FLOOD FLOWS AND POPULATION DYNAMICS OF ARIZONA SYCAMORE (*PLATANUS WRIGHTII*)

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ABSTRACT.—*Platanus wrightii* is a pioneer tree species of warm-temperate riparian deciduous forests in southwestern United States and northern Mexico. Dendrochronological analysis of populations in central and southern Arizona indicated that *P. wrightii* seedlings establish episodically. Long intervals (10–40 years) elapsed with no apparent establishment. Seedling establishment years were positively associated with winter flood size and annual flow rate, and weakly negatively associated with summer flood size. Large floods sometimes preceded multi-year establishment waves. During the past 2 decades an abundance of winter floods and very wet springs has allowed frequent establishment of *P. wrightii.* For example, plants established at many sites during the winter flood years of 1993 and 1995, particularly along channels scoured and widened by flood waters. *Platanus wrightii* also reproduces asexually. Ramets were more abundant than genets in all populations, and ramets established more frequently than seedlings. Ramet density (mean number per genet) varied widely between populations, from 2 (Huachuca Canyon) to 9 (Haunted Canyon), and increased with tree size within 4 of 9 populations. Population size structure varied across a gradient of watershed area. Populations along streams draining the largest watersheds had an abundance of small trees (mean trunk diameter of <10 cm), while those at headwater sites were dominated by mature trees with trunk diameter ≤190 cm and age ≤235 years. These observations suggest that population structure of *P. wrightii* is influenced by temporal as well as spatial differences in stream flow regimes.

Key words: Platanus wrightii, *floods, riparian habitat, seedling establishment, age structure, ramet.*

Population dynamics of many riparian tree species are influenced by flood disturbance (Duncan 1993, Hughes 1994, Scott et al. 1996, Cordes et al. 1997, Timoney et al. 1997, Rood et al. 1998, Sakai et al. 1999). Patterns of riparian tree mortality and establishment vary widely depending on frequency, magnitude, timing, and duration of floods (Poff et al. 1997). In arid regions flood patterns are highly variable between and within years, and flood flows can be very large relative to base flows. Large floods cause mortality of riparian trees by eroding sediments from root zones and uprooting trees, breaking plant stems or burying them with sediment, and causing mass wasting of flood plains. Floods also intermittently create conditions that allow establishment of pioneer species by changing channel and flood plain geomorphology, clearing competing vegetation, and moistening frequently dry flood plain surfaces.

Hydrologic and geomorphic controls on establishment of *Populus fremontii* and *Salix gooddingii*, the dominant pioneer species of Sonoran riparian deciduous forests, are fairly well understood. Both *P. fremontii* and *S. gooddingii* disperse short-lived seeds in spring and have narrow windows of opportunity for seedling establishment (Horton et al. 1960, Shafroth et al. 1998). Establishment of these species depends on winter floods to erode or deposit alluvium, high spring stream flows to moisten seed beds, and slowly receding flood waters to allow seedling roots to remain in contact with declining groundwater. Large winter floods of long duration can extensively widen channels and facilitate large-scale replenishment of *Populus-Salix* stands (Stromberg 1997, Stromberg et al. 1997, Mahoney and Rood 1998). Along some perennial to intermittent alluvial rivers in the Sonoran Desert, flood sequences that allow establishment of *P. fremontii* occur approximately once every 7–10 years. These generally do not occur regularly over time (Stromberg et al. 1991, Stromberg 1998). Establishment frequency varies among rivers, and some populations are dominated by a single age cohort (Everitt 1995). Rates of population turnover appear to be higher on lower reaches of rivers, as suggested

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by patterns of decreasing tree age with decreasing elevation (Stromberg and Patten 1992, Stromberg 1998).

Less is known about establishment patterns of *Platanus wrightii*, a dominant species of warm-temperate riparian deciduous forests in the southwestern United States and northern Mexico (Brown 1994). *Platanus wrightii* occurs in Arizona, New Mexico, western Texas, and northern Mexico at elevations of approximately 400–2000 m (Kearney and Peebles 1960). At lower elevations *P. wrightii* co-occurs with *Populus fremontii and Salix gooddingii.* At higher elevations it grows with *Populus angustifolia* and *Alnus oblongifolia,* among other species. Floods are a primary disturbance factor that structures these warm-temperate riparian plant communities (Campbell and Green 1968). Floods occur during late summer after convective thunderstorms, during winter and spring after Pacific frontal rainstorms and snow, and occasionally in fall as a result of dissipating tropical storms.

Life history traits of *P. wrightii* suggest that it is adapted to disturbance. Each year trees produce many small seeds (achenes) with tufted hairs that are suited to wind dispersal. Seeds persist in clusters of 2–4 round balls (multiple achenes), each about 2.5 cm in diameter, that gradually become detached from the tree throughout fall, winter, and spring. Seeds ripen in November, germinate in April or May following several weeks of winter stratification, and lose viability about 6 months after maturation (Zimmerman 1969, Bock and Bock 1989, Brock 1994). *Platanus occidentalis*, a species that occurs in eastern North America, germinates at high rates on bare mineral soil exposed to high light intensities (Fowells 1965, Sigafoos 1976), and the same may be true of *P. wrightii.*

Platanus wrightii reproduces vegetatively as well as by seed. Shanfield (1984) suggested that *Platanus racemosa,* a California species that is closely related to *P. wrightii,* may maintain its population size by relying on vegetative reproduction. However, factors that stimulate production of vegetative sprouts (ramets) by *P. wrightii* are not known. Along one stream in southern Arizona, Glinski (1977) found no correlation between *P. wrightii* sprout densities and several parameters including percentage of canopy dieback, soil texture, and distance to stream channel. In other woody species ramet production has been shown to be stimulated by a variety of factors including disturbance and changes in resource availability (Ischinger and Shafroth 1995).

My objective was to determine the influence of temporal and spatial variability in stream flow regimes on establishment processes and population size structure of *P. wrightii.* I hypothesized that *P. wrightii* seedlings would establish episodically in response to flood disturbance and that establishment would occur in years with large winter floods and high spring flows, similar to patterns for *P. fremontii* and *S. gooddingii.* I expected that recruitment frequency and abundance of young trees would increase along a downstream gradient as drainage area, flood magnitude, and channel instability increased. I also hypothesized that ramets would establish more frequently than seedlings and that production of ramets would increase during years with above-average stream flow.

MATERIALS AND METHODS

Study Sites

Nine *Platanus wrightii* study sites were selected along 7 rivers in southern and central Arizona (Table 1). Each site spans a river length of 1–3 km. At 7 of the sites, data were collected on tree age and population size structure; at 2 sites (Sycamore Creek–Round Valley and Huachuca Canyon), data were collected only on size structure. The Haunted Canyon and Pinto Creek sites were combined for some analyses, as were the Sycamore Creek–Bushnell and Sycamore Creek–Work Station sites. Some sites were selected because they allowed investigation of other biohydrology relations of *P. wrightii,* including relationship of groundwater level to bioproductivity (Stromberg 2001a). Other sites were added to provide a wide range of watershed sizes and elevations.

