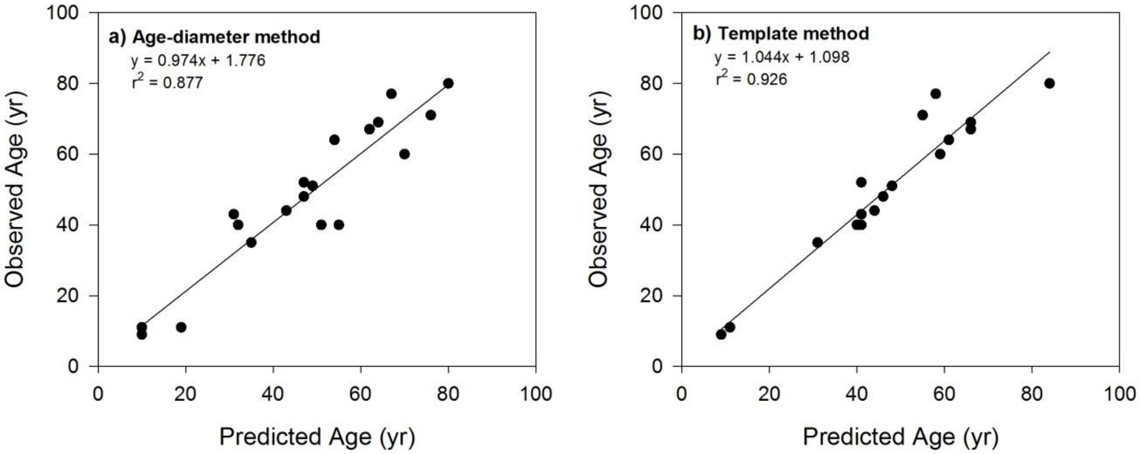

Figure 2. Relationship between observed and predicted tree ages of *P. angustifolia* at Reach 1/Segment 1 using: a) an age-diameter at coring height model to predict tree age (y = 1.519*dch), and b) a template method to estimate tree age. Regression equations for observed versus predicted ages are included in each figure.

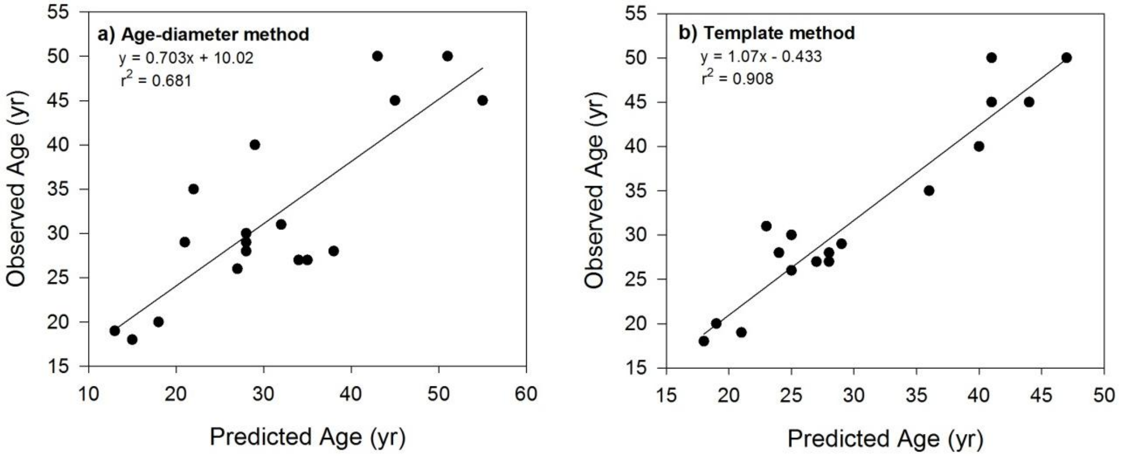

Figure 3. Relationship between observed and predicted tree ages of *P. deltoides* subsp. *wislizenii* at Reach 4/Segment 5 using: a) an age-diameter at coring height model to predict tree age (y = 0.853*dch + 0.544*BA), and b) a template method to estimate tree age. Regression equations for observed versus predicted ages are included in each figure.

