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VARIABILITY AMONG FIVE RIPARIAN COTTONWOOD  
(*POPULUS FREMONTII* WATS.) POPULATIONS: AN EXAMINATION  
OF SIZE, DENSITY, AND SPATIAL DISTRIBUTION

Diane L. Rowland<sup>1</sup>, Beth Biagini<sup>2</sup>, and Ann S. Evans<sup>2</sup>

**ABSTRACT.**—Various abiotic and biotic factors are known to affect tree size, including age, genetics, and environment. Knowledge of size variation within natural riparian tree populations has both ecological and restorative importance. We determined tree sizes, basal area densities, and spatial distributions of 5 *Populus fremontii* Wats. populations within the Rio Grande watershed in New Mexico. At each site 10 randomly spaced plots, perpendicular to the river and extending from the river to the end of the forest, were established. Diameter at breast height (DBH) and distance to the river were determined for 1803 trees within the 5 populations, and stand cover (measured as basal area [BA] per hectare) was determined for each population. Significant variation in tree size and basal area density existed among sites. Mean DBH per site ranged from 11.7 to 58.4 cm and differed significantly ( $P < 0.0001$ ) among sites. Mean BA per hectare also varied significantly ( $P < 0.0001$ ) among sites and ranged from 13.2 to 28.9 m<sup>2</sup> ha<sup>-1</sup>. Spatial distribution of trees in relation to the river also differed among sites. Mean distance from the river ranged from 50 to 353 m and differed significantly ( $P < 0.0001$ ) among sites. Tree size was both linearly and nonlinearly related to distance from the river, with models varying among sites. Patterns of distribution in these New Mexico *P. fremontii* populations may be influenced by differences in water availability across a site; trees farthest from water sources may experience greater water stress and, therefore, growth limitation. Increasing BA cover with increasing tree size indicated no real thinning of mature trees within a population. Recruitment and establishment of cottonwood seedlings and saplings was evident only at sites with newly formed floodplains. For these 5 populations tree size appeared to be affected by environmental factors.

*Key words:* *Populus fremontii*, Rio Grande, riparian ecosystem, tree size variation, water stress, tree spatial distributions, basal area.

Researchers from the disciplines of ecology and forestry focus on determining causes behind variation in growth and size among individual plants because such variation can indicate important differences in age, competition, genetics, and environment (Stoll et al. 1994). For a single tree, size can be determined by both biotic and abiotic factors and their interactions. Biotic factors include genetics, age, sex, herbivore impact, and inter- or intraspecific competition; abiotic factors include availability of nutrients, water, and light. Populations of riparian trees provide unique opportunities to study the factors that affect tree size, density, and distribution. During periodic flood events, trees often are established in even-aged cohorts or “isochrones” (Stromberg et al. 1991, Braatne et al. 1996) at various distances from the river channel. Thus, isochrones may be composed of even-size trees due to their common age. In addition, spatial distribution of isochrones is dependent upon

flood events that lead to seedling establishment. However, some environmental factors may affect tree growth and spatial distribution even more than age. For example, Roberts (1993) found that floodplain *Eucalyptus coolabah* growth and survival were more strongly affected by saline soils and dry conditions than by age. Other factors within riparian ecosystems can also affect tree growth, including distance to groundwater, nutrient status, stand density, reproductive mode (either sexual or asexual), and herbivore pressure (Stromberg 1993). Stand density and tree size are closely linked as well. Density-dependent effects on tree size are strong for many species (Condit et al. 1994, Stoll et al. 1994). However, despite this close relationship, riparian forest stand densities can be highly variable (Braatne et al. 1996).

One such riparian species with potential size and stand density variability among populations is *Populus fremontii* Wats. (Fremont

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cottonwood). This native riparian tree is the dominant forest species within the Rio Grande watershed in New Mexico and historically dominated other riparian zones of the south-western United States. *Populus fremontii* forests provide canopy and understory habitats that are preferred by many animal species including spiders (Jennings 1972), beavers (Irvine and West 1979, Crawford et al. 1993), and birds (Johnson et al. 1990, Crawford et al. 1993). Cottonwood forests are found in diverse areas along the Rio Grande basin; these areas vary in precipitation, temperature, elevation, and soil characteristics. Some riparian populations of *P. fremontii* are also isolated by geographic distance and by natural river constrictions that may serve as barriers to seed dispersal. Such environmental variation and possible genetic differentiation could lead to variability among populations in such stand characteristics as tree size, basal area, and spatial distribution.

