

TREE GROWTH AND REGENERATION RESPONSE TO CLIMATE AND STREAM FLOW IN A SPECIES-RICH SOUTHWESTERN RIPARIAN FOREST

Donna M. Galuszka¹ and Thomas E. Kolb^{1,2}

ABSTRACT.—We studied the influence of climate variables, stream flow, and topography on regeneration and growth of several riparian tree species (*Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Juglans major*, *Platanus wrightii*, *Populus fremontii*, *Salix* spp.) at an unregulated perennial stream, West Clear Creek, in central Arizona. A pulse of seedling regeneration occurred for *Alnus*, *Fraxinus*, *Platanus*, *Populus*, and *Salix* in 1995 and 1996 following high winter and spring surface flows in 1993 and high spring surface flow in 1995. In contrast, little regeneration occurred for *Acer* and *Juglans* under these conditions. Most seedlings occurred at the active channel topographic location, and few seedlings occurred at abandoned channel, gravel-boulder bar, and bench locations. Relationships between environmental variables and annual radial stem growth varied among species and between constrained and unconstrained reaches. High spring or winter surface flows were negatively related to growth of *Acer*, *Alnus*, and *Platanus*, whereas high spring surface flow was positively related to growth of *Fraxinus*. Positive relationships between precipitation and growth occurred only for *Fraxinus* and *Juglans*, suggesting greater use of surface soil water by these species. Annual radial growth was high for *Platanus* and *Alnus*, medium for *Acer* and *Fraxinus*, and low for *Juglans*. Overall, the tree species in our study responded individually, rather than collectively, in regeneration and growth to changes in stream flow and climatic variables.

Key words: Arizona, *Acer negundo*, *Alnus oblongifolia*, climate, dendrochronology, *Fraxinus velutina*, *Juglans major*, *Platanus wrightii*, *Populus fremontii*, regeneration, riparian, *Salix*, tree ring, stream flow.

Riparian areas are physically linked to and dependent upon perennial, ephemeral, or intermittent surface or subsurface waters (Arizona State Parks 1994). These areas provide critical habitat for wildlife and vegetation across the United States (Brinson et al. 1981) and are important for maintaining regional biodiversity (Naiman et al. 1993). Riparian areas in the southwestern United States support forests that resemble the mesophytic humid forests that were widespread in the Early Tertiary era (Minckley and Brown 1982). The development of a drier climate after this era in the Southwest limited riparian forests to sites with dependable water sources (Minckley and Brown 1982). More recently, southwestern riparian forests have been depleted by human impacts such as flow regulation, dewatering, groundwater pumping, and grazing (Johnson and Haight 1984, Swift 1984, National Research Council 1992, Rood and Mahoney 1993, Stromberg 1993, Busch and Smith 1995, Stromberg et al. 1996). Given the high value and increasing scarcity of southwestern riparian forests,

factors that influence the regeneration and growth of riparian trees need to be better understood.

Flooding and resulting geomorphic changes in riparian ecosystems often cause changes in their biotic communities (Vannote et al. 1980). For example, recruitment of riparian *Populus* species has been linked to high surface flows in western North America (Everitt 1968, Brady et al. 1985, Howe and Knopf 1991). High flows scour openings along stream banks, widen floodplains, and deposit alluvium, thus creating extensive open fluvial surfaces for recruitment of pioneer trees such as *Populus* (Stromberg et al. 1991, 1993, Scott et al. 1997, Stromberg 1997). Moreover, seedfall for many riparian trees coincides with spring flooding (Everitt 1968, McBride and Strahan 1984, Fenner et al. 1985, Bock and Bock 1989, Siegel and Bock 1990, Stromberg 1993, Friedman et al. 1995). Further, overland flows created by spring flooding can promote seedling establishment by providing a moist seedbed for germination (Bock and Bock 1989, Stromberg 1997).

¹School of Forestry, Northern Arizona University, Box 15018, Flagstaff, AZ 86011-5018.

²Corresponding author.

Survival of riparian tree seedlings can be influenced by environmental factors such as temperature, pH, and salinity (Siegel and Bock 1990), as well as their location on the floodplain. Optimal germination sites for long-term survival of riparian trees are at elevations high enough on the floodplain to protect the substrate and new seedlings from scouring, yet low enough to provide direct contact with moist sediments (McBride and Strahan 1984, Stromberg et al. 1991, 1993, Scott et al. 1997, Stromberg 1997). Riparian forests also have been shown to develop successfully in abandoned channels created by fluctuating seasonal flows (Brady et al. 1985). Further, the topography of the floodplain may also affect long-term survival of riparian trees. Trees growing in broad floodplains may suffer lower mortality during high flows than those growing in narrow, constrained reaches due to high flow velocity and inundation in narrow reaches (Palik et al. 1998, Friedman and Auble 1999).

Most research on southwestern riparian forests has concentrated on low-elevation forests dominated by trees in the genera *Populus* and *Salix* and has focused on the impacts of stream flow or groundwater regulation by humans (e.g., Brady et al. 1985, Stromberg and Patten 1990, 1991, 1996, Howe and Knopf 1991, Stromberg et al. 1991, 1993, 1996, Stromberg 1993, 1997, Busch and Smith 1995, Cooper et al. 1999, Shafroth et al. 2000, Horton and Clark 2000, Horton et al. 2001). Factors that affect regeneration and growth of species-rich riparian forests of higher elevations in the Southwest (Brown 1982, Szaro 1990) are poorly understood, and yet these forests are widespread in the region and may be increasingly threatened by anthropogenic impacts as human populations grow in the Southwest. Our study addressed the influences of topographic location, stream flow, and climatic variables on regeneration and growth of several riparian tree species (*Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Juglans major*, *Platanus wrightii*, *Populus fremontii*, and *Salix* spp.) growing in a relatively pristine, species-rich riparian forest along an unregulated perennial stream in central Arizona, West Clear Creek.