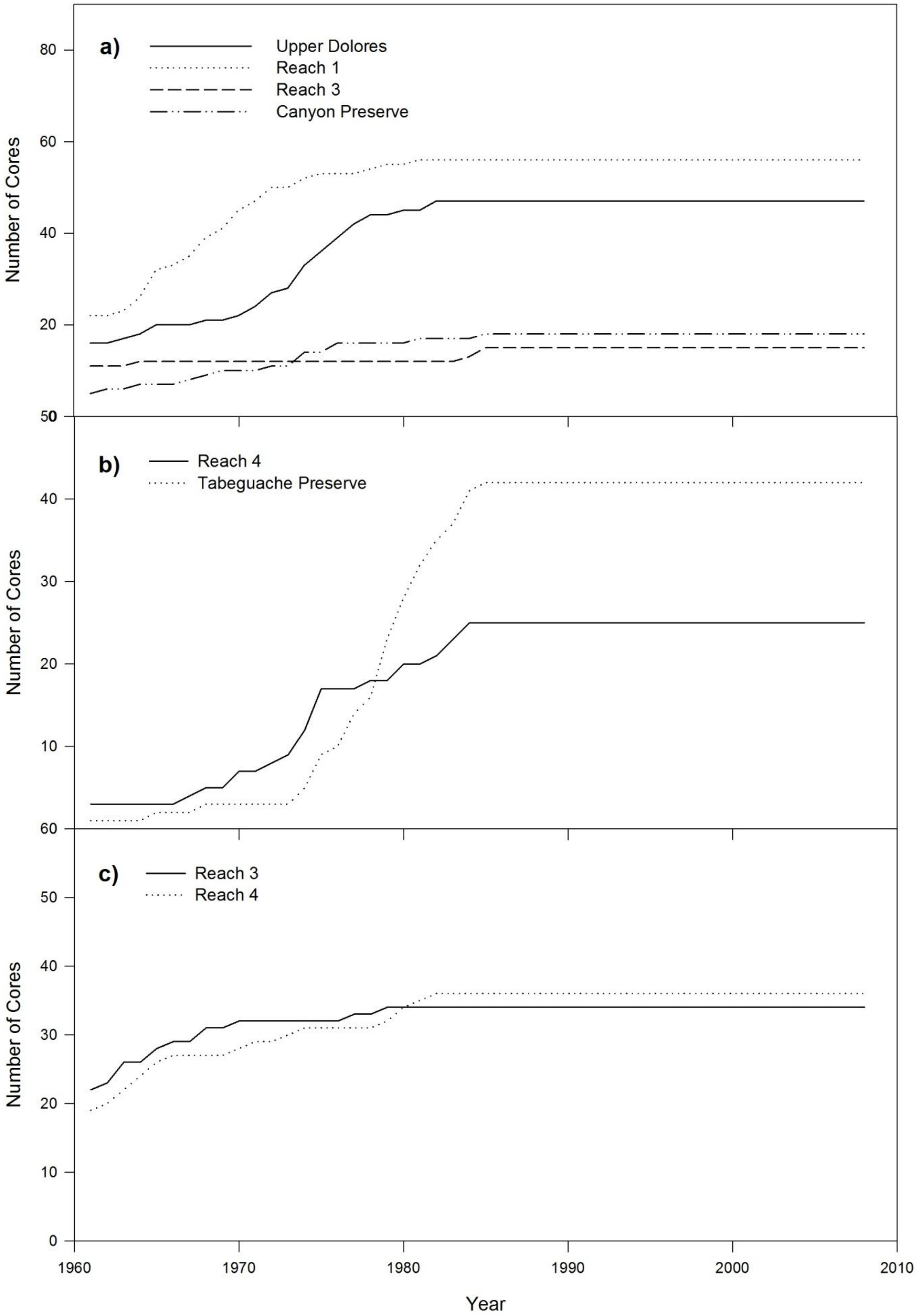

Figure 4. Sample depth of number of cores for: a) *P. angustifolia*, b) *P. deltoides* subsp. *wislizenii*, and c) *A. negundo* along reaches of the Dolores and San Miguel Rivers.

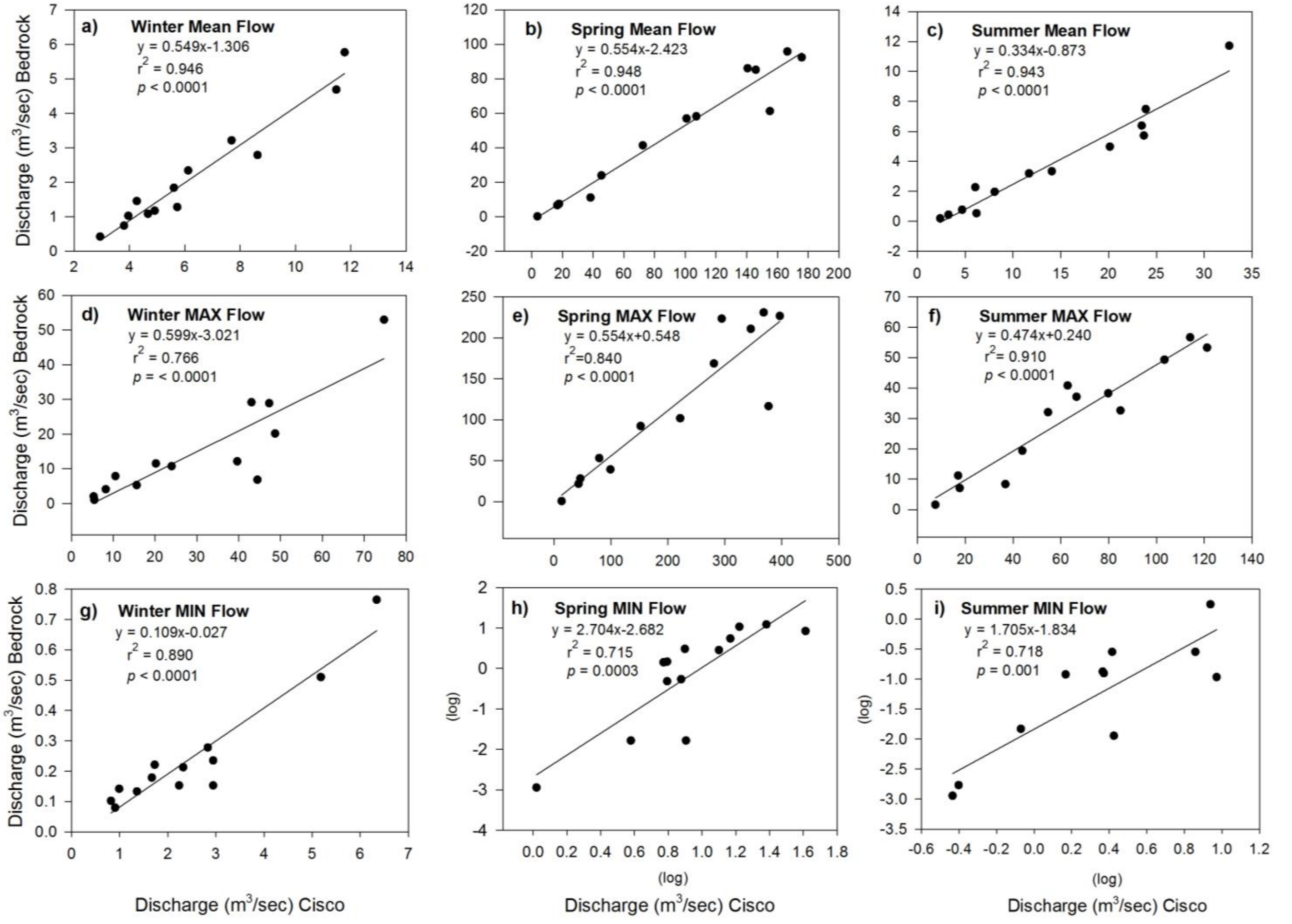

Figure 5. Relationship between seasonal stream discharge (a-i) at the Bedrock and Cisco Gauge Stations for years 1972 to 1984. Data were log transformed on both the y and x axes for plots h and i. Equations within each graph were used to predict seasonal flow from 1961-1971at the Bedrock Gauge Station.