Although riparian forests in New Mexico are of prime ecological importance, their fate is uncertain. Due to perturbations such as construction of dams and channelization, Rio Grande cottonwood forests are likely to disappear in the next 50 yr (Howe and Knopf 1991, Crawford et al. 1993). Factors contributing to this demise include increased competition from exotic tree species (e.g., *Tamarix ramosissima*; saltcedar), reduced water availability, and a lack of germination sites due to elimination of flood events. High use of groundwater from tree competitors, combined with restricted aboveground stream flow, may be causing water stress for cottonwood trees in New Mexico riparian zones (Crawford et al. 1993, Stromberg 1993). Aboveground stream flow is a significant water source for New Mexico riparian populations of *P. fremontii*; stream flow explains 68% of tree ring growth variation for these cottonwoods (J. Leffler personal communication). In addition, *Tamarix* trees in these riparian communities are known to increase soil salinity, possibly causing surface and leachate water to be unavailable to cottonwoods (Stromberg 1993, Busch and Smith 1995). Water stress, in turn, may limit the capacity of adult trees to grow and thrive. Several studies have concluded that these factors will lead to eventual elimination of cottonwood in the Southwest (Irvine and West 1979, Fenner et al. 1985, Asplund and Gooch 1988, Busch and Smith

1995). Deterioration of *Populus* populations due to strict river control measures is not uncommon in western North America (Rood and Heinze-Milne 1989, Rood and Mahoney 1990, Braatne et al. 1996).

Because of these threats to the survival of riparian cottonwood forests, documentation of forest stand parameters such as tree size, basal area, and spatial variation among natural riparian populations of *Populus fremontii* in New Mexico is of particular importance, both for ecological and conservation reasons. Knowledge about these characteristics gives a basis for further investigations into possible environmental factors (e.g., water availability) that affect these characteristics. If adverse environmental characteristics can be ameliorated, then such intervention may ensure the future survival of *P. fremontii* populations. If tree size and basal area variation is due to genetic differences, then future studies determining this genetic variability could identify genotypes that might be utilized in restoration efforts.

In 1994 we conducted a study to measure tree size, stand density, and spatial variation among 5 *P. fremontii* populations in central New Mexico. Howe and Knopf (1991) concluded that cottonwood populations in central New Mexico are even-aged. The apparent absence of extensive cottonwood regeneration along the Rio Grande since the introduction of upstream dams in the past half century supports this conclusion. However, for *P. fremontii*, an even-age distribution is not necessarily reflected in an even-size distribution. Differences among individuals in traits such as suckering, sex-specific growth, genotype, and environmental variability all contribute toward tree size differences in an even-aged stand.

We took forest stand measurements to explore population level differences in tree size, basal area, and spatial variation of *P. fremontii*. First we asked: Do tree sizes and basal area densities of cottonwoods differ among riparian populations? We hypothesized that if most cottonwood populations along the Rio Grande basin had been established during 1 or 2 common flood events prior to dam construction, then most populations would be composed of 1 or 2 even-aged isochrones. Furthermore, because of strict water control along the Rio Grande and its tributaries, these cohort populations may have similar water availability and therefore be of similar size.

Secondly, we asked: If size variation were observed, is this variability related to distance to a water source in the environment? We hypothesized that water stress would likely be more acute farther from the river, so that tree sizes would decrease as distance to the river increased. This is because aboveground stream flow can serve as an important water source for *P. fremontii*, and stream flow greatly impacts groundwater, the primary source of water for cottonwoods (Leffler and Evans 1999).