We addressed the following hypotheses. First, high stream flow promotes seedling regeneration of all these tree species. Second, seedling density would be distributed unevenly across different topographic locations, with

the greatest densities occurring in abandoned channels, low benches, and adjacent to the active channel. Third, seedling density and annual radial growth of all species would be greater in unconstrained areas of the floodplain compared with bedrock-constrained areas. Fourth, annual radial growth of all tree species would be correlated with stream flow and climate characteristics. Specifically, we expected positive correlations between growth rate and surface flow and precipitation based on the premise that tree growth in the southwestern United States is often strongly limited by water availability (Fritts 1974). We also expected negative correlations between growth and air temperature during the growing season because high temperatures would limit photosynthesis due to high vapor pressure deficit, as shown for *Acer negundo* at a perennial stream near our study site (Kolb et al. 1997). Last, we hypothesized that radial growth rate would differ among species.

METHODS

Study Site

The study location is West Clear Creek, a free-flowing perennial stream within the sub-Mogollon region (Minckley and Brown 1982) of the Colorado Plateau in central Arizona (Fig. 1). West Clear Creek flows approximately 48 km through a deep canyon to its confluence with the Verde River. The geology of the watershed comprises sedimentary rocks overlain with basalt in some areas. Elevations in the West Clear Creek watershed range from approximately 2300 m to 945 m. Our study site is located at the Bull Pen U.S. Geological Survey gaging station (lat. 34°32'19", long. 111°41'36", in NW1/4, NW1/4, sec 11, T13N, R6E, Yavapai County, Hydrologic Unit 15060203) 14.5 km east of Camp Verde and 17.7 km upstream of the mouth in the Coconino National Forest at 1106 elevation (Fig. 1).

Surface flow at West Clear Creek varies seasonally. Between 1969 and 1992 average monthly base flow varied between 0.42 and 0.57 m³ sec⁻¹ from May through January (Galusky 1994). Surface flows were highest in February and March due to runoff from snowmelt and averaged 1.13 m³ sec⁻¹ (Galusky 1994). Temperatures at highest elevations in the watershed (Happy Jack Ranger Station, Coconino National Forest) average 7.8°C annually,

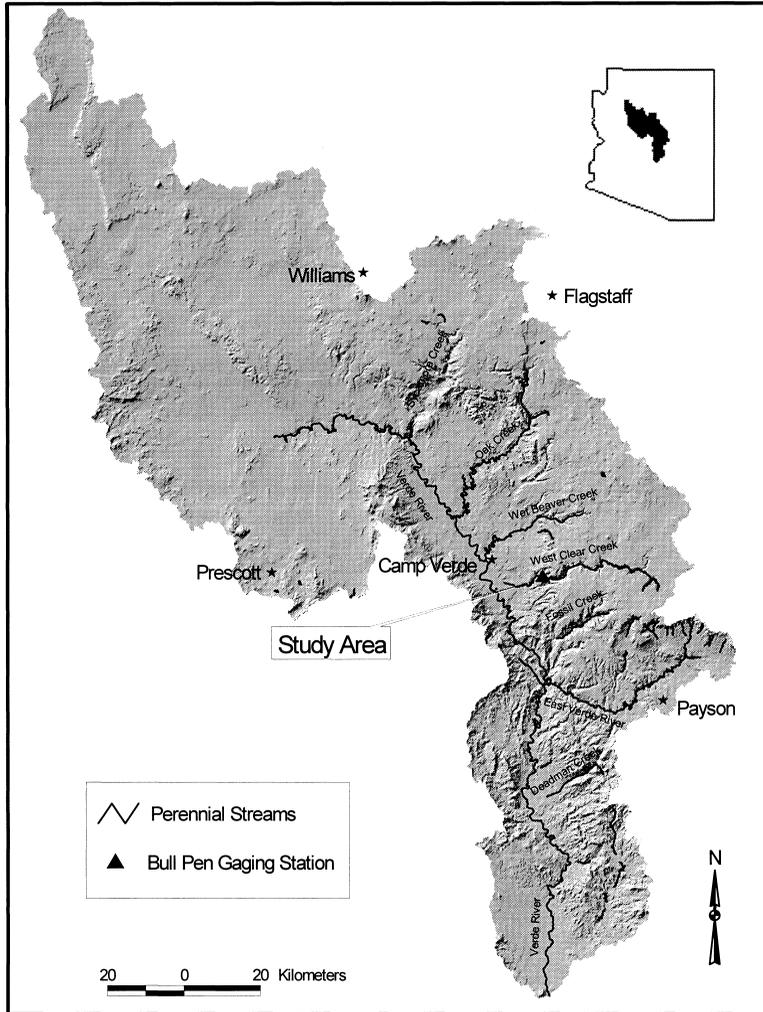


Fig. 1. Location of West Clear Creek and the study area in the Verde River Watershed, Arizona.

17.2°C in July, and -2.8°C in January (Western Regional Climate Center). Average annual precipitation at the highest elevations is 68.6 cm, which includes an average of 223.5 cm of snowfall. Temperature at Beaver Creek Ranger Station (Coconino National Forest), which is located within approximately 15 km of the study site at a similar elevation to the lower parts of the watershed, averaged 16.7°C annually, 27.2°C in July, and 6.7°C in January (Western Region Climate Center). Average annual precipitation at the Beaver Creek Ranger Station is 40.6 cm, which includes only a few centimeters of snowfall per year (Galusky 1994).

A variety of biotic communities occur in the West Clear Creek watershed. In upland parts of the watershed (elevations >1823 m), *Pinus ponderosa* dominates (Plan West Associates 1994). Between elevations of 1822 m and approximately 1372 m, *Pinus edulis*, *Juniperus scopulorum*, *J. deppeana*, *J. osteosperma*, and *J. monosperma* woodland communities (Minckley and Brown 1982) dominate. The lowest upland elevations of the watershed (<1372 m elevation) support interior chaparral and desert scrub communities (Galusky 1994). The interior canyon of West Clear Creek supports a deciduous broadleaf forest of riparian trees typical of mid-elevation, warm temperate,

riparian ecosystems in Arizona (Minkley and Brown 1982). The riparian tree species at our study site include *Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Juglans major*, *Platanus wrightii*, *Populus fremontii*, *Salix* spp., and a few *Amorpha fruticosa*, *Robinia neomexicana*, and *Tamarix chinensis*.