The streams mainly flow through alluvial sediments that are readily reworked by flood flows; there also are areas within sites where channel morphology is controlled by exposed bedrock. *Platanus wrightii* is a dominant species at all sites. Riparian ecosystems at the low-elevation study sites are bordered by Sonoran desertscrub and interior chaparral; those at higher elevations are bordered by desert grassland, Great Basin conifer woodland, and

TABLE 1. Description of study sites.

Site name	Land owner	Elevation (m)	Watershed area (km^2)
Oak Creek	Red Rock State Park	1171	770
Sycamore Creek–Round Valley	Tonto National Forest	718	230
Sycamore Creek–Bushnell	Tonto National Forest	1040	133
Sycamore Creek–Work Station	Tonto National Forest	1090	115
Pinto Creek	Tonto National Forest	976	84
Haunted Canyon	Tonto National Forest	988	43
Garden Canyon	Fort Huachuca (DOD)	1600	30
Ramsey Canyon	The Nature Conservancy	1739	13
Huachuca Canyon	Fort Huachuca (DOD)	1650	13

Madrean evergreen woodland (Brown 1994). Sycamore Creek is in the Mazatzal Mountains of central Arizona. Study sites are on Tonto National Forest land. The Sycamore Creek–Bushnell site experienced heavy recreational use and was grazed by domestic livestock. The grazing regime was changed from year-round to winter-only use in the early 1990s. Recreational impacts (mainly camping and hiking) were concentrated on higher flood plains and at river crossings. The Sycamore Creek–Work Station site is in a cattle grazing exclosure, but it was used as a pasture for horses. Stream flow is spatially intermittent, with short segments of perennial flow interspersed with intermittently flowing segments. Mean annual discharge at Sycamore Creek is 0.5 m^{3}s^{-1}.

Pinto Creek and its tributary Haunted Canyon are in the Pinal Mountains of central Arizona. Study sites at these 2 rivers are on Tonto National Forest land and were grazed by domestic livestock (cattle). Stream flow is spatially intermittent.

Oak Creek, on the southern escarpment of the Colorado Plateau, is the largest of the study streams. The study site is in Red Rock State Park, which was established in 1986. The park lands are managed for natural area values, recreation, and environmental education. The area has not been grazed by livestock since about the 1950s. Oak Creek has perennial flow and a mean annual daily discharge of 2.8 m^{3}s^{-1}.

Garden Canyon, Huachuca Canyon, and Ramsey Canyon are in the Huachuca Mountains of southeastern Arizona. None of the Huachuca Mountain study sites has been grazed by domestic livestock for several decades. Garden Canyon and Huachuca Canyon are located on Fort Huachuca military base.

Ramsey Canyon is managed as a natural area by The Nature Conservancy. Stream flow was diverted from Garden Canyon in the early part of the 20th century for use by military personnel prior to the shift to groundwater as a water source. During the late 19th century and early 20th century, Ramsey Canyon harbored a sizable, but short-lived, town during an active period of mining in southeastern Arizona. These 3 headwater streams are in narrow mountain canyons and have narrower riparian corridors than the central Arizona study sites. Garden Canyon has spatially intermittent stream flow and mean annual discharge of 0.03 m^{3}s^{-1}. Stream flow is temporally intermittent at Ramsey and Huachuca canyons.

Tree Age and Population Size Structure

Slabs or increment cores were collected from over 500 *Platanus wrightii* trees. Slabs and cores were collected when trees were dormant (1996, 1997, or 1998, depending on site) in 4 to 9 belt transects per site. The belts, approximately 10 m wide, extended from the channel to the edge of the riparian zone. There was age zonation at most sites, with young stands of dense trees close to the channel and sparse stands of older trees farther away. All live *P. wrightii* in the belts were measured for diameter at breast height (dbh). Cores or slabs were taken from trees in all apparent size classes. If trees were <4 cm in stem diameter, pruning clippers were used to clip slabs near the ground surface. For trees >4 cm diameter, increment borers were used to collect cores at 0.1–0.2 m above the ground surface. One to 4 replicate cores were collected

per tree, with the larger numbers of cores being collected if first attempts did not penetrate the center of the tree. Very large trees were underrepresented in the samples. Some of the largest trees had hollow interiors or extensive heart rot, and cores were not collected. Interior portions of some of the collected cores also showed evidence of decay and were discarded. Those that did not have heart rot and that had rings that extended to the center of the tree were retained for analysis. This group of usable cores and slabs encompassed 104 from Garden Canyon, 42 from Ramsey Canyon, 228 from Sycamore Creek, 114 from Haunted Canyon/Pinto Creek, and 92 from Oak Creek. Sample size was small at Ramsey Creek because there were very few trees in small size classes.

Trees were classified as to seed origin (genets) or sprout origin (ramets). Ramets were distinguished from genets based on their position (arising from the base of a larger tree or within a few meters of the base), size, and location within the flood plain (i.e., there was apparent age zonation at the sites, with seedlings located along channel edges and larger trees with associated small sprouts on flood plains farther from and above the channel). In most cases the origin of the trees was clear. At many sites there were stands of small, single-trunked trees, distributed in nonaggregated fashion along the stream channel; these were classified as genets. Some of these young trees had smaller stems arising from their bases; these were classified as ramets. Some of the larger trees were single-trunked and were classified as genets. More often the large trees occurred in clumps or aggregations. The largest tree within the clump was classified as a genet. Small-diameter stems arising from the base of the larger tree or emerging from the ground and forming a ring around the larger tree were classified as ramets (Glinski 1977). Most ramets arose directly from or just above the base of parent trees. Older genets generally were widely spaced on the flood plain and surrounded by a ring of smaller ramets. In some cases, however, there was a circle of trees of relatively similar size. Tree aging indicated that in some cases one of the trees in the circle was older than the others, in which case it was classified as a genet. In cases where all trees in the circle were of similar age, all were classified as genets. Some of these may have been ramets from a long-dead parent tree and may be incorrectly classified. Also, some trees classified as genets may have arisen from buried branches of old trees (Bock and Bock 1989). Analysis of covariance (tree age as covariate, tree dbh as dependent variable) was conducted to determine if there were significant differences in size and thus growth rate between genets and ramets. These analyses were conducted within sites, stratified by stream flow reach type. These analyses indicated that there were significant differences between groups, with ramets growing significantly slower than genets (Table 2).

In the laboratory, cores were glued to wood mounts and some slabs were re-sawn to produce smooth surfaces (Stokes and Smiley 1968). Cores and slabs were sanded with a belt sander using a graded series of sandpaper (100–600 grit) and viewed under a dissecting microscope to mark (score) the annual rings. After scoring, annual rings were measured for annual ring width with a Bannister-type automated measuring system. Site chronologies were generated by successively cross-dating within trees (using the replicate cores) and then between trees within sites. Trees were aged by counting annual rings. For the majority of young trees (Figs. 1, 2, 3), the core contained the center of the tree (as indicated by the presence of the persistent pith that is produced in the initial growing season), allowing for precise aging. In other cases the core was slightly off center. These trees were aged by estimating distance from the end of the core to the tree center (in cm), calculating average annual growth rate for the oldest section of the increment core, and adding to the annual ring count the estimated number of years to reach the center of the tree. Regression analyses showed high correspondence between annual radial growth and annual stream flow rate and air temperature, providing confirmation that rings were correctly scored (Stromberg 2001b). Age of the largest uncored trees at the sites was estimated from reach-specific regression equations that predicted age from dbh (Table 2).