## METHODS

### Study Sites

We established 5 study sites to sample the *Populus fremontii* forest that spans 480 km along the Rio Grande and a major tributary, the Rio Chama (Fig. 1). The northernmost site is north of White Rock Canyon and includes a single site at Abiquiu (36°12'30"N, 106°19'06"W, 1807 m elev) along the Rio Chama. The following study sites were established south of White Rock Canyon: Corrales (35°14'16"N, 106°36'22"W, 1552 m elev), Los Lunas (34°48'22"N, 106°43'58"W, 1479 m elev), Bernardo (34°25'06"N, 106°50'06"W, 1444 m elev), and San Antonio (33°55'06"N, 106°52'06"W, 1380 m elev). These sites were chosen to sample the contiguous cottonwood forest within the Rio Grande basin in New Mexico; this forest runs just below Taos Gorge south to Elephant Butte Reservoir. Because of extensive channelization and levee construction, cottonwood populations south of Elephant Butte have been reduced to isolated patches (personal observation).

At each study site ten 10-m-wide randomly located plots were established within an approximate 0.5-km section of forest. Each plot was perpendicular to the associated river and extended from the riverbank to the outer edge of the riparian forest. Distances between plots ranged from 0 to 50 m. At the 4 Rio Grande sites, forest edge coincides with a levee road and water diversion channel, both parallel to the river. These diversion channels are common along the length of the western edge of the Rio Grande. At Abiquiu, the Rio Chama and an abandoned agricultural field border the forest. Within each plot all live cottonwood trees were tagged and mapped; over all plots a total of 1803 trees were catalogued.

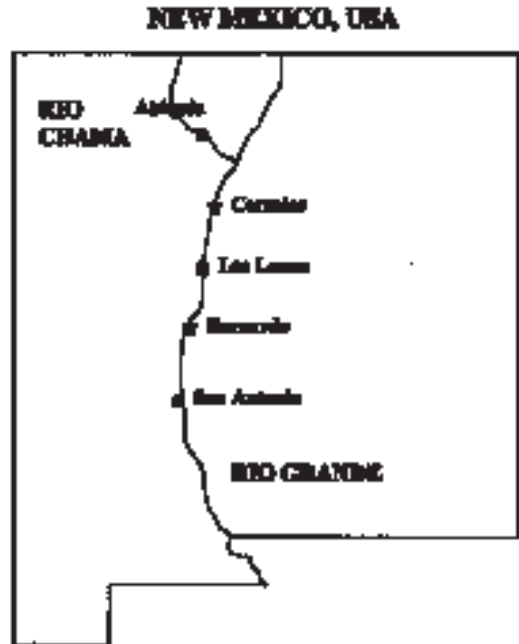


Fig. 1. Location of *Populus fremontii* study populations in New Mexico located at Abiquiu along the Rio Chama, and at Corrales, Los Lunas, Bernardo, and San Antonio along the Rio Grande.

In general, sampled cottonwood stands were mature and continuous throughout each study area; however, minor recruitment was observed at Corrales and San Antonio. At these sites the gallery forest ends abruptly with a 50-m (Corrales) or 200-m (San Antonio) stretch of newly established floodplain situated between the mature forest and the river. Young cottonwood trees inhabit these floodplains. At Corrales, the floodplain was sampled because most juvenile trees were large in size and many were of reproductive age. However, at San Antonio, the floodplain was not sampled because most trees were too small to tag (<4 cm DBH) without causing significant mortality.

### Measurements

For all plots and sites, tree diameter at breast height (DBH) (ca 1.45 m) was measured to the nearest centimeter for all live cottonwoods. We measured distance to the river to the nearest 0.1 m for each tagged tree. To determine the cross-sectional area of each tree, we calculated basal areas from DBH measurements using the general equation of Avery and Burkhart (1994) for any tree species, where:

$$\text{Basal Area (BA) (m}^2\text{)} = 0.00007854 (\text{DBH}^2).$$

Mean basal area per hectare, a measure of stand density, was calculated for each of 10 plots at all 5 sites using the area of each plot.