Field Sampling

We conducted all field sampling in October and November 1996. Our study area included the riparian forest corridor from approximately 760 m upstream to 100 m downstream of the Bull Pen gaging station. At the gaging station, West Clear Creek was characterized by a broad, unconstrained floodplain and a shallow braided channel of sand and cobbles. Approximately 360 m above the gaging station, the canyon narrows and forms a bedrock-constrained narrow channel characterized by little sediment accumulation.

Because West Clear Creek supports a continuous riparian forest, we used a systematic sampling approach with a randomly placed origin to sample trees. We established transects beginning 100 m below the gaging station. In all, 8 transects were established, 4 in the constrained reach and 4 in the unconstrained reach. Of the 8 total transects, 7 were above the gaging station and 1 was below. With this placement, flow data from the gaging station could be used reliably for all transects. We oriented each transect parallel to the stream channel, choosing the side with the broadest floodplain to maximize the number of trees available for sampling. Therefore, the width of each transect varied and included the riparian forest from the edge of the active stream channel to its outer edge. All transects were 20 m long and spaced 100 m apart. However, we did not sample upper peripheral terraces that were characterized by a mixture of xeric shrubs and old, decaying riparian trees with rotten centers.

We recorded the species, diameter at breast height (dbh), and topographic location of every tree in all transects. The following topographic location descriptors were used: active channel, abandoned channel, gravel-boulder bar, first bench, and second bench. We defined the active channel as the area directly adjacent to the stream bank characterized by shallow (<10 cm deep), low-velocity surface flow that covered fine sediments and small cobbles. The

abandoned channel location was an older stream channel that was dry at low flows but had recently been within the active channel prior to high flows which rerouted the stream. Abandoned channels were lower in elevation than gravel-boulder bars or benches. Gravel-boulder bars were remnant alluvial bars, deposited during recent high flows. These bars, elevated at least 1 m above stream base flow, were composed of large cobbles and boulders; fine sediment was generally absent. The first bench location included stream banks immediately adjacent to the active channel; it was characterized by fine sediments deposited among cobbles. This location was raised above the stream base flow up to 1 m. Finally, second bench described the terrace above and peripheral to the first bench location. These areas were raised 1 m or more above stream base flow and were covered in sand, fine sediment, and cobbles.

We established smaller plots within each transect to sample seedlings. These plots were positioned along the upstream border of the transect and were 5 × 5 m in size. We counted and recorded the species, age, and topographic location of all seedlings in these plots. This sampling occurred at each topographic location where seedlings occurred. Therefore, 1 transect could have up to 4 seedling plots, 1 for each topographic location. We aged seedlings by visual observation of terminal bud scars. We practiced this technique of estimating seedling age by comparing ages estimated from bud scars with counts of tree rings from increment cores taken at the soil surface.

Tree Ring Measurement

We excavated each tree with a dbh >5 cm to expose the root collar and extracted 2 increment cores spaced 90° apart just above the root collar to ensure accurate determination of the date of regeneration (Sigafoos 1964, Scott et al. 1997). The cores were prepared for analysis using standard dendrochronological techniques (e.g., Schweingruber 1988). We measured the width of annual growth rings under 20X magnifying power with an automated computer counter accurate to the nearest 0.01 mm. Any cores with questionable rings were evaluated by 2 other experienced people. We cross-dated growth rings of all trees using skeleton plotting (Stokes and Smiley 1968, Schweingruber 1988) and made

modifications to the tree-ring database for obvious missing or false rings.

To standardize annual radial growth of each tree, we divided radial growth in each year by the mean annual radial growth over all years for that tree (Stromberg and Patten 1990). We developed annual radial growth indices for each species for the period between 1964 and 1996 averaged over transects, topographic locations, reaches, and streamwide. Trees <5 years old were excluded from the indices. The number of radial growth increments used to develop the indices varied among years, sites, and species because of differences in spatial occurrence and age among trees. The number of streamwide cores used for the indices was greater for *Fraxinus velutina* ($n = 27\text{--}60$, depending on year) and *Alnus oblongifolia* ($n = 21\text{--}40$) than for *Acer negundo* ($n = 3\text{--}13$), *Juglans major* ($n = 1\text{--}8$), and *Platanus wrightii* ($n = 6\text{--}8$; Fig. 2).

Hydrologic and Climatic Variables

We obtained flow data for the Bull Pen gaging station (number 09505800) from the U.S. Geological Survey (U.S. Geological Survey 2000). These data included daily flow records from October 1964 through October 1996. Climate data were obtained from the Western Regional Climate Center, Desert Research Institute, on CD-ROM for the Beaver Creek Ranger Station (climate station number 020670, 1164 m elevation), located approximately 15 km from the study site and at a similar elevation. The climate data included precipitation and temperature summaries from 1964 through 1996. From the National Oceanic and Atmospheric Administration, we obtained Palmer Drought Severity Index (PDSI; Palmer 1965) values for the region of our study location. PDSI values show departures from average soil water availability. Increasing drought severity results in decreasing (more negative) PDSI values.

Data Analysis

SAS (Version 6.12, SAS Institute Inc., Cary, NC, USA) and SPSS (Version 9.0, SPSS Inc., Chicago, IL, USA) statistical software were used for all analyses. We evaluated the effect of stream reach and species on seedling density and mature-tree radial growth rate (nonstandardized) of the 5 most prevalent riparian tree

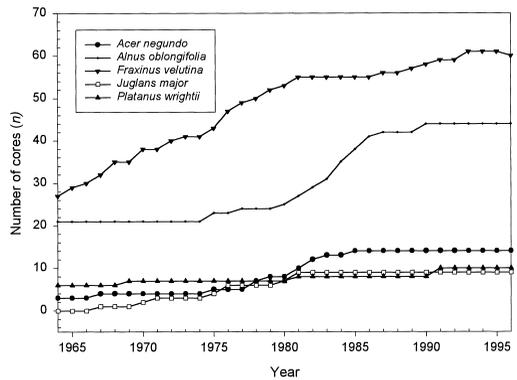


Fig. 2. Number of cores (n) for 5 tree species in 1996 at West Clear Creek used to develop streamwide standardized growth indices.

species (*Alnus oblongifolia*, *Fraxinus velutina*, *Platanus wrightii*, *Populus fremontii*, and *Salix* spp.) using 2-factor, fixed-effects ANOVAs. Factors in the ANOVAs were species, reach, and their interaction. A Tukey multiple-range test was used to compare means among species using a significance level of $P \leq 0.05$. For seedling density this analysis was limited to the active channel location because >90% of all seedlings were located there (Table 1).