Data Analysis

Forward-stepping multiple regression analysis was used to identify hydrologic factors associated with seedling and sprout establishment years for the 3 populations (Sycamore

TABLE 2. Regression equations predicting age (years) from trunk diameter (dbh in cm) of *Platanus wrightii*. All regression models are significant at $P < 0.05$.

	Regression equation	n	r^2
Ramsey Canyon			
genets*	y = 1.22x + 10.5	16	0.67
ramets	y = 1.79x + 16.1	26	0.45
Garden Canyon			
genets*	y = 1.71x + 1.1	46	0.77
ramets	y = 2.51x – 6.6	55	0.76
Oak Creek			
genets*	y = 1.84x – 2.2	38	0.70
ramets	y = 2.25x – 0.2	54	0.80
Haunted Canyon			
genets*	y = 1.79x + 11.7	17	0.79
ramets	y = 2.70x – 6.4	23	0.84
Pinto Creek (perennial)			
genets*	y = 1.91x – 3.9	23	0.90
ramets	y = 2.38x – 1.4	21	0.90
Pinto Creek (intermittent)			
genets*	y = 2.32x + 3.9	12	0.83
ramets	y = 3.13x – 1.6	18	0.95
Sycamore Creek–Work Station (intermittent 1)			
genets*	y = 2.11x – 8.6	24	0.69
ramets	y = 3.13x – 3.5	15	0.87
Sycamore Creek–Work Station (intermittent 2)			
genets	y = 3.24x – 13.0	23	0.75
ramets	y = 3.82x – 16.6	15	0.87
Sycamore Creek–Bushnell Tanks (perennial)			
genets*	y = 1.61x – 6.0	22	0.77
ramets	y = 2.15x – 3.6	20	0.84
Sycamore Creek–Bushnell Tanks (intermittent 1)			
genets*	y = 1.84x – 5.7	24	0.81
ramets	y = 2.05x + 1.5	17	0.75
Sycamore Creek–Bushnell Tanks (intermittent 2)			
genets*	y = 3.11x – 15.8	32	0.89
ramets	y = 3.54x – 5.2	36	0.85

*Significant difference between genets and ramets at $P < 0.05$, ANCOVA

Creek–Bushnell and Work Station, Oak Creek, and Haunted Canyon/Pinto Creek) located near long-term United States Geological Survey (USGS) stream gages. The independent variables in the analyses were mean quarterly discharges (mean daily flow during October through December, January through March, April through June, and July through September), mean annual discharge during the water year, size of the largest winter flood (October through March), size of the largest summer flood (April through September), and size of the largest respective winter and summer floods during the preceding 3-year period. The following stream flow chronologies were used in the analyses: 1962–1996 for Sycamore Creek, 1981–1996 for Haunted Canyon/Pinto Creek, and 1949–1996 for Oak Creek. Data for the Sycamore Creek analysis were from the Sycamore Creek Fort Mcdowell gage (09510200), 20 km downstream of the study site. The Sycamore Creek Sunflower gage (09510150) is closer to the site, but stream flow data were collected only for 1962–1976. Mean annual flow rates and peak annual flood sizes at the Fort Mcdowell and Sunflower gages are highly correlated ($r = 0.97$ and $r = 0.94$, respectively, $n = 15$ years of overlapping record). Peak annual flows average about 25% higher at Fort Mcdowell than at Sunflower. Data for the Haunted Canyon/Pinto Creek analysis were from the nearby Pinal Creek Inspiration Dam gage (09498400). Oak Creek stream flow data were from the Cornville gage (09504500), located 8 km downstream of the study site.

The dependent variable in the regression analyses was categorical. A value of 1 was assigned to establishment years and a value of zero to nonestablishment years. Number of trees per establishment year was not used as the dependent variable to avoid confounding
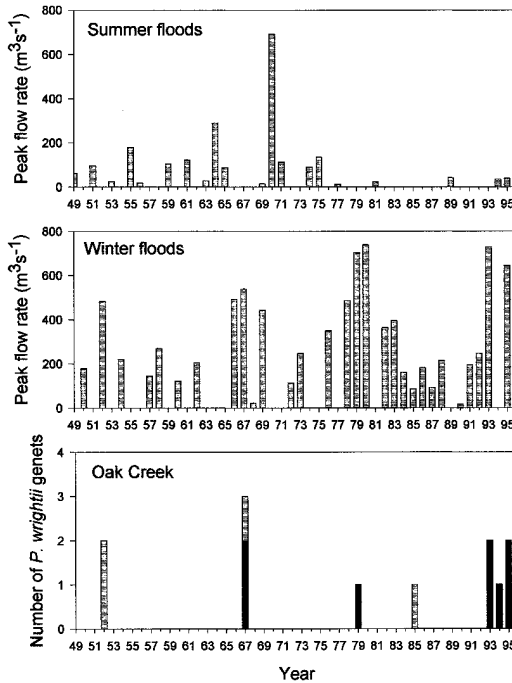
Fig. 1. Size of largest recorded flood during winter (October–March) and summer (April–September) at Oak Creek (USGS gage 09504500), 1949–1996. Also shown are numbers of aged *Platanus wrightii* genets dating from this period. Black portions of the bars indicate trees for which at least one core or slab penetrated the center of the tree; gray portions indicate trees with cores that were slightly off center.
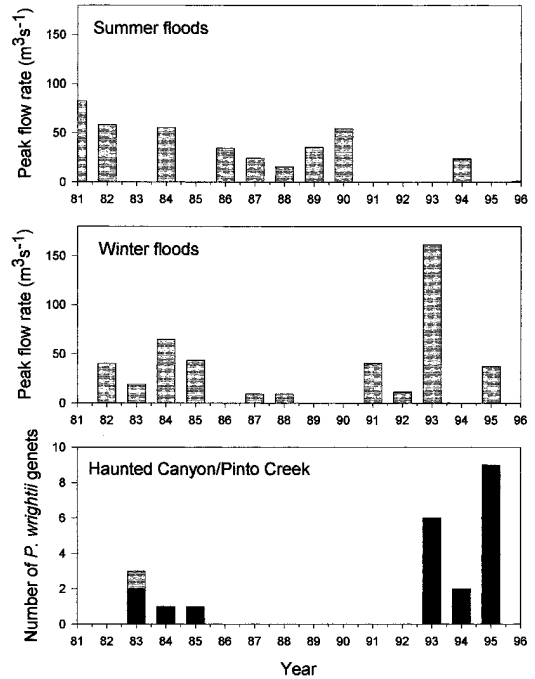
Fig. 2. Size of largest recorded flood during winter (October–March) and summer (April–September) at Pinal Creek (USGS gage 09498400), 1981–1996. Also shown are numbers of aged *Platanus wrightii* genets from nearby Haunted Canyon and Pinto Creek.

demographic effects such as age-dependent mortality processes. Regression analyses were conducted separately for genets and ramets. Analyses were conducted using only those trees that were clearly distinguishable as ramets or genets. Two sets of analyses were conducted for each to test the robustness of the results. For one of the analyses, the data set was based on all of the aged trees. For the other a year was classified as an establishment year only if at least 2 trees dated from that year. The analyses were based on 22 genets and 26 ramets that established during the 16-year period of analysis for Haunted Canyon/Pinto Creek, 85 genets and 70 ramets from Sycamore Creek (35-year period), and 12 genets and 45 ramets from Oak Creek (48-year period).