#### Analyses

For each site and over all sites, descriptive statistics were performed for tree size distributions. Differences among sites for mean tree size (DBH), distance to the river, and basal area per hectare were analyzed using fixed ANOVA and Bonferroni multiple range tests (SYSTAT 1996). Before analyses, DBH data were log-transformed to comply with normality assumptions of ANOVA. To investigate possible relationships between tree size and tree-spatial distributions, we performed least-squares regression analyses (both linear and nonlinear models) for each site separately, and for all sites pooled (SAS Institute 1989).

### RESULTS

#### Variation Among Sites in Tree Size, Spatial Distribution, and Basal Area

Contrary to our expectation of size uniformity, there was extensive variation among cottonwood populations in tree size within the Rio Grande watershed. Mean tree size (DBH)

was significantly different among sites and ranged from 11.7 cm at Corrales to 58.4 cm at Los Lunas (Table 1). The Los Lunas population contained extremely large trees compared to the other sites. Mean distance to the river for trees was significantly different among sites, ranging from 50.3 m at Los Lunas to 352.9 m at San Antonio (Table 1). Multiple range tests showed that all sites differed from one another for DBH and distance to the river. Basal area per hectare also differed significantly among sites (Table 1) and ranged from 28.9 m<sup>2</sup> ha<sup>-1</sup> at San Antonio to 13.2 m<sup>2</sup> ha<sup>-1</sup> at Corrales. Multiple range tests showed Los Lunas and San Antonio had similarly large basal area per hectare, while Abiquiu, Bernardo, and Corrales had comparable values.

#### Size and Distance to the River

The relationship between tree size and distance to the river was more complex than a simple linear function of distance from this possible water source. For data pooled over all 5 sites, the relationship was linear; in general, small trees were near the river and large ones farther away ( $F = 199.5$ ,  $P < 0.0001$ ,  $r^2 = 0.0993$ ; Fig. 2). However, this overall picture is somewhat misleading because spatial distribution of trees differed among individual sites and was often nonlinear. The least-squares line that best described tree distribution at

TABLE 1. ANOVA table for variation in tree size (DBH), distance to river, and basal area per hectare among 5 riparian *Populus fremontii* populations in New Mexico (AB = Abiquiu, CO = Corrales, LL = Los Lunas, BE = Bernardo, SA = San Antonio). Different letters denote significant differences among groups at  $P < 0.05$ .

Trait	Site	Trait mean ( $\pm s_{\bar{x}}$ )	df	F-value	P-value
DBH (cm)	AB	25.3 (0.5) a	4	480.5	0.0001
	CO	11.7 (0.9) b			
	LL	58.4 (2.7) c			
	BE	20.0 (0.6) d			
	SA	39.2 (0.8) e			
Distance to river (m)	AB	147.9 (2.8) a	4	2111.4	0.0001
	CO	65.5 (1.5) b			
	LL	50.3 (3.3) c			
	BE	95.2 (1.5) d			
	SA	352.9 (2.7) e			
Basal area per hectare (m <sup>2</sup> ha <sup>-1</sup> )	AB	14.3 (1.5) a	4	18.0	0.0001
	CO	13.2 (2.3) a			
	LL	28.0 (1.9) b			
	BE	14.0 (1.5) a			
	SA	28.9 (2.2) b			

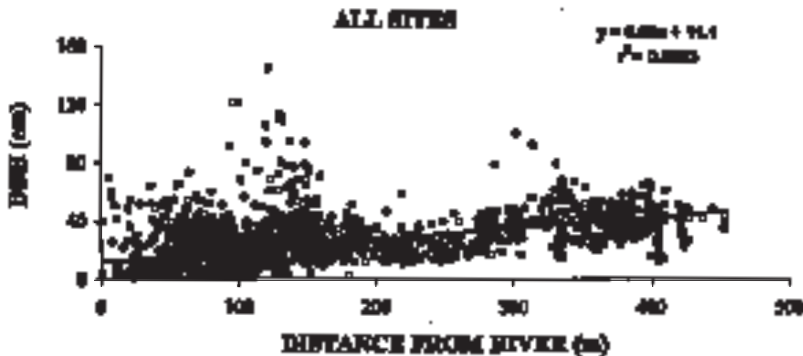


Fig. 2. Relationship between tree size (DBH) and distance to the river among 5 *Populus fremontii* populations in New Mexico. Data are pooled from all 5 sites (see Fig. 1).