We developed 28 environmental variables (Table 2) to describe variations in temperature, precipitation, and stream flow for West Clear Creek between 1965 and 1996. We examined the relationships between these environmental variables and standardized annual radial stem growth of *Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Juglans major*, and *Platanus wrightii* averaged streamwide and over constrained and unconstrained reaches separately using forward multiple regression that allowed testing of the independent influence of each variable on growth (Neter et al. 1996). Coefficients of partial determination (r^2) were considered significant at $P \leq 0.05$.

Finally, we constructed a histogram that showed the number of trees that established for each species in each year and West Clear Creek's seasonal flow regime from 1966 through 1996. Using this histogram, we graphically evaluated the relationship between stream flow characteristics and the date of establishment of 7 tree species (*Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Populus fremontii*, *Juglans major*, *Platanus wrightii*, and *Salix* spp.) Because we aged only living trees, and because of our inability to account for trees

TABLE 1. Distribution of seedlings of different species in 1996 at 3 topographic locations along West Clear Creek. Totals are combined across constrained and unconstrained reaches.

Species	Total seedlings counted	Topographic location	Total seedlings at each location	% of total for location
<i>Acer negundo</i>	1	Active channel	1	100
<i>Alnus oblongifolia</i>	877	Abandoned channel	70	7.98
		Active channel	807	92.02
<i>Amorpha fruticosa</i>	3	Active channel	3	100
<i>Fraxinus velutina</i>	356	First bench	12	3.37
		Abandoned channel	16	4.49
		Active channel	328	92.13
<i>Juglans major</i>	1	Abandoned channel	1	100
<i>Platanus wrightii</i>	161	Abandoned channel	6	3.73
		Active channel	155	96.27
<i>Populus fremontii</i>	285	Abandoned channel	4	1.40
		Active channel	281	98.60
<i>Robinia neomexicana</i>	1	First bench	1	100
<i>Salix</i> spp.	102	Active channel	102	100
<i>Tamarix chinensis</i>	5	Active channel	5	100

swept away during past floods, this analysis was limited to a visual interpretation of the number of sampled trees that established during different years.

RESULTS

Seasonal Stream Flow and Recruitment of Riparian Trees

Our analysis of the relationship between seedling establishment and seasonal stream flow revealed evidence of frequent germination between 1966 and 1992 by *Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Juglans major*, and *Platanus wrightii* (Fig. 3). Seedling establishment of all species was low the first (1993) and second (1994) springs after a winter high-flow event in 1993 that scoured the West Clear Creek channel (Fig. 3). In spring of 1993 only 12 individuals of all species established, and in spring of 1994 only 13 individuals of all species established on our plots. However, the winter of 1995 had low winter flow followed by a moderately high spring flow, and these conditions produced 486 *Alnus oblongifolia*, 99 *Fraxinus velutina*, 85 *Platanus wrightii*, 214 *Populus fremontii*, and 63 *Salix* spp. seedlings on our plots. An additional 392 *Alnus oblongifolia*, 250 *Fraxinus velutina*, 76 *Platanus wrightii*, 70 *Populus fremontii*, and 39 *Salix* spp. seedlings established on these plots in 1996. In contrast, no *Juglans major* and only 1 *Acer negundo* seedling established on our plots in 1995 and 1996 (Fig. 3).

TABLE 2. Environmental variables used in multiple regression analyses. Chronologies for 1965 through 1996 were developed for each variable.

Variables
Winter precipitation (1 October–31 January)
Spring precipitation (1 February–30 April)
Summer precipitation (1 May–30 June)
Monsoon precipitation (1 July–30 September)
Annual precipitation (1 October–30 September)
Winter mean maximum 24-hour temperature (1 October–31 January)
Spring mean maximum 24-hour temperature (1 February–30 April)
Summer mean maximum 24-hour temperature (1 May–30 June)
Monsoon mean maximum 24-hour temperature (1 July–30 September)
Winter mean minimum 24-hour temperature (1 October–31 January)
Spring mean minimum 24-hour temperature (1 February–30 April)
Summer mean minimum 24-hour temperature (1 May–30 June)
Monsoon mean minimum 24-hour temperature (1 July–30 September)
Mean winter temperature (1 October–31 January)
Mean spring temperature (1 February–30 April)
Mean summer temperature (1 May–30 June)
Mean monsoon temperature (1 July–30 September)
Winter surface flow (1 October–31 January)
Spring surface flow (1 February–30 April)
Summer surface flow (1 May–30 June)
Monsoon surface flow (1 July–30 September)
Annual surface flow (1 October–31 January)
Maximum winter surface flow (1 October–31 January)
Maximum spring surface flow (1 February–30 April)
Maximum summer surface flow (1 May–30 June)
Maximum monsoon surface flow (1 July–30 September)
Maximum annual surface flow (1 October–30 September)
Palmer Drought Severity Index (PDSI)