Population Size Structure

Population size structure data were collected at all 9 sites to allow examination of changes across a gradient of watershed area. Watershed area was presumed to be a surrogate for flood magnitude, given that rivers situated lower in the watershed collect runoff over a much larger area (Ribeiro and Rousselle 1996). At each site stem diameter (dbh) of all living *P. wrightii* was measured in a minimum of 4 belt transects spanning the riparian corridor. The number of ramets per genet (i.e., number of trees per cluster) was counted for a minimum of 25 genets per site.

Pearson's correlation coefficient was calculated to determine whether mean trunk diameter of the *P. wrightii* population, diameter of the largest measured tree, and mean ramet density per genet were significantly related to log-transformed watershed area. Watershed area was measured from USGS 15- or 7.5-minute topographic maps or obtained from published USGS records. Pearson's correlation coefficient also was calculated to test for significant relationship between tree size (dbh) and ramet density within sites. SYSTAT 7.0 and 8.0 were used for all statistical analyses.
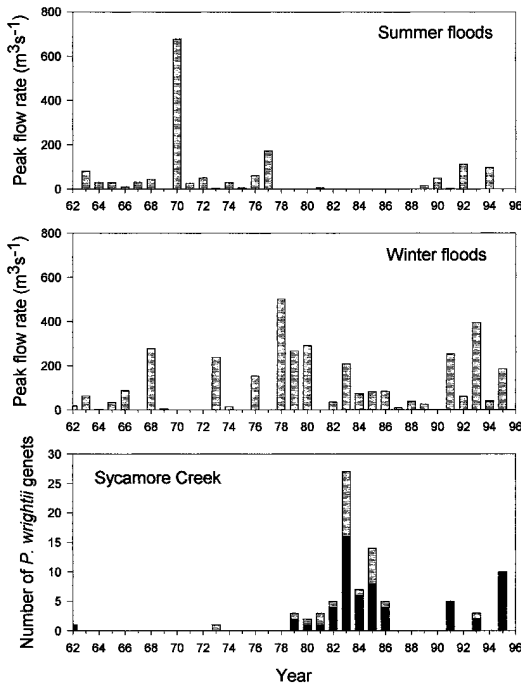
Fig. 3. Size of largest recorded flood during winter (October–March) and summer (April–September) at Sycamore Creek (USGS gage 09510200), 1962–1996. Also shown are numbers of aged *Platanus wrightii* genets.

Fig. 4. Mean daily flow during the water years 1986–1996 at Sycamore Creek (USGS gage 09510200).

RESULTS

Flood-flow Patterns

Annual discharge and size of winter and summer floods in the study rivers varied considerably over time. At all sites there were several large winter floods in recent decades. Winter floods during the 1992–93 El Niño event were particularly large and long. At Oak Creek the 2 largest recorded floods occurred in February 1993 (instantaneous peak discharge of 736 m^3s^{-1}) and February 1980 (748 m^3s^{-1}), both of which resulted from rain on snow (Fig. 1). According to USGS records, a very large flood also occurred in March 1938 in Oak Creek, for which discharge was not recorded. At Pinal Creek the 1993 flood was the largest during the past 2 decades, with a peak flow rate of 161 m^3s^{-1} in January (Fig. 2). The largest recorded flood in Sycamore Creek occurred in September 1970, with a flow rate of 685 m^3s^{-1} (Fig. 3). The largest winter flood at Sycamore Creek occurred in March 1978, with a flow rate of 501 m^3s^{-1}. Peak flow during winter 1993 (January) was 399 m^3s^{-1}. At Gar-
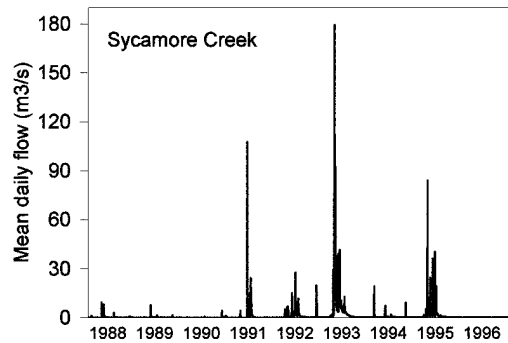
den Canyon the 2 largest recorded floods during the short period of stream flow data collection (1959–1965, 1993 to present) occurred in February 1995 (1.6 m^3s^{-1}) and July 1964 (1.6 m^3s^{-1}; data not shown).

During years with large winter floods, such as 1993, stream flows tended to be high throughout the spring season (Fig. 4). Total annual discharge also was higher than average during years with winter floods. At Sycamore Creek, for example, peak winter flood size was significantly correlated with January–March discharge ($r = 0.90$, $n = 35$), April–June discharge ($r = 0.88$), and mean annual discharge ($r = 0.86$, $n = 35$, $P < 0.05$). Peak summer flood size was not significantly correlated with annual discharge ($r = –0.18$, $n = 35$).

Summer floods generally were small or absent during years with large winter floods. Correlations between log-transformed sizes of the largest winter and largest summer flood were significantly ($P < 0.05$) negative at Oak Creek ($r = –0.68$, $n = 48$), Sycamore Creek ($r = –0.43$, $n = 35$), and Pinal Creek ($r = –0.59$, $n = 16$). Compared to winter floods, summer floods tended to have low mean daily flow rate relative to their instantaneous peak flow rate, reflecting their tendency to be "flashy." For example, the linear regression equation predicting mean daily discharge from instantaneous peak flow rate in Pinal Creek has a lower slope for summer floods ($y = 0.086x – 0.67$; $r^2 = 0.54$, $n = 12$) than for winter floods ($y = 0.63x – 12.8$; $r^2 = 0.94$).

Seedling Establishment Patterns

Platanus wrightii seedlings established episodically (Figs. 1, 2, 3). Establishment events

TABLE 3. Multiple regression models predicting *Platanus wrightii* seedling establishment years from hydrologic variables. For the conservative data set, establishment years were based on a minimum sample size of 2 trees per year.