Abiquiu was linear but negative; larger trees were near the river while smaller trees were close to the agricultural field (Fig. 3a). Tree distribution at Los Lunas also was linear but positive, with large trees clustered farther away from the river (Fig. 3b). However, tree distributions at both Corrales and Bernardo were nonlinear. At Bernardo large trees were found near the river and also near the diversion channel, whereas smaller trees were centered in the plots (Fig. 3c). Largest trees at Corrales were near the diversion channel, medium-small trees near the river, and smallest trees centered in the plots (Fig. 3d). No significant relationship was evident at San Antonio between DBH and distance to nearest water source (Fig. 3e).

#### DISCUSSION

##### Size, Distance, and Basal Area Variation Among Sites

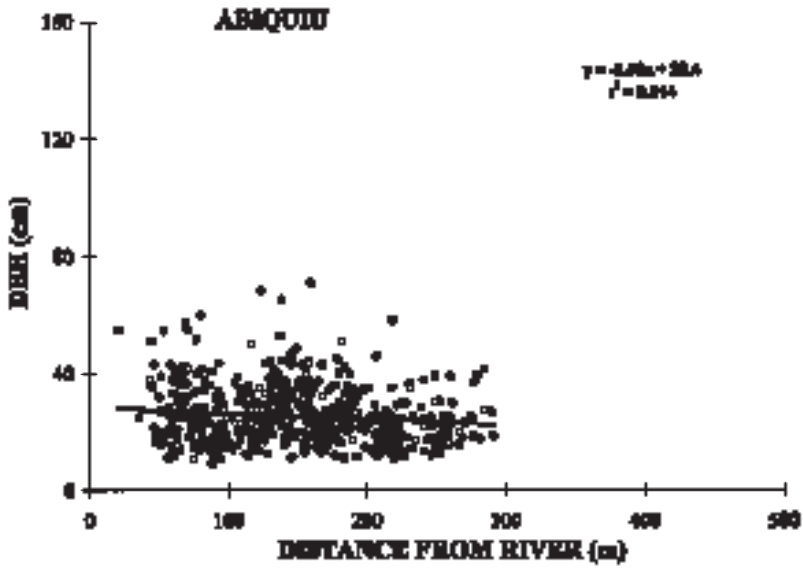
In New Mexico we found significant variation in tree size among 5 riparian populations of *Populus fremontii* along the middle Rio Grande and one of its northern tributaries. This is contrary to what we expected because of the purported even-aged structure of these populations (Howe and Knopf, 1991) and because recruitment in these populations has virtually ceased with the construction of dams in the past 50 yr. Therefore, other factors besides age must be affecting growth rate. Tree size often is an indicator of physiological activity (Dickson 1991, Avery and Burkhardt 1994), and specifically for *P. fremontii* where size per se is not a good indicator of age (Howe and Knopf

1991). However, some size differences may be accounted for by age among *P. fremontii* populations. For example, at Corrales a portion of the population was established recently. Preliminary dendrochronological analysis shows that trees closest to the river at Corrales are approximately 15 yr old (Rowland et al. unpublished data), while the dominant forest at this site may be closer to 50 yr of age (C. Crawford personal communication).

Nonetheless, due to the purported even-aged structure of most middle Rio Grande *P. fremontii* populations, dramatic differences in tree size among populations in this study may not be age related. For example, large trees at Los Lunas recently have experienced overbank flooding, followed by establishment and luxuriant growth of herbaceous species in the understory. Such growth is indicative of a moist habitat. Sediment deposited by overbank flooding is a rich source of nutrients (Stromberg 1993). Such favorable moisture and nutrient conditions could have led to enhanced tree-growth rates at Los Lunas. Cottonwoods are known to require groundwater; however, surface soil moisture also is important to cottonwoods because they have extensive lateral root systems (Dickmann and Pregitzer 1992, Stromberg 1993). All 5 sites showed some within-site diversity of tree sizes. We suspect that such size ranges are due to within-site variability of nutrients, moisture, and sunlight. Intra- and interspecific competition for these favorable environmental conditions also may affect tree growth and size within a site.