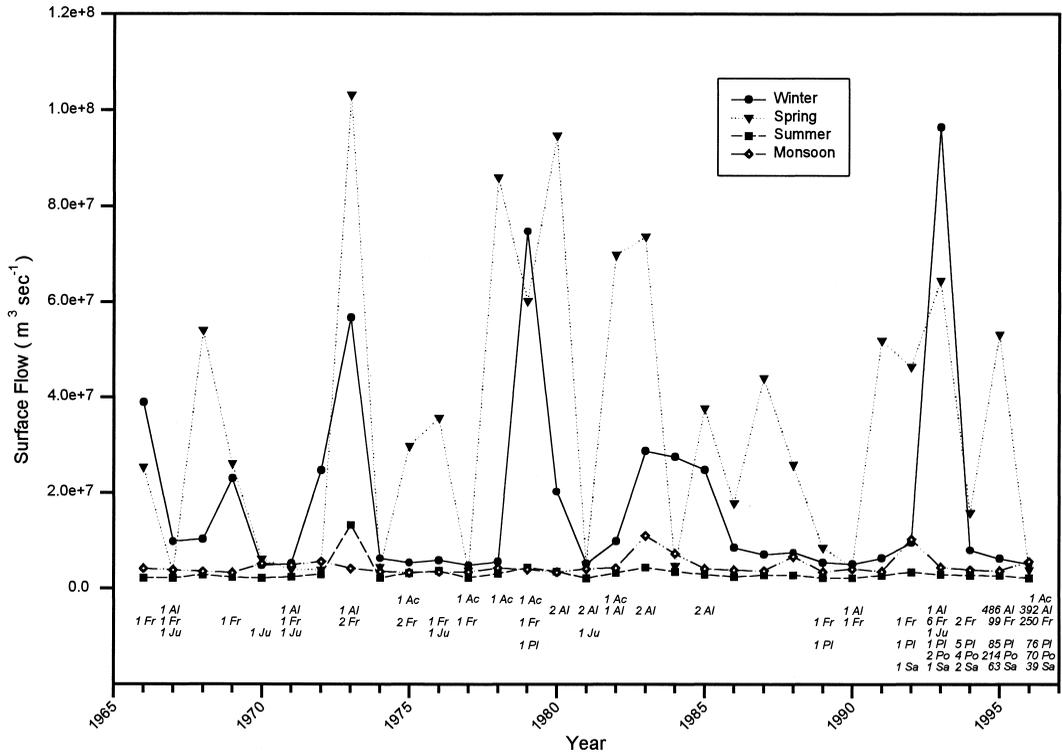


Fig. 3. Seasonal surface flow ($\text{m}^3 \text{sec}^{-1}$) for winter (1 October–31 January), spring (1 February–30 April), summer (1 May–30 June), and monsoon (1 July–30 September) periods from 1965 through 1996 at West Clear Creek. Numbers and codes above the x-axis show the number of individuals that established for 7 tree species (Ac = *Acer negundo*, Al = *Alnus oblongifolia*, Fr = *Fraxinus velutina*, Ju = *Juglans major*, Pl = *Platanus wrightii*, Po = *Populus fremontii*, Sa = *Salix* spp.) for each year.

Seedling Density

The active channel was the preferred location for seedling recruitment, with 92% of *Alnus oblongifolia* seedlings, 92% of *Fraxinus velutina* seedlings, 96% of *Platanus wrightii* seedlings, 99% of *Populus fremontii* seedlings, and 100% of *Salix* spp. seedlings occupying that topographic location (Table 1). Seedling density at the active channel location differed significantly among species ($P = 0.005$) but not between constrained and unconstrained reaches ($P = 0.13$). Further, the reach \times species interaction was not significant ($P = 0.404$), indicating a similar effect of reach on seedling density for each species. Mean seedling density along the active channel was highest for *Alnus oblongifolia*, intermediate for *Fraxinus velutina* and *Populus fremontii*, and lowest for *Platanus wrightii* and *Salix* spp. (Table 3).

Radial Growth

Of 28 environmental variables tested (Table 2), several were significantly related to annual

TABLE 3. Mean seedling density (number individuals m^{-2}) in 1996 along the active channel topographic location of 5 tree species averaged over constrained and unconstrained reaches at West Clear Creek. Means followed by the same letter do not differ significantly ($P \leq 0.05$) with Tukey's Multiple Range test.

Species	Mean density	s
<i>Alnus oblongifolia</i>	4.04 ^a	1.13
<i>Fraxinus velutina</i>	1.64 ^{a,b}	0.69
<i>Platanus wrightii</i>	0.78 ^b	0.33
<i>Populus fremontii</i>	1.41 ^{a,b}	0.56
<i>Salix</i> spp.	0.51 ^b	0.21

variation in standardized radial stem growth. Growth of *Acer negundo* streamwide was significantly ($P = 0.026$) and negatively related to high spring surface flow (Table 4), which accounted for 16% of the yearly variability in growth. *Acer negundo* growth streamwide was also negatively related to summer mean maximum temperature (partial $r^2 = 0.29$, $P = 0.0007$; Table 4); this pattern also occurred at

TABLE 4. Results of forward multiple regression analyses for 5 tree species at West Clear Creek using standardized tree-ring indices averaged streamwide from 1965 through 1996 as the dependent variable and 28 environmental independent variables.

Species	Environmental variable	Partial r^2	Slope direction	P
<i>Acer negundo</i>	Summer mean maximum temp.	0.2885	–	0.0007
	Spring surface flow	0.1578	–	0.0269
	Monsoon mean temp.	0.0584	+	0.0743
	Winter precipitation	0.0561	+	0.0923
<i>Alnus oblongifolia</i>	Monsoon mean minimum temp.	0.0980	+	0.0863
<i>Fraxinus velutina</i>	Mean winter temp.	0.2570	–	0.0036
	Summer precipitation	0.1494	+	0.0129
<i>Juglans major</i> ^a	Winter mean maximum temp.	0.1845	+	0.0121
	Palmer Drought Severity Index	0.1569	+	0.0334
	Mean spring temperature	0.0745	–	0.0862
<i>Platanus wrightii</i>	Maximum spring surface flow	0.0951	–	0.0913

^aFound only at the constrained reach.

TABLE 5. Results of forward multiple regression analyses for 5 tree species at West Clear Creek using standardized tree-ring indices averaged over the constrained reach from 1965 through 1996 as the dependent variable and 28 environmental independent variables.

