11-15-2001

Physiological, morphological, and environmental variation among geographically isolated cottonwood (Populus deltoides) populations in New Mexico

Diane L. Rowland
USDA-ARS, National Peanut Research Lab, Dawson, Georgia

Lucille Beals
University of New Mexico, Albuquerque

Amina A. Chaudhry
University of New Mexico, Albuquerque

Ann S. Evans
University of New Mexico, Albuquerque

Larry S. Grodeska
University of New Mexico, Albuquerque

Follow this and additional works at: https://scholarsarchive.byu.edu/wnan

Part of the Anatomy Commons, Botany Commons, Physiology Commons, and the Zoology Commons

PHYSIOLOGICAL, MORPHOLOGICAL, AND ENVIRONMENTAL VARIATION AMONG GEOGRAPHICALLY ISOLATED COTTONWOOD (*POPULUS DELTOIDES*) POPULATIONS IN NEW MEXICO

Diane L. Rowland[1], Lucille Beals[2], Amina A. Chaudhry[2],
Ann S. Evans[2], and Larry S. Grodeska[2]

ABSTRACT.—The ability of a plant population to respond and eventually adapt to environmental stress ultimately determines that population's survival. This becomes especially significant in environments where important plant resource levels have radically decreased. Southwestern riparian areas have numerous plant species that are experiencing radical changes in water availability due to construction of dams, and thus their ability to respond to such changes is critical. One such species likely to be greatly affected by these hydrological changes is *Populus deltoides* var. *wislizenii* (cottonwood) because it relies heavily on both groundwater and river surface volume as primary water sources. Both water sources have been extremely impacted by impoundments along southwestern rivers. To understand how New Mexico populations of cottonwood may respond to environmental changes, we quantified environmental differences and characterized physiological and morphological variation among 4 cottonwood populations. Significant differences among study sites in water availability were indicated by both soil and groundwater salinity. The northernmost site, at Abiquiu, had the highest salinity levels in both soil and groundwater, followed by Bernardo, while San Antonio and Corrales sites had the lowest soil salinity. As expected, variation in physiological and leaf morphological characters existed among and within the tree populations, most likely in response to environmental factors. Midday xylem pressure potentials indicated that Abiquiu individuals suffered the greatest water stress and they also had the highest transpiration levels. Because of high specific leaf weights and high photosynthetic levels, cottonwoods at Corrales may better mitigate lower water availability. Such physiological and morphological trait variability among populations is ecologically important and may be of use in present reclamation and conservation efforts in these areas.

Key words: Rio Grande, Populus deltoides, ecophysiology, soil salinity, groundwater, cottonwood.

Studies in plant physiological ecology strive to provide an understanding of the diversity of plant physiological functions and how such diversity allows plants to interact favorably with their changing environment (Jacquard and Urbanska 1988). Many of these environmental changes eventually impose selection that acts on plants functioning as physiological units (Chapin and Oechel 1983). The end result of selection varies depending upon the nature of environmental change and the concomitant plant response. Variation among populations in their abilities to respond to environmental change is important in understanding the result of ecosystem perturbations and in our ability to predict a population's ability to adapt and survive. Therefore, it is ecologically and evolutionarily important to study the amount and direction of physiological variation in natural plant populations that experience environmental changes.

The riparian ecosystem along the middle Rio Grande and its major tributaries in New Mexico is an ideal model for studying physiological plant response to environmental change. In the last 80 years, this ecosystem has experienced dramatic hydrologic perturbations that, in turn, may have induced physiological and morphological variation among these riparian populations. Construction of dams and extensive channelization of this river system have increased salinization of soil and groundwater, eradicated most flood events, and decreased water availability (Crawford et al. 1993). With the control of flooding and the construction of a system of drains paralleling the river through most of the middle Rio Grande basin in the 1930s, the water table was lowered by 1.5 m and the periodic, evenly distributed recharge of groundwater by flood events was virtually eliminated (Crawford et al. 1993). Even now, the storm-water conveyance system along a large portion of the Rio Grande surrounding Albuquerque, New Mexico, delivers most of the water runoff directly to the river channel,

---

[1]USDA-ARS, National Peanut Research Lab, 1011 Forester Dr. SE, Dawson, GA 31742.
[2]Department of Biology, University of New Mexico, Albuquerque, NM 87131.