Besides age, tree size diversity can be attributed to a number of biotic and abiotic

a



b

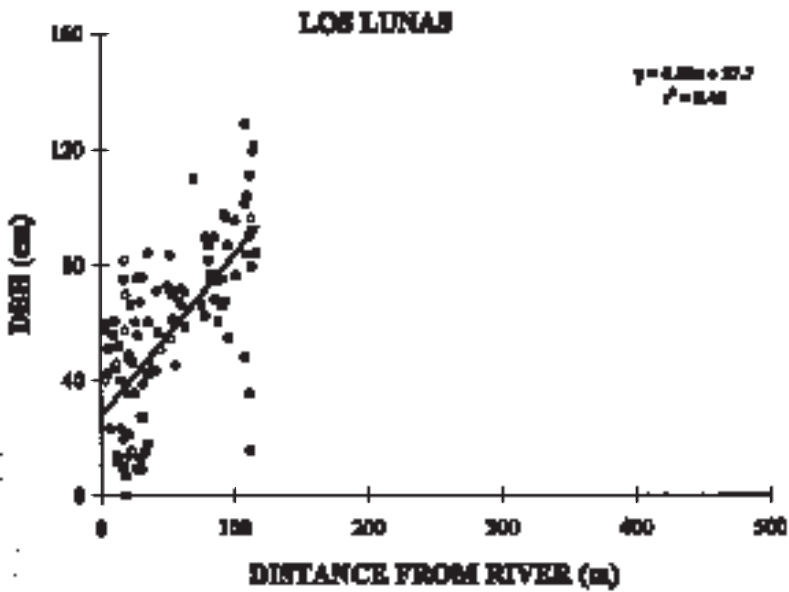
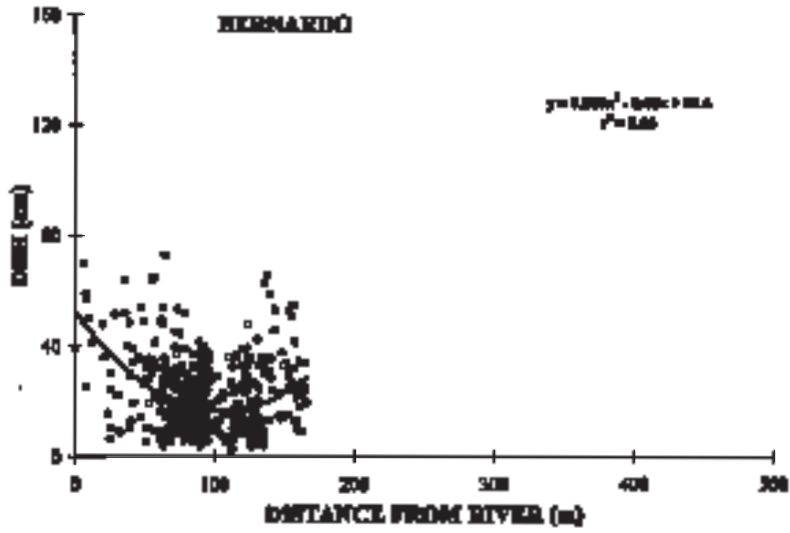


Fig. 3. Relationship between tree size (DBH) and distance to the river for 5 individual populations of *Populus fremontii* in central New Mexico. The data show a significant (3a) negative relationship at Abiquiu and (3b) positive linear relationship at Los Lunas.