Species	Environmental variable	Partial r^2	Slope direction	P
<i>Acer negundo</i>	Annual surface flow	0.1510	–	0.0307
	Summer mean maximum temp.	0.1469	–	0.0222
	Monsoon mean max. temp.	0.1027	+	0.0406
<i>Alnus oblongifolia</i>	Maximum winter surface flow	0.1524	–	0.0299
	Summer mean maximum temp.	0.0851	+	0.0879
	Monsoon mean max. temp.	0.0769	–	0.0932
	Mean monsoon temp.	0.0715	+	0.0937
<i>Fraxinus velutina</i>	Mean winter temp.	0.2050	–	0.0105
	Summer precipitation	0.1924	+	0.0058
<i>Juglans major</i>	Winter mean maximum temp.	0.1845	+	0.0121
	Palmer Drought Severity Index	0.1569	+	0.0334
	Mean spring temp.	0.0745	–	0.0862
<i>Platanus wrightii</i>	None	—	—	—

the constrained reach (partial $r^2 = 0.15$; $P = 0.022$; Table 5). *Acer negundo* growth was negatively related to annual surface flow in the constrained reach only (partial $r^2 = 0.15$, $P = 0.031$; Table 5), a response similar to the negative relationship between spring surface flow and growth of *Acer negundo* streamwide (Table 4). *Acer negundo* growth at the constrained reach was positively related to monsoon season mean maximum temperature (partial $r^2 = 0.103$, $P = 0.041$; Table 5). None of the 28 environmental variables tested was significantly

($P \leq 0.05$) related to *Acer negundo* growth at the unconstrained reach (Table 6).

Growth of *Fraxinus velutina* was negatively related to winter mean temperature streamwide (partial $r^2 = 0.26$, $P = 0.0036$; Table 4) and at the constrained reach (partial $r^2 = 0.21$, $P = 0.011$; Table 5). Summer precipitation was positively related to growth of *Fraxinus velutina* streamwide (partial $r^2 = 0.15$, $P = 0.013$; Table 4) and at the constrained reach (partial $r^2 = 0.19$, $P = 0.0058$; Table 5). Growth of *Fraxinus velutina* at the unconstrained reach

TABLE 6. Results of forward multiple regression analyses for 5 tree species at West Clear Creek using standardized tree-ring indices averaged over the unconstrained reach from 1965 through 1996 as the dependent variable and 28 environmental independent variables. *Juglans major* was found only at the constrained reach.

Species	Environmental variable	Partial r^2	Slope direction	P
<i>Acer negundo</i>	Maximum summer surface flow	0.1180	—	0.0585
<i>Alnus oblongifolia</i>	None	—	—	—
<i>Fraxinus velutina</i>	Maximum spring surface flow	0.1360	+	0.0247
	Monsoon surface flow	0.1249	+	0.0512
	Palmer Drought Severity Index	0.0900	—	0.0840
<i>Juglans major</i> ^a	—	—	—	—
<i>Platanus wrightii</i>	Maximum spring surface flow	0.1314	—	0.0450
	Maximum monsoon surface flow	0.0965	—	0.0719

^aFound only at the constrained reach.

was significantly related to only a single environmental variable, maximum spring surface flow, which was positively related to growth (partial $r^2 = 0.14$, $P = 0.025$; Table 6).

Juglans major growth at the constrained reach was positively related to PDSI (partial $r^2 = 0.16$, $P = 0.033$; Table 5). Winter mean maximum temperature was also positively related to *Juglans major* growth at the constrained reach (partial $r^2 = 0.18$, $P = 0.012$; Table 5), which was the only reach where *Juglans major* occurred. The only variable significantly related to growth of *Platanus wrightii* was maximum spring surface flow at the unconstrained reach (partial $r^2 = 0.13$, $P = 0.045$; Table 6), where growth was lower when spring surface flows were high. The only variable significantly related to growth of *Alnus oblongifolia* was maximum winter surface flow at the constrained reach (partial $r^2 = 0.15$, $P = 0.03$; Table 5), where growth was lower when maximum winter surface flows were high.

Average annual radial stem growth (non-standardized) differed significantly among species ($P < 0.001$) and reaches ($P < 0.001$), and the species \times reach interaction was significant ($P < 0.001$). Radial growth averaged over reaches was significantly higher for *Alnus oblongifolia* and *Platanus wrightii* than for *Acer negundo*, *Fraxinus velutina*, and *Juglans major* (Table 7). Radial growth averaged over all species was greater at the unconstrained reach (mean = 5.75 mm, $s = 0.39$) than the constrained reach (mean = 2.43 mm, $s = 0.45$). Further, the significant reach \times species interaction indicates that differences in radial growth

TABLE 7. Mean annual radial growth (mm) from 1965 through 1996 at West Clear Creek for 5 tree species averaged over constrained and unconstrained reaches at West Clear Creek. Means followed by the same letter do not differ significantly ($P \leq 0.05$) with Tukey's Multiple Range test.

Species	Mean annual radial growth	s
<i>Acer negundo</i>	2.49 ^a	0.84
<i>Alnus oblongifolia</i>	5.29 ^b	0.47
<i>Fraxinus velutina</i>	2.62 ^a	0.39
<i>Juglans major</i>	1.18 ^a	1.04
<i>Platanus wrightii</i>	6.57 ^c	0.74

between reaches varied among species. Specifically, growth of *Alnus oblongifolia* and *Platanus wrightii* was significantly higher at the unconstrained versus the constrained reach, whereas reach had little effect on radial growth of *Acer negundo* and *Fraxinus velutina* (Fig. 4).

DISCUSSION

We hypothesized that high surface flow events are necessary to recruit seedlings of all tree species at our West Clear Creek study site. However, we could evaluate this hypothesis only for seedling recruitment that followed the 1993 and 1995 floods because the 1993 flood removed many existing younger trees (T.E. Kolb personal observation, unpublished photo documentation by U.S. Geological Survey) and may have removed entire age classes of some tree species. Large numbers of *Alnus oblongifolia*, *Fraxinus velutina*, *Platanus*

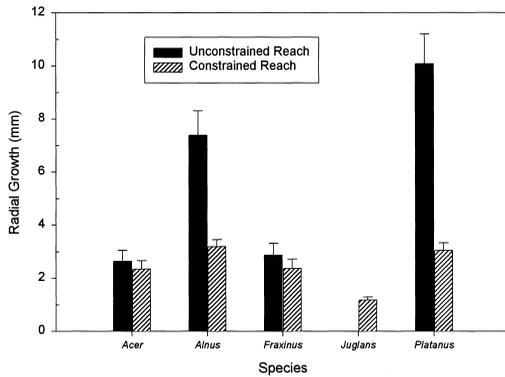


Fig. 4. Average annual radial stem growth (1965–1996) for the 5 most prevalent mature tree species at constrained and unconstrained reaches of West Clear Creek. Bars indicate 1 s. Note: *Juglans* was not found at the lower reach.