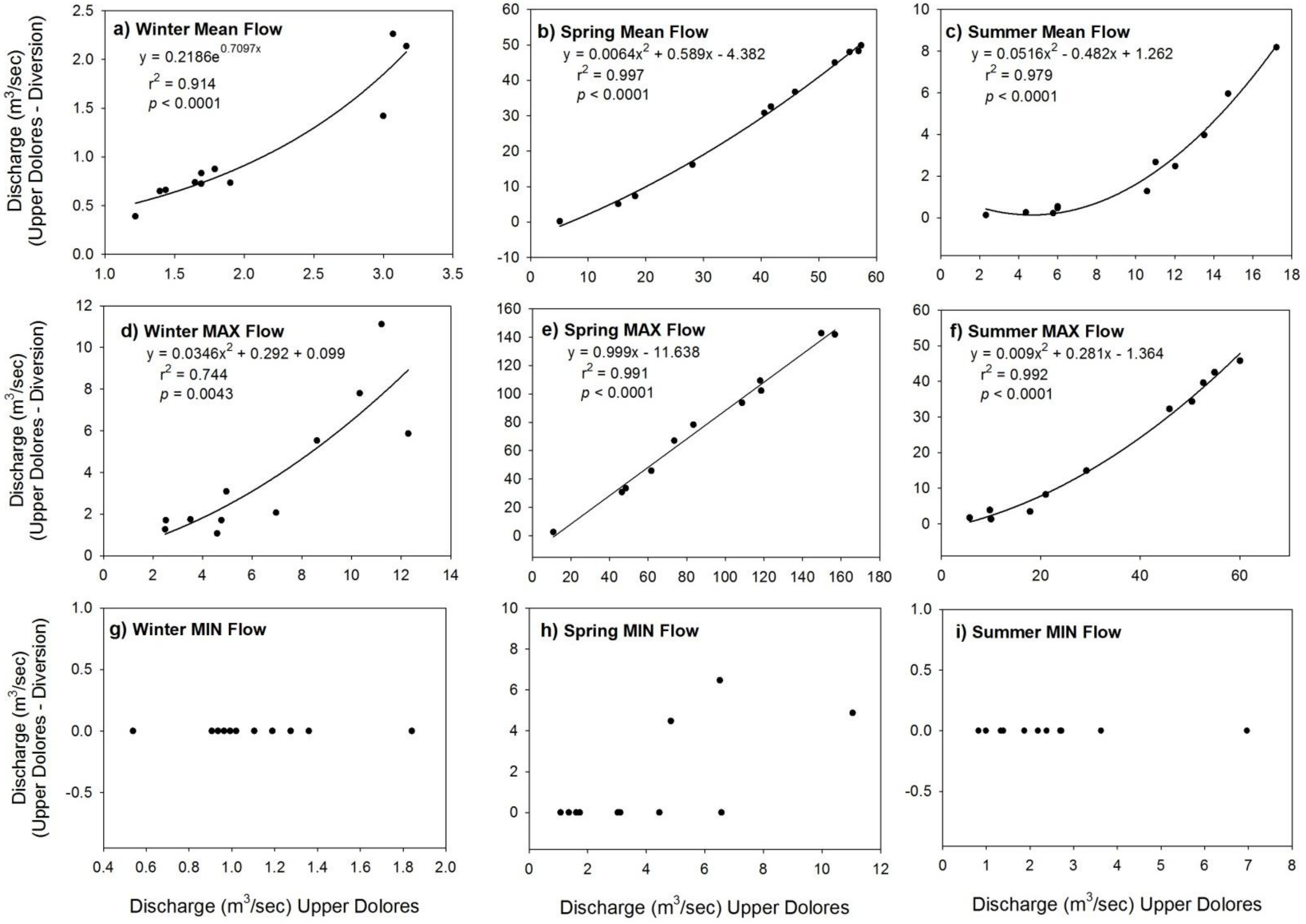

Figure 6. Relationship between seasonal stream discharge (a-i) at the Upper Dolores Gauge Station and calculated discharge values (Upper Dolores – Diversion) for years 1974 to 1984. Equations within each graph were used to predict seasonal flow from 1961-1973 at the McPhee Gauge Station.