c



d

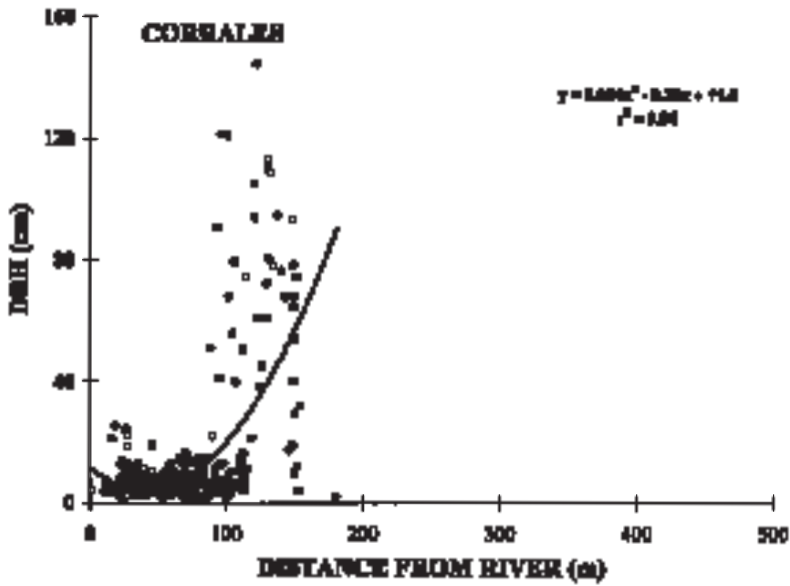


Fig. 3. Continued: (3c) nonlinear, quadratic relationship at Bernardo and (3d) nonlinear, quadratic relationship at Corrales.



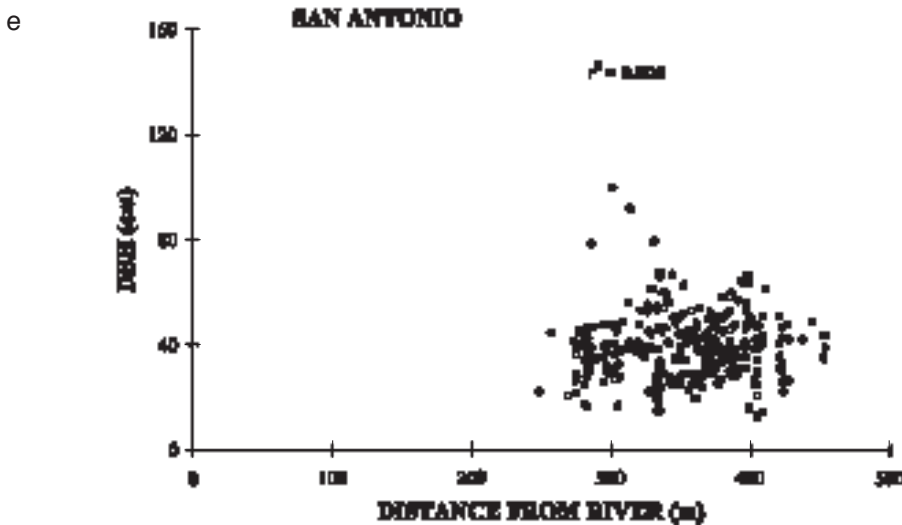


Fig. 3. Continued: (3e) no detectable relationship at San Antonio.

factors. Biotic factors affecting size variability in *P. fremontii* include suckering, sex-specific differences, genetic differences, and competition. Presence of abundant saplings only at Corrales and San Antonio indicates that recruitment of riparian cottonwoods in the recent past was limited to these sites. Asexual reproduction also may have contributed to some observed size variation. Howe and Knopf (1991) noted clonal reproduction for *P. fremontii* along various areas of the Rio Grande. Such asexual reproduction may explain the preponderance of smaller size classes (DBH = 10–20 cm) at Bernardo, where multiple-bole trees were common. However, to our knowledge quantitative assessments of asexual reproduction in riparian cottonwoods have not been made. To do so would require physical excavation of roots or, preferably, genetic identification of clones. Genetic variation also may have contributed to observed size differences among and within *P. fremontii* populations in New Mexico. For sugar maple (*Acer saccharum* Marsh.), recent studies (Perry and Knowles 1991, Young and Merriam 1994) have emphasized that, even at a small spatial scale, genetic variation can be substantial. Whether such genetically based small-scale spatial variation exists for *P. fremontii* remains to be seen. However, if present, it would be an invaluable source of genetic diversity that could be utilized in forest-stand restoration (Stromberg 1993).