wrightii, *Populus fremontii*, and *Salix* spp. seedlings established in 1995 and 1996, suggesting that germination and establishment of these species were promoted by the high winter and spring surface flows in 1993 or the high spring surface flow in 1995. In contrast, there was only 1 *Juglans major* seedling on our plots, and it germinated in 1993 in an abandoned channel. Similarly, we observed only 1 *Acer negundo* seedling, which germinated in 1996 in an abandoned channel. These observations suggest that regeneration of *Juglans major* and *Acer negundo* at our study site was not stimulated by the high surface flow events of 1993 and 1995 as were *Alnus oblongifolia*, *Fraxinus velutina*, *Platanus wrightii*, *Populus fremontii*, and *Salix* spp. Our results on regeneration of *Populus fremontii* and *Salix* spp. are consistent with other research in the western United States on these species that has documented an increase in seedlings following high surface flows (Howe and Knopf 1991, Stromberg et al. 1991, 1993, Scott et al. 1997, Stromberg 1997).

We also hypothesized that topographic location and stream reach would influence recruitment of riparian trees at West Clear Creek. We found that *Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Platanus wrightii*, *Populus fremontii*, and *Salix* spp. regenerated almost exclusively at the active channel topographic location (>90% for all seedlings). The nearly exclusive active channel preference was unexpected because other research in Arizona riparian forests has documented that high

winter surface flows with slowly subsiding spring runoff increased sediment deposition and provided a moist seedbed along peripheral floodplains which then facilitated seedling recruitment in abandoned channels and along upper stream benches (Bock and Bock 1989, Stromberg 1997). West Clear Creek had high winter surface flows that inundated all topographic locations 3 years before our sampling (1993); thus, we expected to find more seedlings at the abandoned channel and first bench topographic locations.

The flood that occurred in December 1993 at West Clear Creek scoured the floodplain and reduced the density of mature trees, thus providing openings along the active floodplain for future seedling recruitment. However, this high winter flow also might have scoured and removed more sediment than it deposited. Additionally, the 1993 flood was a spike winter flood in which flows increased and decreased rapidly. Insufficient soil moisture during early summer months along peripheral topographic locations, such as abandoned channels and benches, may have prevented seedling establishment at all topographic locations except the active channel where seedling roots were in direct contact with saturated soil (Bock and Bock 1989, Stromberg 1997). This interpretation is consistent with other research that has shown the importance of magnitude and timing of floods in reestablishing riparian trees (e.g., McBride and Strahan 1984, Stromberg et al. 1991, 1993, Scott et al. 1997, Stromberg 1997).

We expected greater seedling density along the unconstrained reach compared with the bedrock-constrained reach. This expectation is consistent with research on other riparian systems showing that higher stream velocity in narrow entrenched channels at constrained reaches restricts sediment deposition and therefore offers little habitat for seedling establishment (Palik et al. 1998). However, our results did not support these findings. At West Clear Creek we found similar seedling density between constrained and unconstrained reaches for *Alnus oblongifolia*, *Fraxinus velutina*, *Platanus wrightii*, *Populus fremontii* and *Salix* spp. More than 90% of seedlings occurred at the active channel location, and this location was similar in width at both the constrained and unconstrained reaches. Therefore, we conclude that recent seedling recruitment (1993–

1996) at our study site was not influenced by bedrock constraints because the locations where most seedlings occurred did not differ in size between reaches.

We also hypothesized that seedling density would differ among tree species. We found that seedling density of *Alnus oblongifolia* was significantly higher than densities of *Acer negundo*, *Juglans major*, *Platanus wrightii*, and *Salix* spp. at the active channel topographic position where most seedlings occurred. We suspect that the lower density of *Platanus wrightii* was due to less widespread seed distribution compared to *Alnus oblongifolia*, as *Platanus wrightii* seedlings typically establish in clumps at the location of seed drop (Bock and Bock 1989). Also, we suspect that the lower density of *Salix* spp. seedlings was largely due to fewer mature trees. In fact, we did not include *Salix* spp. in the growth analysis because no mature trees occurred on our plots. *Acer negundo* and *Juglans major* were fairly common mature trees at our sites (both were included in the growth analysis), but seedlings of these species were extremely rare on our plots (1 each) compared to other species. Kolb et al. (1997) observed that most small *Acer negundo* trees at a site similar to West Clear Creek (Oak Creek) originated from sprouting by mature, flood-damaged trees, suggesting an important role of asexual regeneration for *Acer negundo* in frequently flooded southwestern riparian forests.

We hypothesized that annual growth of riparian trees at West Clear Creek would be correlated with stream flow characteristics. We found that high stream flow during the growing season was negatively related to annual growth for *Acer negundo* streamwide, and at both constrained and unconstrained reaches. This finding suggests that growth of *Acer negundo* is sensitive to inundation, which is consistent with research by Friedman and Auble (1999), who documented increased mortality of *Acer negundo* saplings with extended flood inundation on the Gunnison River, Colorado. Moreover, high surface flows at West Clear Creek were also negatively associated with annual growth of *Alnus oblongifolia* (constrained reach) and *Platanus wrightii* (unconstrained reach). Other studies (Reily and Johnson 1982, Astrade and Begin 1997) have also reported negative effects of prolonged saturation and limited root oxygenation on annual

radial growth of riparian trees. Further, inundating flows could have greater negative impacts on riparian trees growing along constrained versus unconstrained reaches due to deeper water and greater physical damage from debris moving in floodwater caused by higher water velocity (Palik et al. 1998).