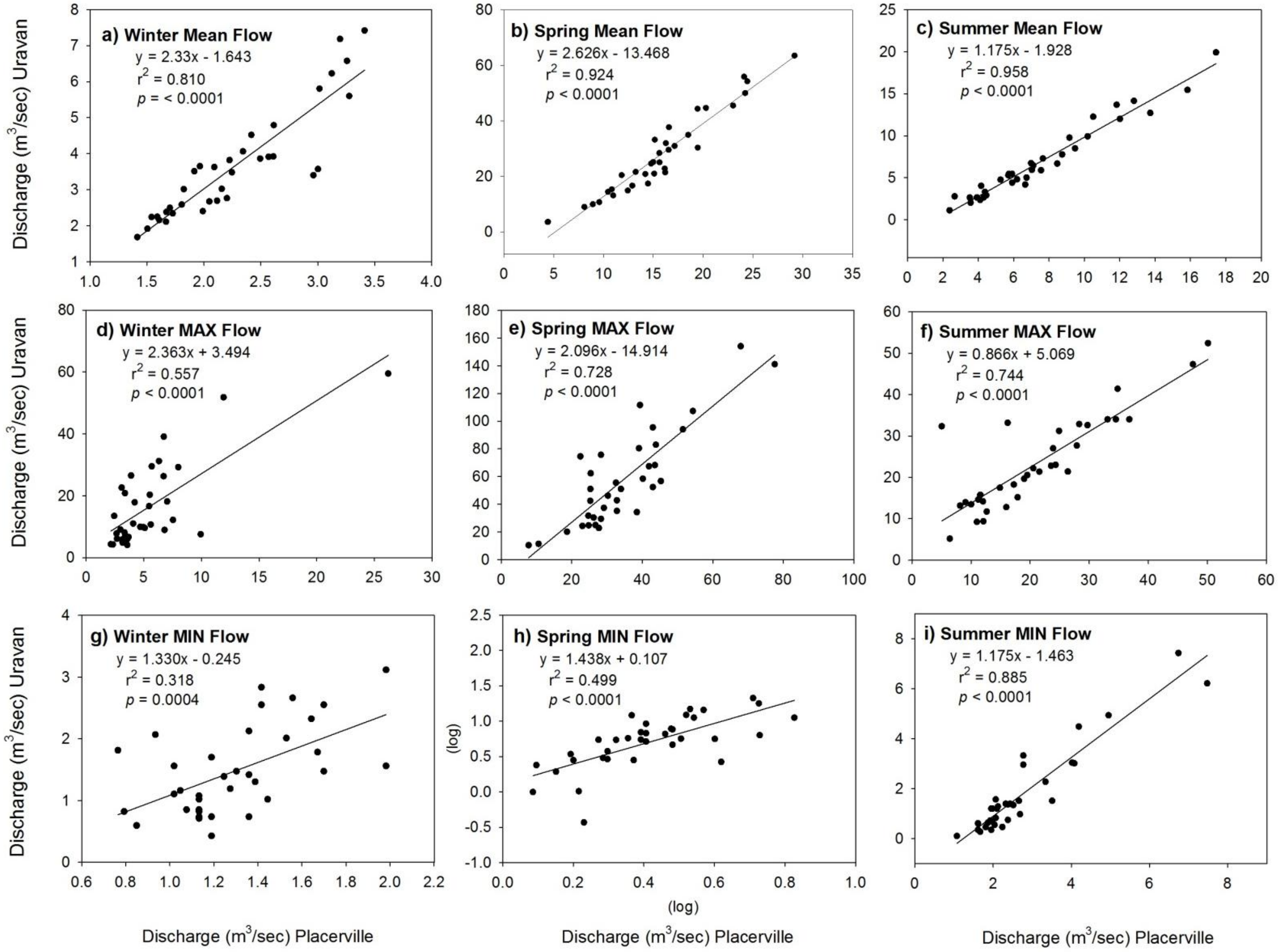

Figure 7. Relationship between seasonal stream discharge (a-i) at the Uravan and Placerville Gauge Stations for years 1974 to 2008 at the San Miguel River. Data were log transformed on both the y and x axes for plot h. Equations within each graph were used to predict missing data on seasonal flow at the Uravan Gauge Station for years 1961 to 1973.

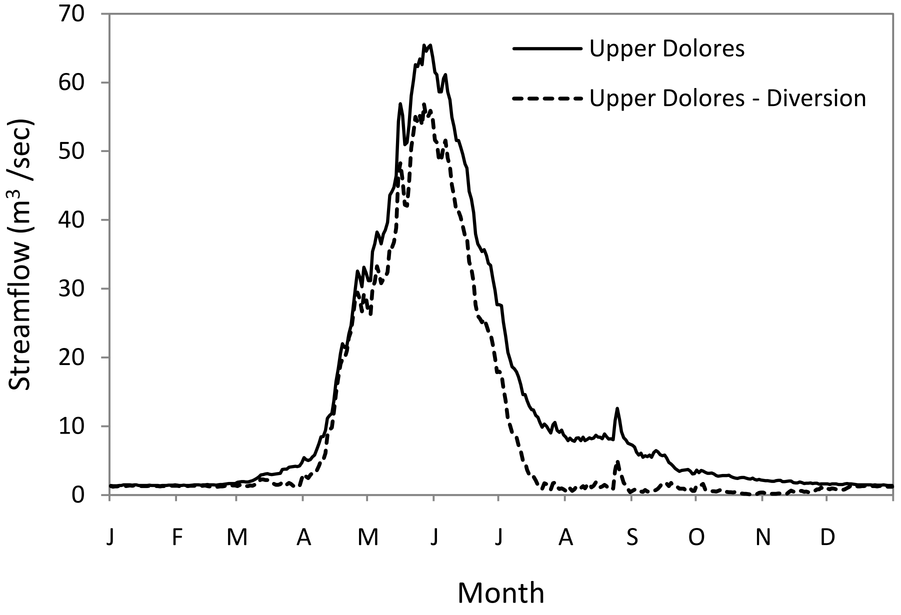

Figure 8. Mean daily streamflow from 1974-1984 at the unregulated Upper Dolores River (Upper Dolores) and calculated values of Dolores Gauge Station minus water diversion into irrigation canals (Upper Dolores – Diversion).

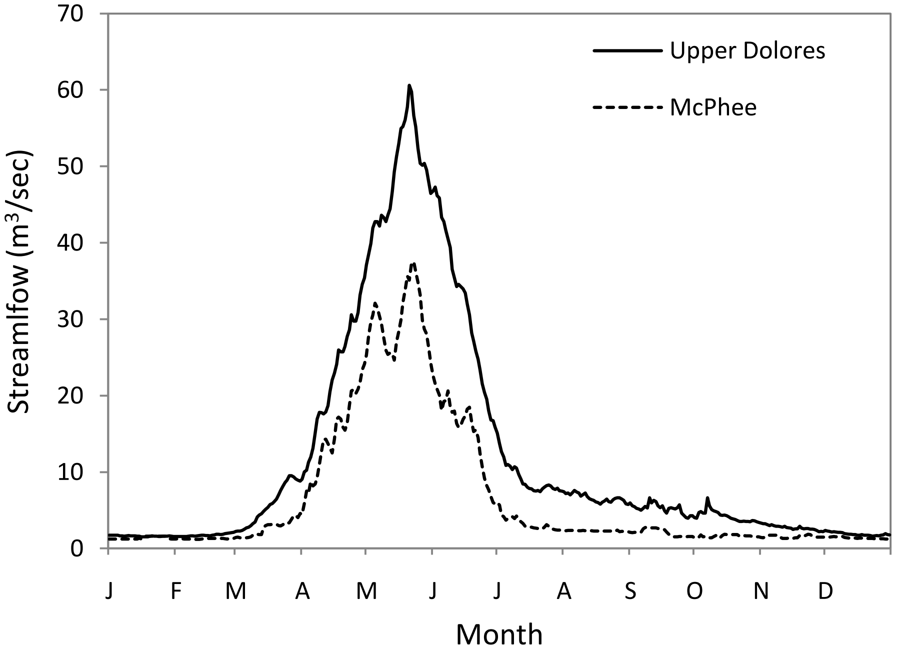

Figure 9. Mean daily streamflow from 1985 to 2008 at the unregulated Upper Dolores River (Upper Dolores) and regulated Lower Dolores River (McPhee).