	Model r^2	Model variables	Direction of correlation	P value
SYCAMORE CREEK				
All genets	0.27	Annual flow rate	+	<0.01
Conservative data set	0.29	Winter flood size (3 yr)	+	<0.01
		Summer flood size	−	0.09
OAK CREEK				
All genets	0.36	Winter flood size (3 yr)	+	<0.01
		Oct–Dec flow rate	+	0.03
Conservative data set	0.21	Winter flood size (3 yr)	+	<0.01
HAUNTED CANYON/PINTO CREEK				
All genets	0.69	Winter flood size (3 yr)	+	<0.01
		Oct–Dec flow rate	+	0.01
		July–Sept flow rate	+	0.02
Conservative data set	0.81	Winter flood size (3 yr)	+	<0.01
		July–Sept flow rate	+	0.04

did not occur regularly over time. At all sites there were periods of over a decade with no apparent establishment: no establishment occurred, no survivors remained, or the trees were too sparse to be detected in the sample of cored trees. For all 3 populations analyzed, winter flood size (over the prior 3 years) was a significant component of the multiple regression models that predicted seedling establishment years (Table 3). Annual discharge, winter-season discharge, and summer-season discharge were components of the models for at least a single population. Summer flood size (negative influence) was a component of 1 of the 2 seedling establishment regression models for Sycamore Creek.

During the 35-year period of hydrologic analysis (1962–1996) at Sycamore Creek, there were 13 establishment years (Fig. 3). In 12 of these 13 years, there was a winter flood but no summer flood. The winter flood was large (at least 150 m^3s^{-1}) in 7 of these years. All establishment years occurred within 3 years of a large winter flood. Not all years with winter floods were establishment years: there were 2 years (1968 and 1978) with large winter floods but no establishment. None of the years with large or small summer floods were establishment years for *P. wrightii* at Sycamore Creek.

At most sites there was a pattern for clusters of establishment years to alternate with quiescent periods. This pattern was particularly strong at Sycamore Creek. A wave of 8 consecutive establishment years began in the winter flood year of 1979 and extended through 1986, with the largest establishment pulse in

1983. Seedlings at this site also established abundantly in 1991, 1993, and 1995, all of which were wet years with relatively large winter or spring floods and small or absent summer floods (Fig. 4). The 1993 and 1995 saplings were abundant along channel margins that had been eroded and widened by flood waters. In some areas the 1993 and 1995 cohorts were spatially intermingled. In other areas the 2 cohorts formed distinct bands, with the 1995 cohorts being closer to the channel.

Platanus wrightii also established frequently at Sycamore Creek in the late 1920s and early 1930s and the 1860s through the 1900 decade (Fig. 5). The oldest cored genet at Sycamore Creek was approximately 207 years, having established during the 1780s. The 3 largest trees measured at the Sycamore Creek–Bushnell and Work Station sites (111, 113, and 131 cm dbh) had predicted ages of 175–200 years, based on extrapolation of age-dbh regression equations (Fig. 7, Table 2). The largest and oldest *P. wrightii* at these sites ranged up to 50 m from the stream channel.

At Haunted Canyon/Pinto Creek, 6 establishment years occurred during the 16-year period of hydrologic analysis (Fig. 2). Four of these 6 years (1983, 1985, 1993, 1995) had winter floods but no summer floods. One (1984) had a winter flood and a summer flood. A small number of plants established in 1994, which had a small summer flood and came immediately after the 1993 flood-of-record. Another active period of seedling establishment at Haunted Canyon and Pinto Creek occurred in the 1900s through 1930s (Fig. 5).
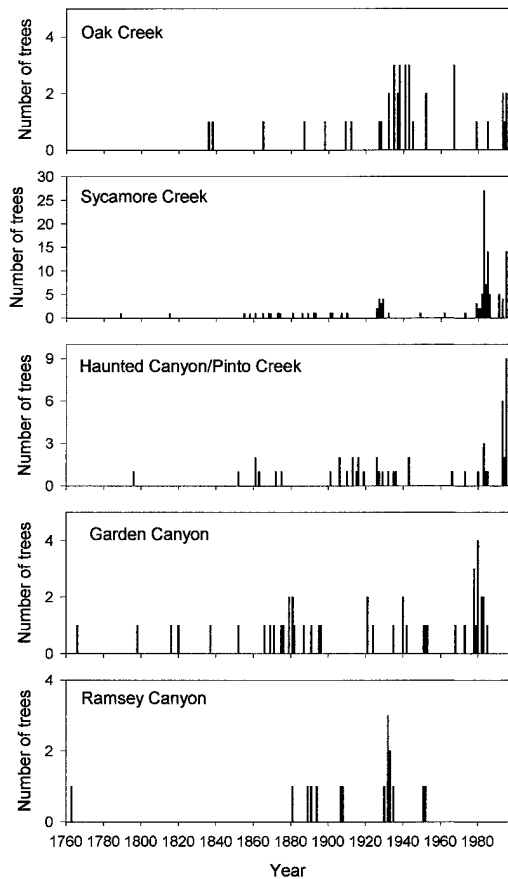
Fig. 5. Age structure histograms for *Platanus wrightii* genets at Oak Creek, Sycamore Creek, Haunted Canyon/Pinto Creek, Garden Canyon, and Ramsey Canyon. The *x*-axis extends from 1760 through 1996.

The oldest cored genet was 200 years (established in the 1790s) and had a dbh of 92 cm. Extrapolation of site-specific age-dbh regression equations yielded ages of 250–310 years for the largest trees at these sites (127, 134, and 160 cm dbh).

In the 48-year period of hydrologic analysis (Fig. 1) at Oak Creek, 7 establishment years occurred. Six of these were in years with winter floods, 5 of which (1952, 1967, 1979, 1993, 1995) had very large floods. No flood occurred in the establishment year of 1994. Only 1 (1985) of the 7 establishment years had a summer flood, and it was small. Over 20 years had winter floods but no detected establishment. Many of the establishment years at Oak Creek overlapped with establishment years at the 2 other central Arizona sites.

Many of the Oak Creek trees established in the 1930s and early 1940s (Fig. 5). The large spring flood of 1938 may have facilitated establishment of some of the trees in this regeneration pulse. The oldest trees cored at this site established in the 1830s (age of approximately 160 years). The largest uncored trees at the site (60–75 cm) had predicted ages of 100–135 years.

At Garden Canyon several trees established during the 1970s and 1980s (e.g., 1973, 1978, 1983; Fig. 5), similar to patterns observed at the central Arizona sites. However, saplings from 1993 or 1995 were not present. Among older cohorts trees established fairly frequently during the 1870s, 1880s, and 1890s. The oldest tree cored at Garden Canyon had a dbh of 122 cm and an estimated age of 175 years (established ca 1766). The largest measured tree at Garden Canyon had a dbh of 139 cm and a predicted age of 215 years.

At Ramsey Canyon roughly 5 decades have elapsed since the last establishment year of 1952 (Fig. 5). Many of the trees at Ramsey Canyon established during the 1930s and between 1880 and 1915. The oldest cored tree at Ramsey Canyon had a dbh of 162 cm and an age of approximately 235 years (established in the 1760s). The largest tree measured at Ramsey had a dbh of 194 cm and a predicted age of 250 years.

Ramet Establishment Patterns

Ramets established more frequently than seedlings (Fig. 6) and were more abundant than genets in all populations. In some cases periods that were favorable for seedling establishment were also favorable for ramet production. In other cases ramets established during times when seedlings did not. For example, during the 1950s several ramets but few genets established at Haunted Canyon/Pinto Creek and at Oak Creek. Neither ramets nor genets established at Sycamore Creek in the 1950s. All recent recruitment at Ramsey Canyon has been due to ramets.