thereby effectively bypassing the recharge of groundwater (Crawford et al. 1993). In addition, the low mean annual rainfall and high summer temperatures of the desert Southwest likely exacerbate these hydrologic impacts. All 3 likely sources of water in these riparian ecosystems, i.e., surface rainfall, channel flow, and groundwater stores, can be highly variable and are often relatively scarce. The effects of low precipitation and flow are exaggerated by the sandy alluvium in the middle Rio Grande valley, which cannot provide a suitable substrate for groundwater storage (Crawford et al. 1993). One might expect, therefore, that geographically separated plant populations within this system are likely to experience differing degrees of water availability. If so, separation by distance combined with changes in the hydrological environment may be driving differential physiological and morphological plant responses to lowered water availability in New Mexico riparian ecosystems.

One species likely to be acutely affected by these hydrologic changes is New Mexico's native cottonwood, *Populus deltoides* var. *wislizenii.* Although primarily phreatophytic, *P. deltoides* relies secondarily on precipitation and stream flow for its water resources (Leffler and Evans 1999). Dams have not only impacted stream flow and groundwater levels, but they have also virtually eliminated germination sites in most *P. deltoides* populations along the Rio Grande. It is therefore expected that these populations will be replaced by exotic plant species within the next 50 years (Howe and Knopf 1991). This is not an uncommon phenomenon; in parts of western Canada, cottonwood forests downstream from dams have virtually been eliminated due to imposed water stress (Rood and Heinze-Milne 1989, Rood and Mahoney 1990). Therefore, studies that examine the physiological-morphological responses of riparian tree populations to imposed changes in water regime provide new insights and predictions about how dams contribute to the decline of downstream ecosystems (Tyree et al. 1994).

To gauge the degree of variation among *P. deltoides* cottonwood populations in New Mexico in both environmental conditions and possible physiological responses to differences in hydrology, we quantified variability among 4 study sites in both soil and groundwater conditions and examined physiological and

morphological characters on trees at these sites. We chose physiological traits that can be indicators of water stress including photosynthesis, water vapor exchange, and water potential (Buxton et al. 1985, Baldocchi et al. 1987, Iacobelli and McCaughey 1993). We also examined several morphological traits that are indicators of changes in water availability, i.e., traits that significantly affect gas exchange characteristics including leaf area, specific leaf weight, and chlorophyll content.

METHODS

Study Sites

Four study sites were established to sample the relatively contiguous cottonwood forest along the middle Rio Grande basin of New Mexico. In New Mexico cottonwood forests are found from just below Taos Gorge south to Elephant Butte Reservoir. Populations south of the reservoir have been reduced to isolated patches due to a variety of anthropogenic impacts. The study sites are located along an approximately 280-km expanse of the Rio Grande watershed in New Mexico (Fig. 1). The northernmost site is Abiquiu (36°12′30″N, 106°19′06″W, elevation 1807 m) on the Rio Chama (a major tributary of the Rio Grande). Along the Rio Grande there are 3 additional study sites: 1 each at Corrales (35°14′16″N, 106°36′22″W, elevation 1552 m), Bernardo (34°25′06″N, 106°50′06″W, elevation 1444 m), and San Antonio (33°55′06″N, 106°52′06″W, elevation 1380 m).

For a previous study, ten 10-m-wide randomly located study plots were established within an approximately 0.5-km section of forest at each study site (Rowland et al. 2000). Each plot is perpendicular to the river and extends from the river's edge to the end of the riparian forest. At 3 of the sites, the forest edge coincides with a levee road and water diversion channel that both parallel the river. At Abiquiu the river and an abandoned agricultural field border the forest. Thirty trees at each site were randomly chosen for measurements. Cottonwood stands sampled tended to be continuously mature throughout each site, and tree age averaged 30–40 years (unpublished data). However, minor recruitment was observed at Corrales and San Antonio. At these latter sites the gallery forest ended abruptly at a 50-m (Corrales) or 200-m (San Antonio) stretch
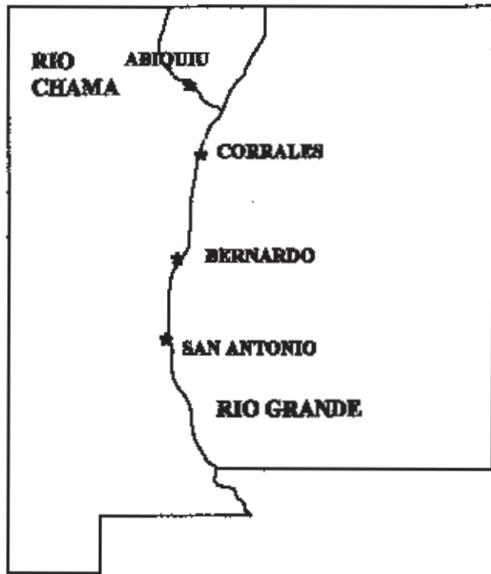
Fig. 1. Study sites within the state of New Mexico. Study populations of *Populus deltoides* are located at Abiquiu along the Rio Chama, and at Corrales, Bernardo, and San Antonio along the Rio Grande.