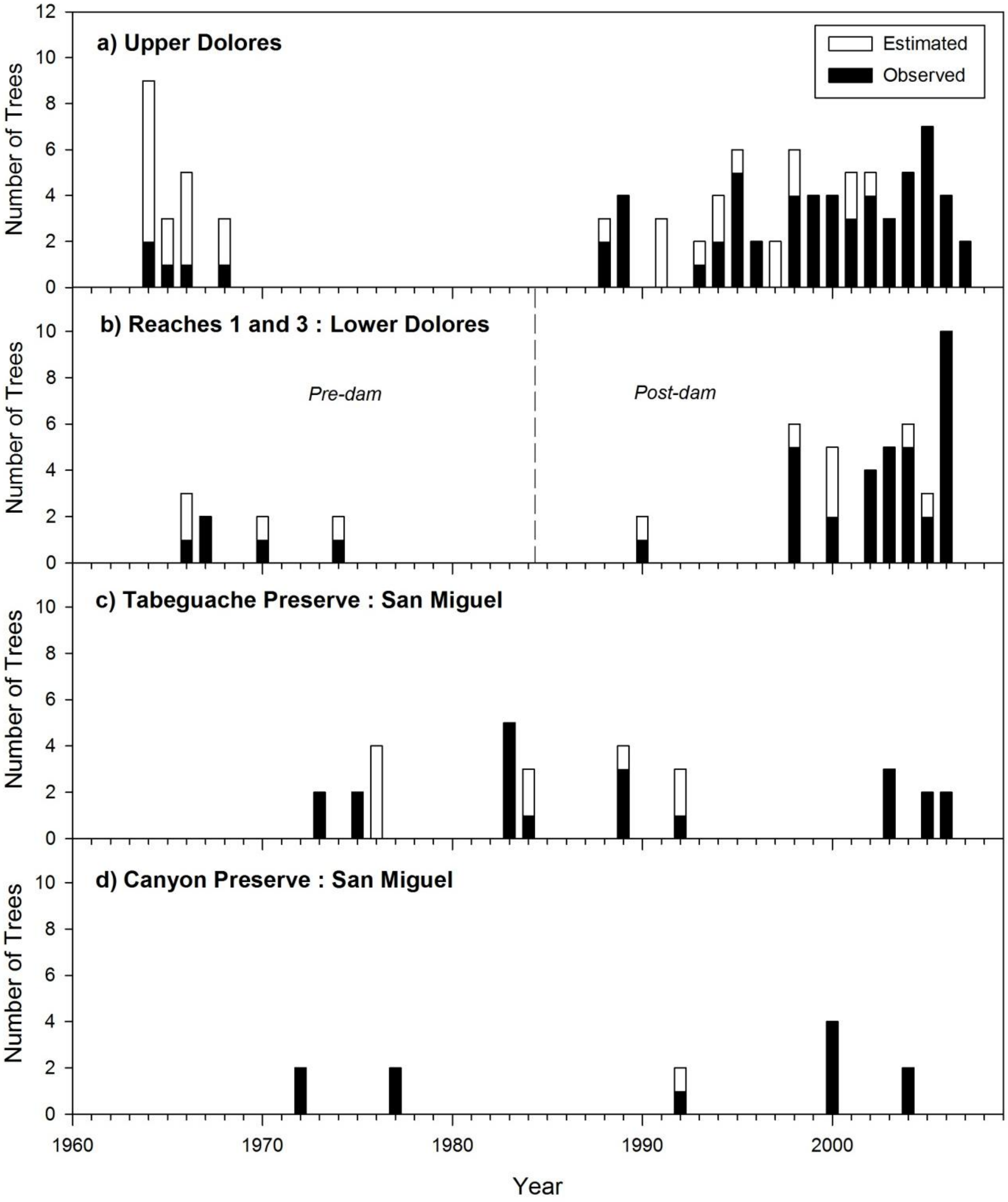

Figure 10. Number of *P. angustifolia* trees that established in sample reaches by year of establishment at the a) Upper Dolores River, b) Reaches 1 and 3, Lower Dolores River, c) Tabeguache Preserve, San Miguel River, and d) Canyon Preserve, San Miguel River. The number of trees is shown separately for tree ages observed directly by counting rings to pith and ages estimated by the template method when pith was missing. At least two trees had to establish at a reach for a year to be defined as an establishment year.