Multiple regression models significantly predicted ramet establishment years for the 2 populations (Table 4). However, ramet models explained less variance than did seedling establishment models, and there were no consistent trends between populations in terms of influential hydrologic variables. Among populations, hydrologic correlates of ramet production
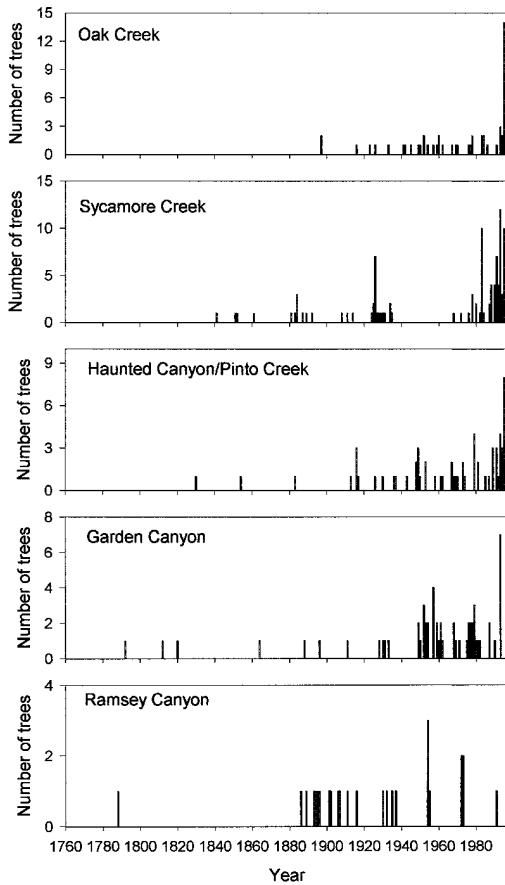
Fig. 6. Age structure histograms for *Platanus wrightii* ramets at Oak Creek, Sycamore Creek, Haunted Canyon/Pinto Creek, Garden Canyon, and Ramsey Canyon. The *x*-axis extends from 1760 through 1996.
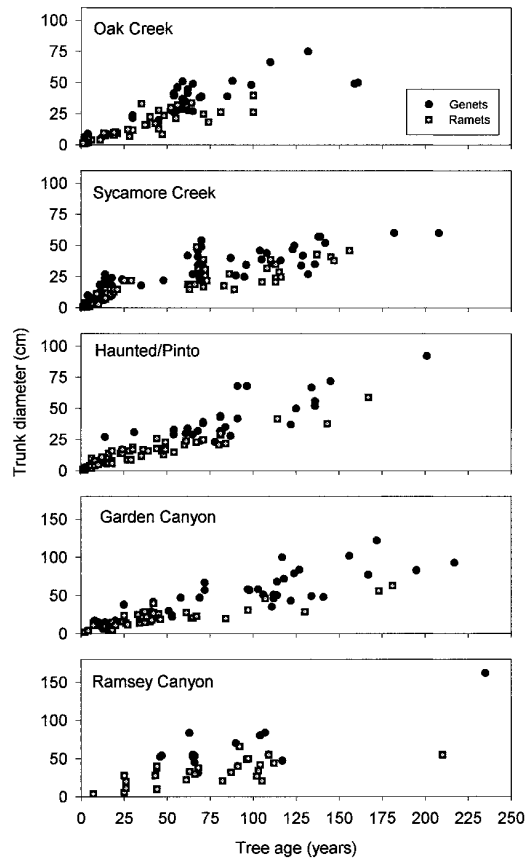

Fig. 7. Trunk diameter vs. age for *Platanus wrightii* at Oak Creek, Sycamore Creek, Haunted Canyon/Pinto Creek, Garden Canyon, and Ramsey Canyon. Data are shown separately for genets and ramets.

included winter flood size, spring-season stream flow rate, and summer dry-season stream flow rate.

Population Size Structure

Mean stem diameter of the *P. wrightii* population (inclusive of ramets and genets; Table 5) declined as watersheds became larger ($r = 0.78$, $n = 9$, $P < 0.05$). At Oak Creek, which drains a watershed of >700 km^2, most trees were <10 cm in diameter (Fig. 8). At the 3 sites draining watersheds of ≤30 km^2 (all of which are in the Huachuca Mountains), the mean diameter of *P. wrightii* stems was >30 cm. At Ramsey Canyon (13-km^2 watershed), most trees were in the 41–50 cm dbh class, and only 7% had stems with diameters <10 cm. Maximum tree size also declined among

sites as watershed size increased ($r = 0.79$, $n = 9$, $P < 0.05$).

Among the 9 sites sampled for population size structure, mean number of live ramets per genet ranged from 1.9 to 8.6 (Table 5). Ramet density was not significantly related to watershed size ($r = 0.38$, $n = 9$, $P > 0.05$). Within sites, ramet density increased significantly with genet size for 4 of 9 populations. The relationship between ramet density and genet size appeared to be curvilinear at many sites, with ramet density declining for the largest trees (Fig. 9). Trees of intermediate size (40–80 cm dbh) generally produced the most ramets. Most ramets on ramet-rich trees were small (<1 m tall) and young (1–3 years old; Fig. 10). Mortality rates for small ramets appeared to be high, based on observations of large numbers of small, dead ramets. Two

TABLE 4. Multiple regression models predicting *Platanus wrightii* sprout establishment years from hydrologic variables.

|	Model r^2	Model variables	Direction of correlation	*P* value
SYCAMORE CREEK				
All ramets	0.25	Winter flood size	+	<0.01
		Oct–Dec flows	−	0.05
Conservative data set	0.31	Annual flow rate	−	0.04
		April–June flow rate	+	<0.01
OAK CREEK				
All ramets	—	Model not significant		
Conservative data set	0.13	Jan–Mar flow rate	+	0.01
HAUNTED CANYON/PINTO CREEK				
All ramets	0.33	July–Sep flow rate	−	0.02
Conservative data set	—	Model not significant		
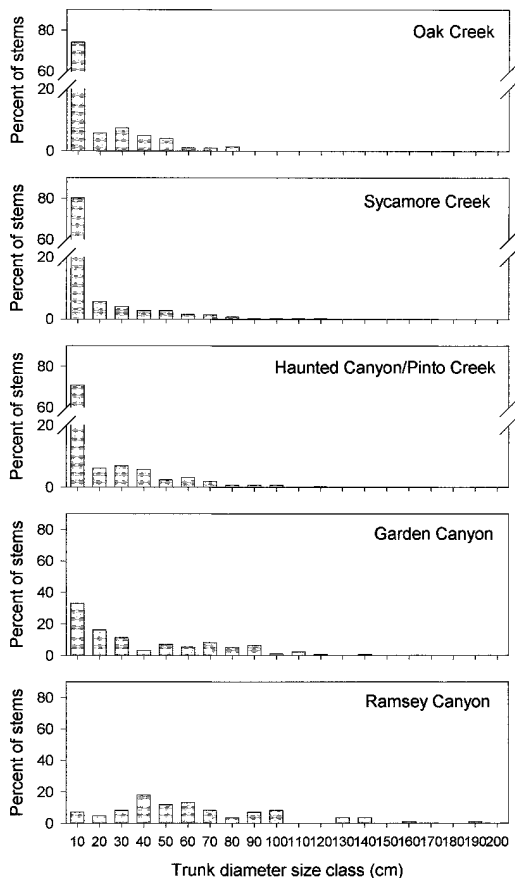
Fig. 8. Size structure histograms (10-cm dbh increments) for 5 populations of *Platanus wrightii*. Values on the *x*-axis indicate the upper range of the size class (i.e., 20 indicates trees with dbh of 11 to 20 cm). Plots are shown in order of descending watershed size.

outliers are not shown on the graphs. One tree at Oak Creek with a dbh of 73 cm had 126 ramets. Another at Haunted Canyon (91 cm) had 137 ramets. Some trees with abundant ramets showed signs of canopy dieback.