of floodplain inhabited by younger trees between the forest edge and the river. These trees were sampled at Corrales and averaged 10–15 years of age, but trees at San Antonio were not measured because they were too small to tag without causing damage and possible mortality.

Measurements

SOIL SITE CHARACTERISTICS.—Soil, physiological, and morphological measurements were made during the same sampling period, June and July 1995. At each of the 4 sites, we randomly chose 30 trees for soil and physiological measurements. Soil samples were taken from the north side of each tree at either 2/3 of the canopy width from the trunk or 1.6 m from the trunk if the canopy was not even; this distance ensured that samples were taken from the active root zone. Samples were taken with a 2-inch (5.08-cm) PVC pipe sharpened at one end. After removing overlying organic material, the PVC pipe was driven into the ground to a depth of 20 cm and withdrawn. We then removed core samples, placed them in plastic bags, and refrigerated them at 4°C until processed. Soils were air-dried and homogenized using a #10 sieve (2.00-mm sieve opening) before analysis.

Following procedures outlined by Black et al. (1965), we prepared saturation paste extracts and analyzed them for salinity by the electrical conductivity (EC) method using an Accumet model 50 pH/ion/conductivity meter. We determined total nitrogen and phosphorus on 10 random samples per site using the Kjeldahl digestion method (Black et al. 1965). Soil texture from 8 randomly chosen samples per site was analyzed by the hydrometer method (Black et al. 1965). After percentages of sand, silt, and clay were calculated, we used a Soil Survey Staff chart to apply textural classifications (e.g., clay, loam, sandy loam).

GROUNDWATER SITE CHARACTERISTICS.—After taking physiological and morphological measurements, we established 3 groundwater wells at each site in a stratified random manner in December 1995. At each site 3 plots were chosen randomly and single wells were installed 20 m from the edge of the river, 20 m from the edge of the forest near the levee road (or near the agricultural field at Abiquiu), and at the center of the plot. All wells were hand-augered to groundwater. Three-inch (7.62-cm) PVC pipe was used for the well body, and approximately 1 m of screened PVC tube was inserted into each well at groundwater. Measurements were taken monthly during the cottonwood growing season from May 1996 until December 1996. Depth to groundwater (m) from the soil surface was measured using a meter tape to the nearest cm. Dissolved oxygen was measured with a YSI dissolved oxygen meter (Yellow Springs Instrument Co., Inc.), and water samples were taken for electrical conductivity measurements (samples were stored in a refrigerator at 4°C until conductivity measurements were made). Conductivity, a measure of salinity, was determined with an Accumet model 50 pH/ion/conductivity meter.

MORPHOLOGICAL AND PHYSIOLOGICAL MEASUREMENTS.—In mid-June 1995 we took morphological and physiological measurements at the southernmost population (San Antonio). Because of seasonal changes in flower production, the delay in leaf development between successively more northern sites was approximately 1 week. To compensate for this seasonal difference, each successive northern site was sampled 1 week later than the previous site. At each of the 4 sites, the same 30 individuals chosen randomly for soil samples were

used for gas exchange, morphological, and water potential measurements. To minimize light-induced developmental differences, we collected 3 shade leaves near the tree bole from the lower canopy of each tree. Branch apices were excised with an extendable pole-cutter and leaf samples analyzed immediately for gas exchange. Although measuring gas exchange, especially photosynthesis, on excised tissue may be problematic (Slavik 1974, Lakso 1982), others have found no appreciable effects (Barden et al. 1980). In this study, measurement of intact leaf tissue was not possible due to inaccessibility of the canopy. Therefore, measurements were standardized across all sites by equalizing time between excision and gas exchange analysis. One fully expanded leaf per cut branch was selected for measurement; selected leaves had blade lengths between 6 and 7 cm, which standardized leaf developmental stage based on the plastochron index for *Populus* (Dickmann 1971, Larson and Isebrands 1971, Isebrands and Larson 1973, Lamoreaux et al. 1978). Gas exchange measurements were made in full sun. Photosynthesis, stomatal conductance, and transpiration were measured with an ADC infrared gas analyzer (The Analytical Development Company Ltd., England; LCA model 3). Water-use efficiency (WUE) was calculated as the ratio of photosynthesis:transpiration. To ensure that gas exchange was measured at maximum levels, all such measurements were taken between 0900 and 1130 hours MDT at all sites. This time interval was previously determined to be within the period of peak gas exchange for *P. deltoides* at the New Mexico sites (unpublished results).