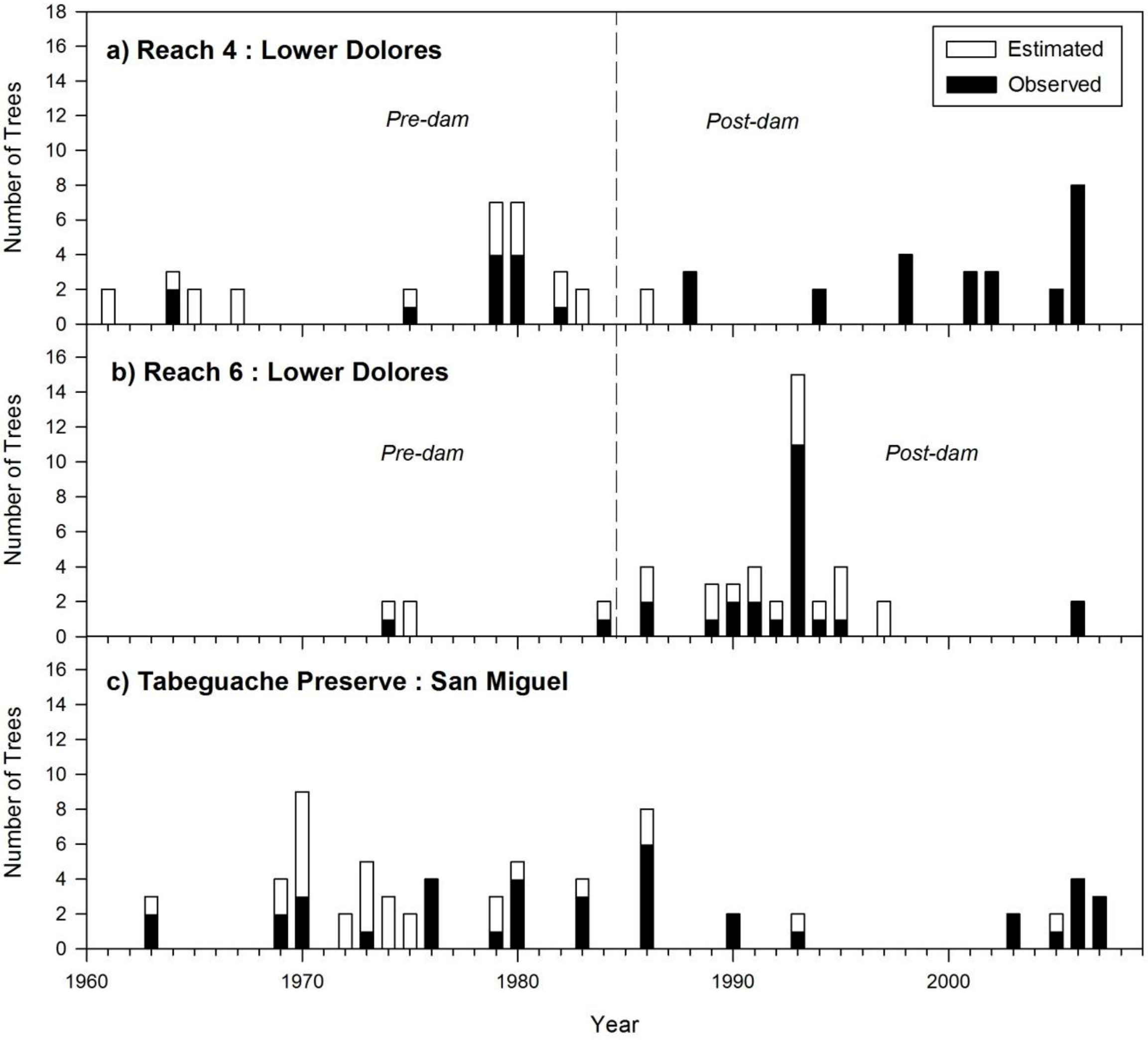

Figure 11. Number of *P. deltoides* subsp. *wislizenii* trees that established in sample reaches by year of establishment at a) Reach 4, Lower Dolores River, b) Reach 6, Lower Dolores River, and d) Tabeguache Preserve, San Miguel River. The number of trees is shown separately for tree ages observed directly by counting rings to pith and ages estimated by the template method when pith was missing. At least two trees had to establish at a reach for a year to be defined as an establishment year.

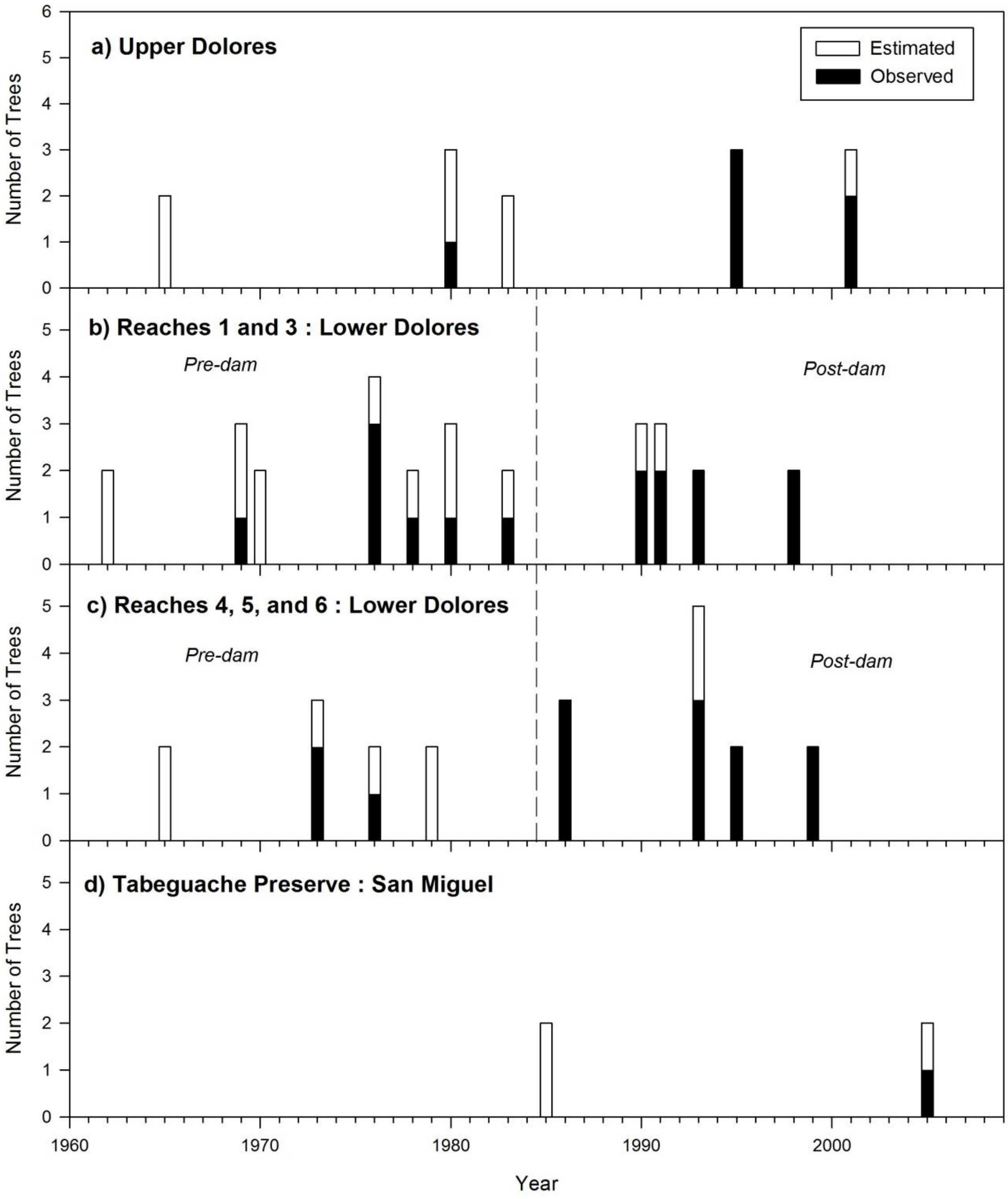

Figure 12. Number of *A. negundo* trees that established in sample reaches by year of establishment at the a) Upper Dolores River, b) Reaches 1 and 3, Lower Dolores River, c) Reach 4, 5 and 6, Lower Dolores River, and d) Tabeguache Preserve, San Miguel River. The number of trees is shown separately for tree ages observed directly by counting rings to pith and ages estimated by the template method when pith was missing. At least two trees had to establish at a reach for a year to be defined as an establishment year.