DISCUSSION

Seedling Establishment Processes

Relationships between flood flow patterns and seedling establishment of *P. wrightii* were similar in many ways to those of dominant pioneers of lower-elevation Sonoran riparian forests. Like *Populus fremontii* and *Salix gooddingii*, *P. wrightii* established episodically, mainly during years with large winter floods and high spring-season stream flows. Large winter floods do the geomorphic "work" that creates seedling safe sites (sensu Harper 1997) by scouring vegetation, eroding sediments, depositing fresh alluvium, or exposing the bare mineral soil that stimulates high rates of germination (Sigafoos 1976). High spring stream flows that typically follow large winter floods serve to moisten seeds and provide adequate water for seedling growth, not always available in these small streams that vary widely in annual flow rates (Sacchi and Price 1992). Stream flows in 1993 and 1995, for example, remained high throughout spring and summer, presumably providing the moisture that allowed high seedling survivorship. At several study sites, including Sycamore Creek and Haunted Canyon, *P. wrightii* saplings from 1993 and 1995 were intermingled with *Salix bonplandiana, S. gooddingii,* and *P. fremontii* in the recruitment zones (Fig. 11), indicating a high

TABLE 5. Population size structure variables. Sites are listed in descending order of watershed size.

Site name	Mean ramet density (no./genet)	Mean trunk diameter (cm)	Maximum trunk diameter (cm)	Correlation coefficient, ramet density vs. genet size (r value)
Oak Creek	6.9	9	75	0.43*
Sycamore Creek–Round Valley	1.9	8	23	0.13
Sycamore Creek–Bushnell	5.2	12	131	0.34
Sycamore Creek–Work Station	4.2	10	67	0.08
Pinto Creek	8.3	15	160	0.23
Haunted Canyon	8.6	10	134	0.49*
Garden Canyon	3.6	35	133	0.32*
Ramsey Canyon	2.4	60	194	0.07
Huachuca Canyon	2.3	31	186	0.34*

*Significant correlation between ramet density and genet size at $P < 0.05$

degree of similarity in regeneration niches among these species. The combination of large winter floods and cool wet springs also creates favorable regeneration conditions for *Populus angustifolia,* a member of the cool-temperate deciduous riparian forest assemblage (Baker 1990).

House and Hirschboeck (1995) describe the 1993 floods as one of the most severe winter flooding episodes in Arizona history, surpassed only by large floods in the 1890s. Regionally, floods were also very large in 1983 and the early 1900s. Large winter floods can extensively modify stream channels and flood plains (Hooke 1994). Floods that are large enough to extensively rework channel and flood plain sediments can facilitate a multi-year wave of *P. wrightii* establishment. Multi-year post-flood establishment also has been documented for *Populus deltoides* subsp. *monilifera* along the Missouri River in Montana (Scott et al. 1997). This differs somewhat from the pattern for *P. fremontii* along the larger alluvial desert rivers in Arizona, where high rates of sedimentation can quickly render the flood plain recruitment zones unsuitable for further seedling establishment. This sedimentation process did not appear to be as evident in the *P. wrightii* study streams, allowing flood-scoured zones to remain suitable for establishment in ensuing wet years.

Platanus wrightii establishment patterns showed a high degree of temporal variation, reflecting highly variable flood patterns both in terms of season and year. Decades with abundant establishment included the 1980s and 1990s, 1920s and 1930s, and those just before and after 1900. High variation in flood
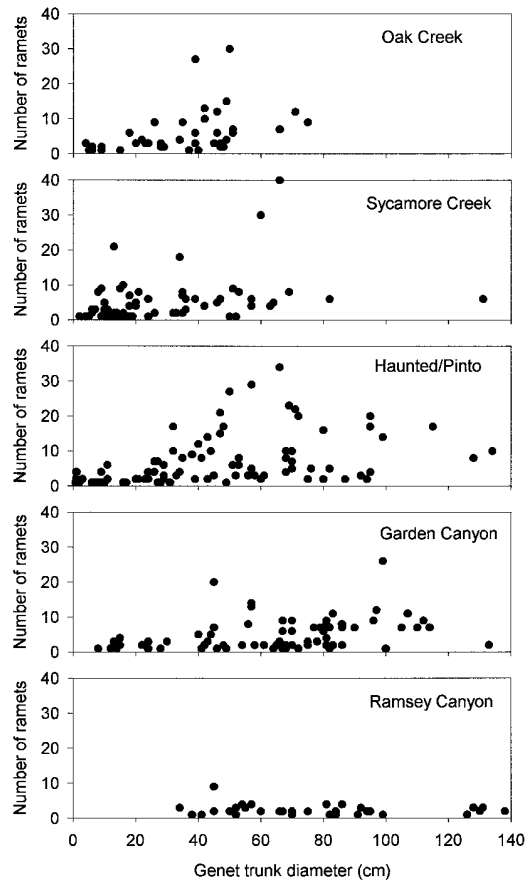

Fig. 9. Ramet density as a function of genet trunk diameter for 5 populations of *Platanus wrightii.*

Fig. 10. Small (above) and large (facing page) ramets of *Platanus wrightii* arising from the

patterns in semiarid regions, on decadal scales, is largely due to influences of El Niño–Southern oscillation (ENSO) weather patterns (Molles et al. 1992, Webb and Betancourt 1992). Swetnam and Betancourt (1998) note that "the post-1976 period shows up as an uprecedented surge in tree-ring growth within millenia-length chronologies" of upland trees in the southwestern United States and reflects a post-1976 shift to the negative phase of the Southern oscillation. The result of this

shift has been a high frequency of El Niño years during the 1980s and 1990s, characterized by wet winters and large winter floods. These hydrologic conditions have provided opportunities for frequent and extensive regeneration of *P. wrightii,* as well as *Populus fremontii* and *Salix gooddingii,* in recent decades (Stromberg 1998).