Immediately after the gas exchange measurements, chlorophyll content was estimated with a Minolta SPAD chlorophyll meter (Minolta Corp., Ramsey, NJ). The SPAD chlorophyll meter measures absorbance by plant tissues of a particular range of wavelengths in the visible spectrum; this is a relative measure of the internal concentration of chlorophyll a and b. Three SPAD measurements were taken per leaf and then averaged to correct for possible non-homogeneous distribution of chlorophyll throughout the leaf (Monje and Bugbee 1992). SPAD measurements were then converted to chlorophyll content using the equation:

$$\text{chlorophyll } (\mu g \cdot cm^{-2}) = (SPAD - 8.1095)/0.855$$

developed for *Populus deltoides* trees in New Mexico (J. Leffler personal communication).

After field measurements of gas exchange and chlorophyll, leaves were placed in plastic bags and kept on ice or refrigerated at 4°C until leaf area and stomatal density measurements were completed. Hence, leaf morphological characters were measured on the same leaves measured for gas exchange. Leaf area was measured to the nearest square centimeter with a model CI-201 leaf area meter (CID, Inc.). For each leaf, 3 area measurements were taken and averaged. Leaves were then dried in a drying oven at 60°C for 5 days and, after drying was complete, leaf mass (g) was determined using an analytical balance. Specific leaf weight (SLW) was calculated for each leaf (i.e., mean leaf area/leaf mass).

Leaf xylem pressure potentials were measured in the field with a pressure bomb (PMS Instrument Company, Corvallis, OR). Using a polecutter, we excised 1 branch from each of the same 30 trees measured for gas exchange. Branches were placed in plastic bags and measured within 15 minutes after excision in a Scholander-style pressure chamber (Scholander et al. 1965). Water potential measurements were taken between 1200 and 1500 hours MDT, the hours of greatest water loss. Predawn measurements were not taken because previous results at the Corrales site indicated no significant differences among individuals for predawn water potentials; therefore, we concluded that midday water potentials would provide a relative index of water stress among sites.

At each site we measured stomatal density on 10 trees randomly selected from the same 30 trees measured for physiology. One branch per tree was collected and frozen at 0°C. One leaf was removed from each branch for stomatal density measurement. For each leaf, we cut 2 samples from the center of the leaf blade, one on either side of the midrib, and mounted them on glass microscope slides with distilled water. Because *Populus* is amphistomatous, stomatal density was counted on both the adaxial and abaxial surfaces of each leaf sample. Samples were observed and stomata counted with a Zeiss Axioskop light microscope at 20× magnification. For each mounted sample, stomata were counted in 4 arbitrary fields (right adaxial, right abaxial, left adaxial, left abaxial).

Statistical Analyses

For environmental variation among sites, 1-way fixed model ANOVAs (SAS Institute 1989), with SITE as a fixed factor, were used to assess possible differences in salinity, total nitrogen, total phosphorus, ratio of nitrogen to phosphorus, and soil texture among sites. Repeated-measures ANOVAs (SAS Institute 1989) were used to assess differences in groundwater depth, dissolved oxygen, and salinity among sites. Physiological and morphological variation both among and within sites was examined with individual mixed-model nested univariate ANOVAs with SITE as a fixed factor and TAG(SITE) or tree nested within site as a random factor (Sokal and Rohlf 1995). Scheffe's multiple range tests were used to determine where differences existed among sites. Pearson correlations (SYSTAT 1996) were used to relate the environmental parameters to physiological and morphological characteristics within a given site. Within each of the 4 sites, we correlated soil salinity and distance to the river of a measured tree with its average measured physiological characters of photosynthesis, stomatal conductance, transpiration, water-use efficiency, chlorophyll content, and water potential.