The only positive relationship between stream flow and annual radial growth in our study occurred for *Fraxinus velutina*. Given the arid climate of our study site, why did this relationship not occur for more species? Stromberg and Patten (1991) showed that the strongest, positive correlation between radial growth of *Populus* spp. and stream flow occurred in areas where low flows were not sufficient to meet tree water requirements. In areas where tree water requirements were met by low flows, there was a low correlation between radial growth and stream flow. In their study (Stromberg and Patten 1991), stream diversions abated high flows, and thus the negative effect of high flow was not tested. At West Clear Creek a consistent perennial base flow likely supplied ample water to most trees, except perhaps *Fraxinus velutina*; thus, high stream flows did not increase water availability to trees.

We also conclude that temperature can be an important influence on annual growth of riparian trees at West Clear Creek. High temperature was significantly and negatively related to streamwide annual radial growth of *Acer negundo* during the dry, early summer months, but it was positively related to growth of *Acer negundo* during the wetter, late-summer monsoon season (constrained reach). Perhaps the detrimental effect of high temperature on *Acer negundo* growth in early summer was ameliorated by more humid conditions during the late-summer monsoon season. Consistent with this idea, Kolb et al. (1997) reported that photosynthesis of *Acer negundo* was negatively affected by high vapor pressure deficit at a riparian site similar to West Clear Creek. High temperatures and low humidity in the dry, early summer season would lead to very high vapor pressure deficits, thus reducing photosynthesis and assimilate available for growth. Streamwide annual radial growth of *Fraxinus velutina* was negatively related to winter mean temperature, suggesting poor growth following warm winters, perhaps because of high respiratory losses of stored

carbohydrates. In contrast, growth of *Juglans major* was positively related to winter mean maximum temperature, suggesting greater growth following warmer winters. Perhaps warm winter temperatures increase subsequent growth of this species because of reduced incidence of xylem cavitation caused by freezing (Kozłowski et al. 1991). Overall, our results suggest that temperature plays an important role in the growth of some riparian trees at West Clear Creek, and that this role depends on species sensitivity to temperature and the season during which temperature extremes occur.

Our hypothesis that tree growth would be positively correlated with precipitation was supported only for *Fraxinus velutina* and *Juglans major*. For *Fraxinus velutina*, growth was positively related to summer precipitation streamwide and at the constrained reach. For *Juglans major*, growth was positively related to PDSI values at the constrained reach. One explanation is that because roots of these species at the constrained reach did not contact groundwater, precipitation thus was an important water source. In addition, *Juglans major* in our study grew only on upper benches away from the active channel, where lack of contact with saturated soil and perhaps groundwater may have made it more susceptible to drought than other species that grew closer to the stream. Our explanations are consistent with other research documenting the influence of recent precipitation on riparian tree growth increases when water is not available from other sources (Reily and Johnson 1982, Stromberg and Patten 1990). In contrast to *Fraxinus velutina* and *Juglans major*, growth of *Acer negundo*, *Alnus oblongifolia*, and *Platanus wrightii* was not strongly related to precipitation or PDSI, suggesting greater use of stream or groundwater by these species.

Our expectation that annual radial growth would vary among species was supported by greater growth for *Alnus oblongifolia* and *Platanus wrightii* than for *Fraxinus velutina*, *Juglans major*, and *Acer negundo*. Differences in radial growth rate of these species might be caused by a tradeoff between allocation of carbon to fast growth (i.e., wide rings) versus dense wood, or they might reflect differences in life history strategy (Grime 1979, Loehle 1988). Additionally, fast growth of *Alnus oblongifolia* might be caused by its symbiotic

nitrogen-fixing relationship with actinomycete fungi (Aber and Melillo 1991), which does not occur in the other species we studied. Riparian restoration programs in the Southwest that include tree establishment should consider *Alnus oblongifolia* and *Platanus wrightii* because of their fast growth.

We expected faster tree growth at the unconstrained reach due to more favorable growing conditions such as closer proximity to alluvial groundwater (Reily and Johnson 1982, Stromberg and Patten 1996) and deeper fine sediments from prior high flows (Palik et al. 1998). However, we found that the effect of stream reach on growth varied among species. *Alnus oblongifolia* and *Platanus wrightii* had significantly higher annual radial growth at the unconstrained reach than at the constrained reach, whereas growth of *Acer negundo* and *Fraxinus velutina* did not differ between reaches. Thus, the fastest growing species, *Alnus oblongifolia* and *Platanus wrightii*, responded more dramatically to changes in resource availability than the slower growing species, *Acer negundo* and *Fraxinus velutina*.

CONCLUSIONS

Environmental requirements for seedling establishment varied among tree species at West Clear Creek. A pulse of seedling establishment occurred in 1995–96 for *Alnus oblongifolia*, *Fraxinus velutina*, *Platanus wrightii*, *Populus fremontii*, and *Salix* spp. following high winter and moderate spring surface flows in 1993, and high spring surface flow in 1995. In contrast, little seedling establishment occurred for *Acer negundo* and *Juglans major* under these conditions despite the common occurrence of mature trees. Most seedlings of all species occurred at the active channel topographic location, with few seedlings at abandoned channel, gravel-boulder bar, and bench locations. Our study did not address the environmental conditions necessary for reproduction of riparian trees by sprouting, although this may be an important factor in the reestablishment of riparian forests at some sites (e.g., Kolb et al. 1997).

Relationships between environmental variables and annual radial growth varied among species and between constrained versus unconstrained stream reaches for some species. Relationships with annual radial growth were

most consistent with surface flow. Surface flows were negatively related to growth of *Acer negundo*, *Alnus oblongifolia* (constrained reach), and *Platanus wrightii* (unconstrained reach), whereas spring surface flows were positively related to growth of *Fraxinus velutina* (unconstrained reach). Precipitation or PDSI was positively related to growth only for *Fraxinus velutina* and *Juglans major*, suggesting greater reliance on water in surface soil by these species. In several cases yearly variations in temperature appeared to influence the growth of these riparian trees, and this influence varied among species and seasons. Overall, annual radial growth was high for *Platanus wrightii* and *Alnus oblongifolia*, medium for *Acer negundo* and *Fraxinus velutina*, and low for *Juglans major*. Of the 28 environmental variables we considered, no category of variable (stream flow, temperature, precipitation) equally affected annual radial growth of all species. Thus, tree species at our study site on West Clear Creek responded individually rather than collectively to changes in stream flow and climatic variables.

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