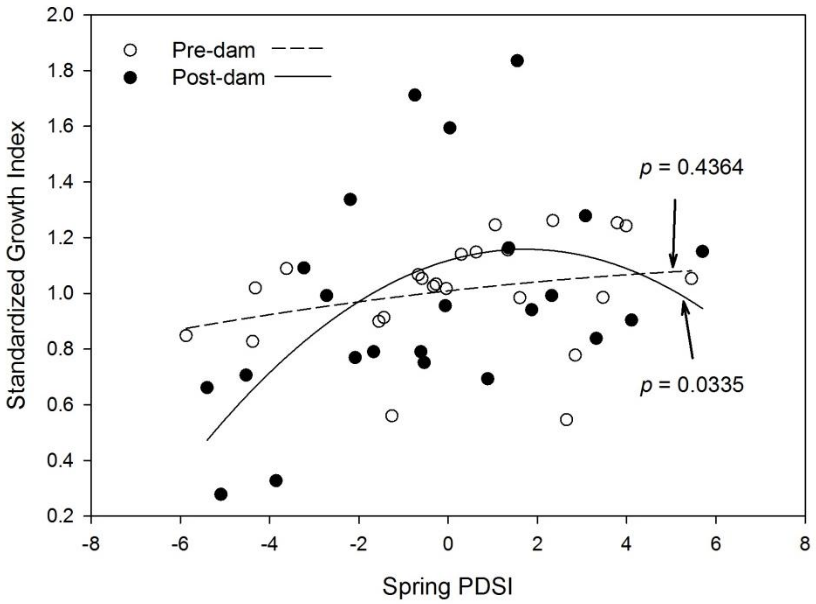

Figure 13. Relationship between standardized growth index of *P. deltoides* subsp. *wislizenii* and spring Palmer Drought Severity Index (PDSI) at Reach 4 of the Dolores River during the pre-dam period (1961-1984) and post-dam period (1985-2008, excluding extreme drought year 2002). Dashed and solid lines correspond with pre-dam and post-dam time periods, respectively.

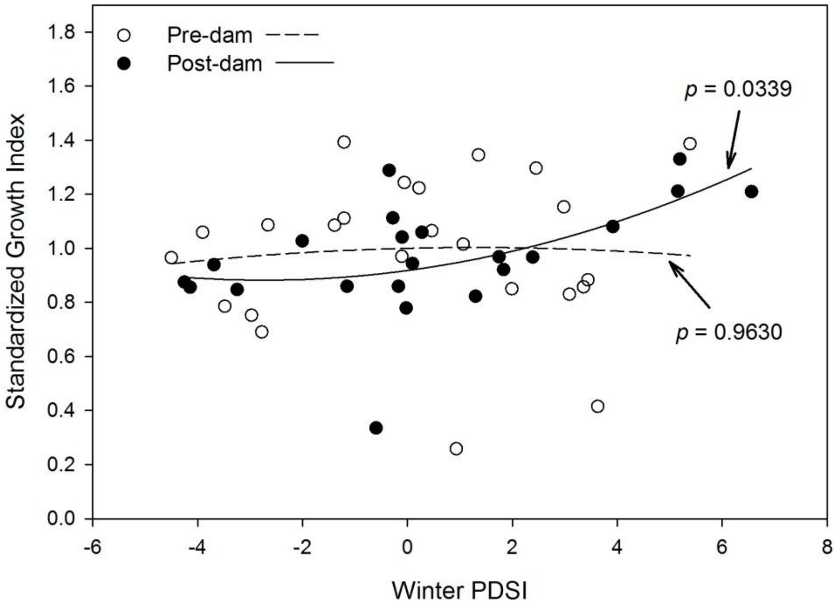

Figure 14. Relationship between standardized growth index of *A. negundo* and winter Palmer Drought Severity Index (PDSI) at Reach 4 of the Lower Dolores River during the pre-dam period (1961-1984) and post-dam period (1985-2008, excluding extreme drought years 2002 and 2003). Dashed and solid lines correspond with pre- and post-dam time periods, respectively.

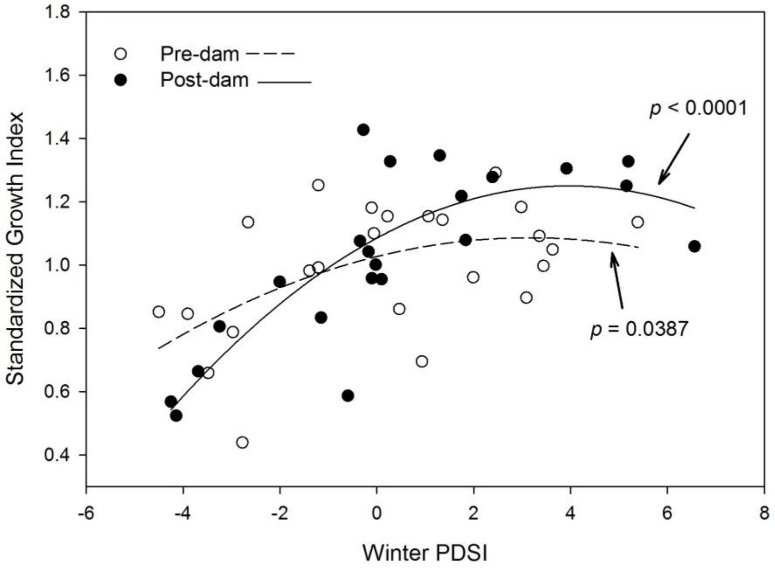

Figure 15. Relationship between standardized growth index of *A. negundo* and winter Palmer Drought Severity Index (PDSI) at Reach 3 of the Dolores River during the pre-dam period (1961-1984) and post-dam period (1985-2008, excluding extreme drought years 2002 and 2003). Dashed and solid lines correspond with pre- and post-dam time periods, respectively.

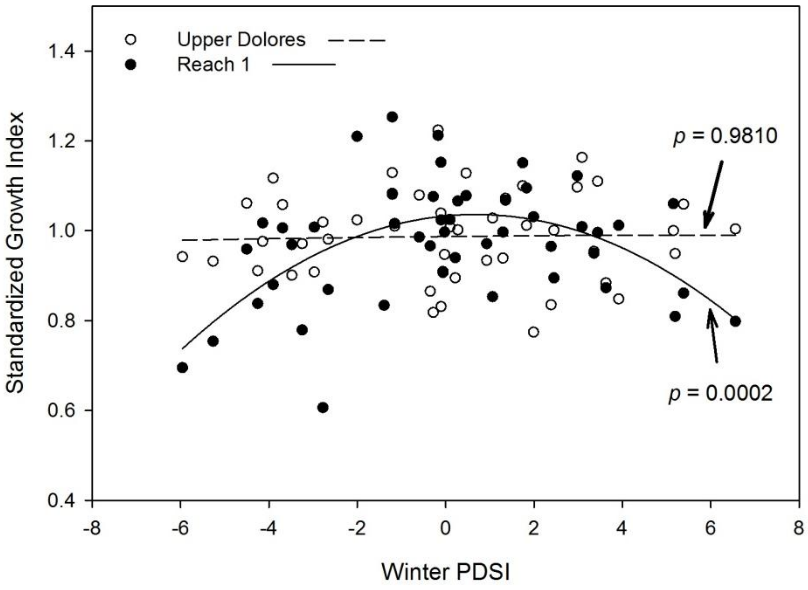

Figure 16. Relationship between standardized growth index of *P. angustifolia* and winter Palmer Drought Severity Index (PDSI) at the unregulated Upper Dolores River and Reach 1 (pre- and post-dam) of the Lower Dolores River for years 1961-2008. Dashed and solid lines correspond with the Upper Dolores Reach and Reach 1, respectively.