RESULTS

Environmental Variation

Significant variation was evident among the 4 sites for all soil characteristics (Table 1). Soil salinity showed a wide range among sites. Abiquiu had the highest mean salinity, followed by Bernardo; whereas San Antonio and Corrales had similarly low soil salinity. Total nitrogen and soil phosphorus content was highest at Abiquiu and lowest at Corrales (Table 1). The nitrogen-to-phosphorus ratio was highest at Bernardo and lowest at Corrales, while San Antonio had an intermediate value. Soil textures ranged widely among sites as well (Table 1). Analysis of variance showed significant differences among sites for both sand and clay. Mean percentages for sand ranged from 11.8 at San Antonio to 57.2 at Corrales; for clay, mean percentages ranged from 19.9 at Corrales to 56.3 at San Antonio. However, silt content did not differ among sites; mean percentages ranged from 22.9 at Corrales to 36.5 at Abiquiu. Corrales samples were extremely sandy (57%), San Antonio was mostly clay (57%), and Bernardo soil was 43% clay. Abiquiu soils were more equally partitioned among 3 soil particle classes (31% clay, 36% silt, 32% sand), i.e., a texture of loam.

TABLE 1. ANOVA results and means for variation in soil characteristics among 4 populations (AB = Abiquiu, CO = Corrales, BE = Bernardo, SA = San Antonio). Values for soil texture are in percentage of each soil type. Means reported with standard error in parentheses; different letters denote significant differences among populations at a 0.05 significance level (Scheffe grouping).

| Trait	Site mean			
	AB	CO	BE	SA
Salinity (dSiemens · m^{-1}) (df = 3, MS = 10543755, F = 86.7, P-value = 0.0001				
	1.33 (0.11) a	0.10 (0.02) c	0.92 (0.05) b	0.18 (0.02) c
Nitrogen (µg · g^{-1}) (df = 3, MS = 1243372, F = 7.7, P-value = 0.0004)				
	1132.9 (142.7) a	331.4 (138.8) b	1010.3 (141.8) a	808.3 (71.0) ab
Phosphorus (µg · g^{-1}) (df = 3, MS =38448.1, F = 7.8, P-value = 0.0004)				
	350.0 (22.8) a	208.9 (29.1) b	292.4 (18.2) ab	328.1 (16.5) a
Nitrogen / phosphorus ratio (df = 3, MS = 9.2584, F = 10.5, P-value = 0.0001)				
	3.2 (0.3) a	1.2 (0.3) b	3.3 (0.3) a	2.5 (0.2) ab
Sand (df = 3, MS = 2574, F = 5.93, P-value = 0.0034)				
	32.3 (5.2) ab	57.2 (8.2) a	33.0 (9.5) ab	11.8 (7.5) b
Clay (df = 3, MS = 1816, F = 8.44, P-value = 0.0005)				
	31.2 (2.3) b	19.9 (1.5) b	42.6 (8.1) ab	56.3 (6.5) a
Silt (df = 3, MS = 291, F = 1.77, P-value = 0.18)				
	36.5 (3.1) a	22.9 (6.9) a	24.4 (3.8) a	31.9 (4.4) a
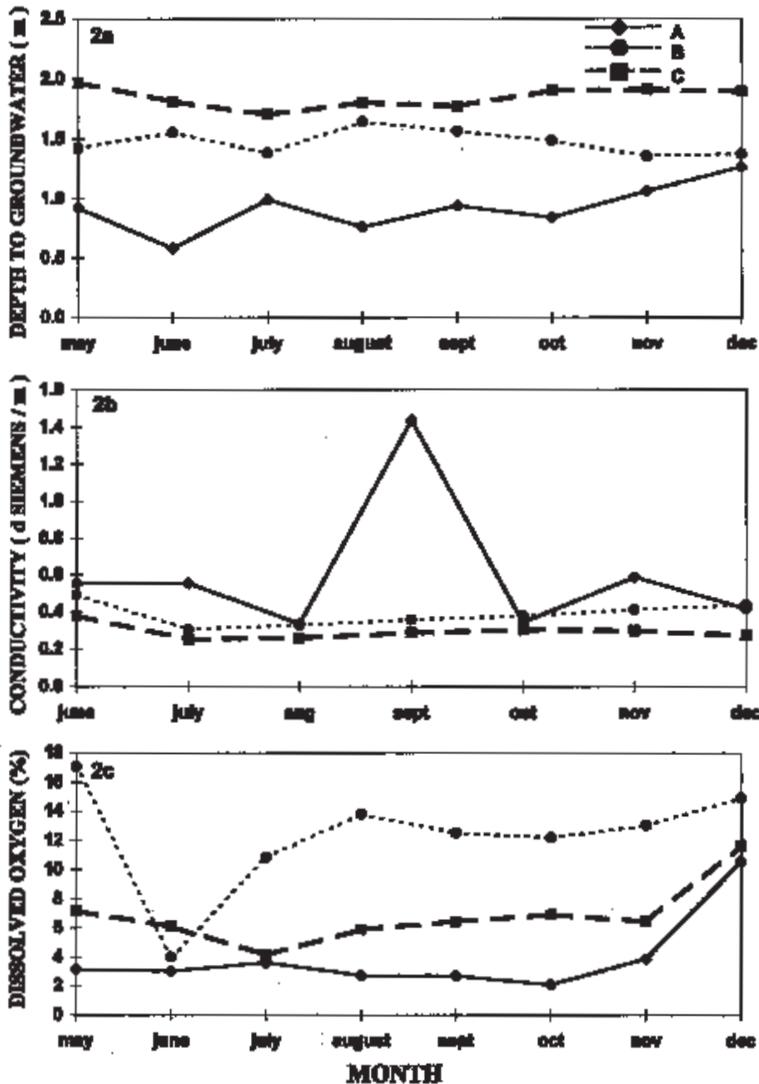
Fig. 2. Groundwater measurements for 3 New Mexico *Populus deltoides* populations during the 1996 growing season (A = Abiquiu, B = Bernardo, C = Corrales). Depth to groundwater (2a) is the depth of the groundwater below the soil surface; conductivity (2b) is a measure of salinity; and dissolved oxygen content (2c) is the percentage of oxygen present in groundwater samples.