The 5 cottonwood populations we observed in New Mexico were highly variable in stand density as well. Mean basal area per tree was significantly different among sites; this was not surprising because basal area is derived from DBH, which was significantly different among sites. As expected from DBH measurements, Los Lunas had the largest mean basal area per tree (0.33 m<sup>2</sup>). However, not as obvious were significant differences among sites in mean basal area per hectare (stand basal cover), with Los Lunas and San Antonio exhibiting higher basal area per hectare than the other 3 populations. These 2 sites had the largest trees as well. Based on these results, it appears that *P. fremontii* trees may not self-thin as they approach maturity; consequently, stand density increases with tree size. Intraspecific competition is likely to be great at these sites where both basal area per tree and stand density are high. Large variability in stand basal cover is a common result for many species of *Populus* (Braatne et al. 1996).

#### Size and Spatial Distribution

The observed diverse spatial distributions of cottonwood trees in New Mexico suggest that tree recruitment and growth might be affected by environmental conditions, possibly water availability, in these riparian communities. If size variability existed among these populations, we expected water availability might be driving much of this variation. We

hypothesized that large trees would be located near the river, a possible important water source for cottonwoods in these dry, southwest populations. However, the nonlinear distribution of trees at Bernardo and Corrales shows that large trees are found not only near the river, but also near the diversion channel, another likely aboveground water source.

Two sites, Abiquiu and Los Lunas, had a linear relationship between tree size and spatial distribution. The nonlinear distribution of trees associated with 2 possible aboveground water sources is absent at Abiquiu, where no 2nd source of water occurs. However, at Abiquiu, the linear relationship is as expected: large trees are located near the river, the only aboveground water source available. The linear relationship at Los Lunas is not as expected if tree size at this population is dependent upon proximity to an aboveground water source because the smallest trees are located near the river. However, this site is currently experiencing overbank flooding that could be influencing tree size by providing water uniformly across the population and by affecting groundwater levels. In addition, because of this overbank flooding, recruitment could have taken place in earlier high-flow years; the pattern of large trees being farther away from the streambed follows what would be expected if different age isochrones had previously been established.

At San Antonio the apparent absence of a significant tree-river spatial relationship may be due to the large stretch (>200 m) of dry floodplain that now separates the forest from the active river channel. The small-sized, abundant saplings in this area indicate this floodplain was established recently. The clustered distribution of more mature trees away from the river might eventually lead to greater dependence on precipitation and levee-channel water for tree water sources.

#### CONCLUSIONS

This study shows a large diversity of tree size, density, and spatial distribution of individuals among populations of *Populus fremontii* within the Rio Grande basin in New Mexico. Such large variation among these populations is surprising since they are found within a relatively small geographic area (480 km)

4500 km. In addition, the Rio Grande basin populations are contained within a contiguous stretch of forest, indicating they may be relatively connected via gene flow. Nonetheless, these populations differ significantly in many environmental parameters including precipitation, temperature, elevation, salinity, and moisture availability (Rowland et al. in press). If the observed size variability is genetically based, then these populations have the potential to evolve in diverse directions.

Fairly recent (within the past 10–15 yr) regeneration or recruitment of young *P. fremontii* saplings appears to be restricted to sites with newly established floodplains (San Antonio and Corrales). It is known that floodplain development and stabilization play significant roles in forest-stand regeneration of *P. fremontii* populations along the middle Rio Grande and its tributaries (Crawford et al. 1993). Extensive channelization and flood control have resulted in the virtual absence of regenerating forests along most of the Rio Grande basin. In this study it appears that, despite this purported cessation of recruitment, variation in size and density among populations of *P. fremontii* is extensive along much of the Rio Grande and one of its tributaries. This variability may be related to differing environmental conditions, either existing before flood control measures or, more likely, exacerbated by such perturbations. Further studies are needed to explore both the possible environmental and even genetic causes behind such variation in size, density, and spatial distribution.

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