Platanus wrightii did not establish in response to summer floods. Monsoon-season floods conceivably could create conditions suit-

base of parent trees (photograph by J. Stromberg).

able for seedling establishment in late summer or the following spring. Optimum germination temperature for some *P. wrightii* is 27°C, consistent with early- or late-summer germination (Siegel and Brock 1990). However, in a growth chamber programmed to simulate field conditions, all *P. wrightii* seeds germinated in April or May (R. Richter personal observation). Summer floods arise due to localized convective thunderstorms and tend to have high instantaneous peak flow rate but short dura-

tion. Compared to a winter flood of the same instantaneous discharge, summer floods cause less geomorphic change (Everitt 1995) and presumably do not moisten soils for a long period after the flood peak. Thus, summer floods probably do not frequently create suitable establishment sites for *P. wrightii.*

Many years, and even one or more decades, elapsed in which conditions apparently were unsuitable for establishment of *P. wrightii.* Some of these periods were characterized by

Fig. 11. Flood-scoured stream channel with bands of *Platanus wrightii* and *Populus fremontii* seedlings that established in 1993 and 1995 (photograph by J. Stromberg).

below-average stream flows. A severe drought occurred in the American Southwest in the 1940s and 1950s (Shelton and Bahre 1993, Swetnam and Betancourt 1998). This drought probably contributed to sparse regeneration by *P. wrightii* (Fig. 8).

Activity of convective summer thunderstorms and floods was high in some parts of Arizona in the decades prior to the 1970s (Webb and Betancourt 1992), perhaps also further contributing to the paucity of cohorts dating from the middle decades of the 1900s. Summer floods have been reported to cause mortality of *P. wrightii* seedlings and trees by uprooting and scouring plants (Bock and Bock 1989). In this study there was a weak negative correlation between summer flood magnitude and *P. wrightii* seedling establishment for a single population. This pattern may directly reflect flood-caused seedling mortality, or may reflect a climatic tendency for summer floods to be small in years with large winter floods.

There was overlap among sites in seedling establishment years, reflecting the trend for winter storms and floods to occur region-wide.

However, although seedlings established during the 1993 and 1995 winter flood years at central Arizona sites, they did not do so at southeastern Arizona sites (Ramsey and Garden canyons). Regional differences in storm tracks may have contributed to this pattern. Between-site differences in stream size and flood power also may have contributed. Populations of *P. wrightii* along small headwater streams were dominated by old trees and had few young trees. Downstream decreases in mean or maximum tree age also have been observed for *Populus* species (Stromberg and Patten 1992, Stromberg 1998). These patterns suggest that size of recruitment events and rates of population turnover are greater on larger streams.

Establishment processes of *P. wrightii* also may have been influenced by domestic livestock and native herbivores. In some circumstances, livestock grazing can favor pioneer woody plants by reducing abundance of herbaceous competitors and maintaining the community in an early successional state. Heavy livestock grazing also can inhibit establishment

of pioneer tree seedlings. Livestock grazing has been identified as a factor contributing to low abundances of *P. wrightii* seedlings and saplings (Glinski 1977, Rucks 1984), although Bock and Bock (1989) attribute the negative effect to legacies of past heavy grazing (such as channel incision) rather than to direct effects of browse or trampling. This study was not designed to assess effects of livestock grazing on *P. wrightii*, in that there was no replication of grazed and ungrazed sites within stream flow regime or watershed size classes. Such a study would be valuable, given the large number of riparian and upland sites on public and private land that are grazed in the American Southwest. This present study does highlight the need to consider a suite of factors that influence seedling establishment when assessing the effects of livestock management changes on riparian vegetation. Spatial controls in reference watersheds are important to allow one to distinguish between land management changes and weather-related influences. Without control sites it is difficult to know whether increases or decreases in seedling numbers are related to livestock management changes or to changes in flood flow and low flow patterns.

Riparian tree age structure, or at least presence of seedlings and saplings, is one measure of ecological health used by land managers to assess impacts from livestock grazing (Prichard et al. 1998). If examined for a larger number of sites, relationships between *P. wrightii* size or age structure and watershed area could provide a reference against which managers could assess a particular *P. wrightii* population for "healthy" structure. To be most useful to managers, the relationships between size/age structure and watershed area should be developed within ecoregions and within flow regime types, thereby taking into account additional site factors that influence population dynamics such as the relative contribution of summer and winter flows to mean annual discharge. For example, regeneration of *P. wrightii* may be inherently less frequent along streams in ecoregions with larger and more frequent summer floods. Results of this study suggest that dominance by old individuals is typical for *P. wrightii* populations along some ungrazed headwater streams. Thus, infrequent regeneration of *P. wrightii* at headwater sites may not necessitate management concern. However,

the contrast between Garden and Ramsey canyons, both of which are headwater streams in the same ecoregion, suggests that some factor may be reducing recruitment rates at Ramsey Canyon. Deer browse, channel incision, dense cover of *Vinca major* in the understory, and canyon shade are factors that may be contributing to the lower abundance of young *P. wrightii* at Ramsey Canyon compared to Garden Canyon.

Vegetative Reproduction

Platanus wrightii, like many riparian plant species that live in temporally unpredictable environments, reproduces by seed and vegetatively. Vegetative sprouts (ramets) comprised over half of the *P. wrightii* stems in all populations. Ramet production may facilitate persistence of *P. wrightii* populations by allowing regeneration during long periods that can occur in which seedling regeneration needs are not met. The large root and stem masses that develop on old *P. wrightii* clones may provide a buffer against flood scour and perhaps increase survivorship over nonclonal species.

Ramet production can be stimulated by many factors, including disturbance, changes in resource availability, and disease. For 2 *P. wrightii* populations, ramet production was associated with winter flood years and/or wet springs, although these trends were not robust. Flood debris can trigger sprouting in riparian trees by causing wounding or stem removal (Rood et al. 1994, Ischinger and Shafroth 1995). Increased ramet production in years with wet springs may be related to weather-induced expression of anthracnose (*Gnomonia platani*). Anthracnose is a systemic fungal disease that is widespread in populations of *P. wrightii* and other *Platanus* species (Svihra and McCain 1992). Cool, wet weather in spring increases susceptibility to the fungus, resulting in canopy dieback. During this study I observed many trees with canopy dieback and other symptoms of anthracnose in 1995, a year with a cool, wet spring. Many of these trees had an abundance of young ramets. Thus, seedlings and ramets both may establish in years with wet winters and springs, although due to different mechanisms.

Ramet density varied substantially among populations but was not significantly related to watershed area. However, the positive correlation coefficient between the 2 variables was

relatively high, warranting further investigation. To understand the causes of between-population variability in ramet densities, a large number of sites should be studied to disentangle effects due to tree size and age. Tree size influences ramet density and co-varies with watershed size. Another factor that might be examined is light availability. Ramet production is higher in open, sunny sites for some, but not all, riparian trees (Shaw 1991, Mishio and Kawakubo 1998). Ramet density may be higher for *P. wrightii* growing in open outwash plains or alluvial valleys than in narrow shady canyons.

Between-site differences in herbivory rates may have contributed to some of the differences in ramet density among populations. Managers at Ramsey Canyon have observed deer browsing on the *P. wrightii* ramets and noted that deer are very abundant in the Ramsey Canyon sanctuary. Deer browsing may have contributed to the low numbers of ramets at Ramsey Canyon as well as to the lack of correlation between ramet density and genet size at this site.

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