Groundwater measures varied significantly among sites. Distance to groundwater (df = 2, SS = 11.317, MS = 5.658, F = 12.65, P < 0.0186), conductivity (df = 2, SS = 1054096, MS = 527048, F = 394.82, P < 0.0002), and dissolved oxygen content (df = 2, SS = 1.39, MS = 0.69, F = 15.84, P < 0.0126) were all significantly different among sites. Depth to groundwater was greatest at Corrales and least at Abiquiu throughout the sampling period (May–December; Fig. 2a). However, Abiquiu groundwater was highly saline and lower in

dissolved oxygen content than Bernardo and Corrales for most months during the measurement period (Figs. 2b, 2c). Bernardo groundwater was higher in dissolved oxygen than the other 2 sites for every month except June 1996 (Fig. 2c).

Physiological and Leaf Morphological Variation

Individual nested ANOVAs, using a significance level of P < 0.0125, adjusted for multiple tests (Sokal and Rohlf 1995), showed signifi-

cant variation among and within populations for specific physiological and morphological characters. Photosynthesis was significantly different among and within populations and ranged from 7.2 μmol C · m^{-2} s at San Antonio to 12.2 μmol C · m^{-2} s at Corrales (Table 2). However, there was no clear geographical (i.e., north–south) pattern for photosynthetic levels, with the northernmost site (Abiquiu) not significantly different from the southernmost site (San Antonio). Nonetheless, stomatal conductance, transpiration, and midday xylem pressure potentials did show geographical trends. Stomatal conductance was significantly different among and within populations (Table 2) and decreased with each site from north to south; Abiquiu had the highest stomatal conductance, while San Antonio had the lowest value. Transpiration also showed significant differences among and within populations and a similar decreasing trend to the south (Table 2); however, the 2 middle geographic populations (Corrales and Bernardo) were not significantly different from one another. Midday xylem pressure potentials were significantly different among populations and showed a geographic trend of increasing xylem pressure potentials to the south (Table 2). The greatest water stress was noted at Abiquiu (–1.9 MPa), the lowest at San Antonio and Bernardo (–1.7 MPa). Although water-use efficiency showed no strong geographic trend, differences among and within populations were significant. All populations were significantly different from one another, with the highest WUE occurring at Corrales (1.8 mmol C · mol H$_2$O^{-1}) and the lowest at Abiquiu (0.8 mmol C · mol H$_2$O^{-1}; Table 2). Water-use efficiency was also significantly negatively correlated with soil salinity at Abiquiu, the site with highest soil salinity (Table 3), but it was not correlated with distance to the river. No other physiological or morphological variables were significantly correlated with these 2 environmental parameters within individual sites.