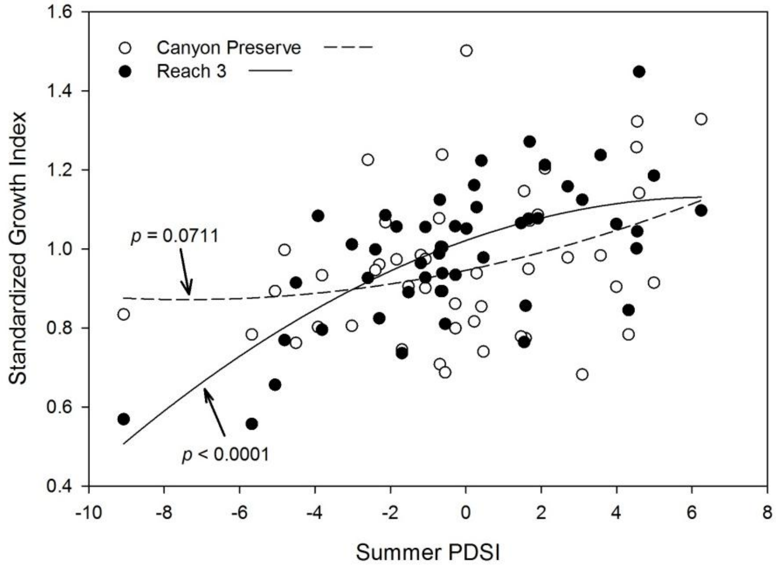

Figure 17. Relationship between standardized growth index of *P. angustifolia* and summer Palmer Drought Severity Index (PDSI) at the unregulated San Miguel River, Canyon Preserve and Reach 3 (pre- and post-dam) of the Lower Dolores River for years 1961-2008. Dashed and solid lines correspond with the Canyon Preserve and Reach 3, respectively.

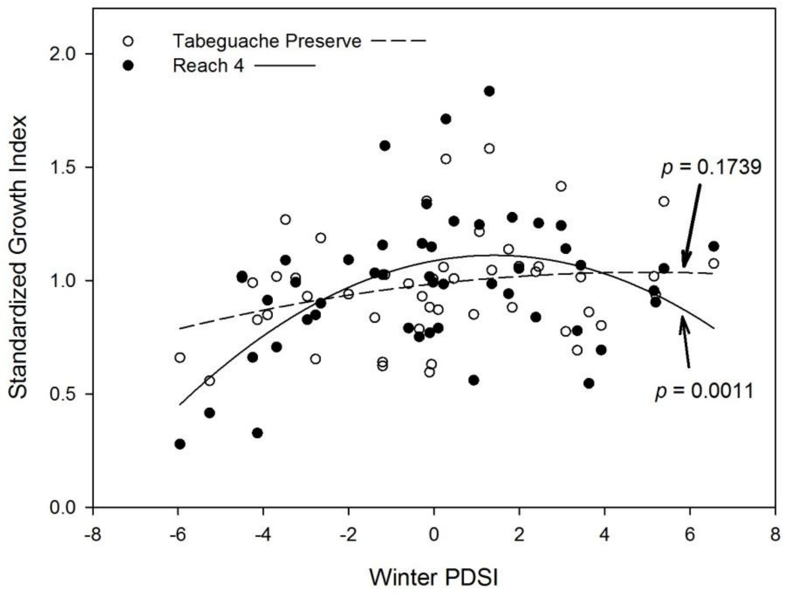

Figure 18. Relationship between standardized growth index of *P. deltoides* subsp. *wislizenii* and winter Palmer Drought Severity Index (PDSI) at the unregulated San Miguel River, Tabeguache Preserve and Reach 4 (pre- and post-dam) of the Lower Dolores River for years 1961-2008. Dashed and solid lines correspond with the Tabeguache Preserve and Reach 4, respectively.

Chapter 4

Management Recommendations

The goal of this chapter is to offer streamflow recommendations for land and water managers to promote the establishment and sustain appropriate growth of native riparian trees along the Lower Dolores River. For *Populus deltoides* subsp. *wislizenii* we observed ample recruitment throughout the post-dam period at Reaches 4 and 6 which suggests healthy conditions for establishment of that species along the Lower Dolores River at these reaches. Thus, seasonal variation in streamflow should be maintained along the Lower Dolores River, such as high streamflow during the months of May and June followed by receding flows into the summer months of July through September.

Based on the work of Merritt and Cooper (2000), extreme departure from seasonal variation in streamflow can have detrimental effects on the recruitment of *P. deltoides* subsp. *wislizenii*. Merritt and Cooper (2000) observed little seasonal variation in streamflow along the regulated Green River compared to the unregulated Yampa River. Mean daily streamflow was greatly reduced through the months of April through June, while mean daily streamflow was greater through the months of October through February and August. This should be avoided on the Lower Dolores River because reduced seasonal variation in streamflow could reduce the number of establishment events for *P. deltoides* subsp. *wislizenii*.

In our study, the establishment of *A. negundo* was associated with higher flows throughout the spring and summer seasons. DeWine and Cooper (2007) found that high spring maximum flows along the regulated Green River facilitated the establishment of

A. negundo. Annual variation in seasonal streamflow should be maintained, such as above average spring maximum flows (> 38 m^3/sec) at the end of May followed by above-average summer streamflow through the months of July through September. Based on our results and the work of DeWine and Cooper (2007), releases that follow this recommendation should support *A. negundo* recruitment along the Lower Dolores River.

We found evidence that river damming and water diversion through irrigation canals increased tree growth sensitivity to drought for all species along the Lower Dolores River. For the remainder of the 21st century, climate models have predicted more frequent drought years for the Southwestern U.S. (Seager et al., 2007). With respect to flow releases from McPhee Dam, particular attention should be directed towards years with little snowpack or low levels of snow water equivalencies at higher elevations within the Dolores River watershed. During extreme drought years, water releases from McPhee Dam should be planned accordingly so that releases do not fall below critical levels that are damaging for riparian trees. Based on tree growth and streamflow relationships for all species, we recommend that during drought years mean spring (April through June) and summer (July through September) flow does not fall below 10 and 3 m^3/sec, respectively. During the post-dam period, decline in tree growth across all reaches was apparent when values fell below this threshold.

References

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