Leaf morphological traits were also significantly different among and, in most cases, within populations (Table 4). Mean chlorophyll content (converted values, μg · cm^{-2}) showed significant differences among and within populations and ranged from 28.1 at San Antonio to 23.6 at Abiquiu. Chlorophyll levels showed a geographic trend of increasing to the south; like transpiration, chlorophyll levels were not significantly different between Corrales and Bernardo. Leaf area also showed significant variation among and within populations. Leaf area was largest at the 2 southernmost populations, Bernardo (31.7 cm^2) and San Antonio (29.5 cm^2), while leaves were smallest at Corrales (20.1 cm^2; Table 4). Specific leaf weight (SLW) differed among and within sites; it was highest at Corrales (100.0 g · m^{-2}) and lowest at San Antonio (62.9 g · m^{-2}; Table 4). Although leaves were smaller at Corrales, they were thicker, thus contributing to high SLW. Adaxial (upper) stomatal density did not significantly differ among sites; however, abaxial (lower) density approached significance (Table 4). Abiquiu had the lowest mean values for both adaxial stomatal density (67.2 · mm^{-2}) and abaxial (53.4 · mm^{-2}). A paired t test across populations showed that the adaxial surface had a significantly higher stomatal density than the abaxial surface (df = 39, tcrit = 2.02, $P < 0.0001$).

DISCUSSION

Our study provides evidence of considerable variation in environmental, physiological, and morphological characteristics within and among natural riparian populations of *Populus deltoides* in the New Mexico Rio Grande basin. While many studies have addressed physiological variation among and within *Populus* species, most were conducted on limited, clonal material (e.g., Ceulemans and Impens 1980, 1983, 1987, Blake et al. 1984, Liu and Dickmann 1992, Dunlap et al. 1993, Donahue et al. 1994). Those studies comparing the degree and type of physiological differences among natural *Populus* populations of contrasting environments, as in our study, are quite scarce (see McGee et al. 1981). Our study is ecologically important for detecting and describing the partitioning of physiological and morphological variation among populations. These descriptions assist us in predicting future population survival because variability among populations in physiological and morphological characteristics will eventually impact their ability to respond to these environmental differences. In addition, studies that examine variation within natural populations are a mainstay of silviculture research for screening and identifying new candidate genetic stock (Bassman and Zwier 1991). Because *Populus* is

TABLE 2. Variation in physiological characteristics among 4 populations (AB = Abiquiu, CO = Corrales, BE = Bernardo, SA = San Antonio). Mixed-model nested ANOVAs were performed to determine both among- (SITE) and within-population (among individuals) (TAG[SITE]) differences for all traits except water potential. A fixed-model ANOVA was performed to determine among-population differences in water potential. Means reported with standard error in parentheses; different letters denote significant differences among populations at a 0.05 significance level (Scheffe grouping).

Trait	Source of variation			
	AB	CO	BE	SA
Photosynthesis (μmol C $\cdot$ m^{-2} s)				
Site: df = 3, MS = 455.3, F = 42.7, P-value = 0.0001;				
Tag(Site): df = 116, MS = 10.7, F = 2.3, P-value = 0.0001				
	7.8 (0.3) c	12.2 (0.3) a	9.0 (0.2) b	7.2 (0.2) c
Stomatal conductance (mmol H$_2$O $\cdot$ m^{-2} s)				
Site: df = 3, MS = 468899.6, F = 68.5, P-value =0.0001				
Tag(Site): df = 116, MS = 6869.4, F = 3.8, P-value = 0.0001				
	265.8 (7.8) a	225.0 (6.9) b	165.3 (4.2) c	102.6 (5.0) d
Transpiration (mmol H$_2$O $\cdot$ m^{-2} s)				
Site: df = 3, MS = 430.0, F = 123.7, P-value = 0.0001				
Tag(Site): df = 116, MS = 3.5, F = 4.0, P-value = 0.0001				
	9.8 (0.1) a	6.7 (0.1) b	6.8 (0.2) b	4.5 (0.1) c
Water-use efficiency (mmol C $\cdot$ mol H$_2$O^{-1})				
Site: df = 3, MS = 18.4, F = 62.6, P-value = 0.0001				
Tag(Site): df = 116, MS = 0.3, F = 6.2, P-value = 0.0001				
	0.8 (0.0) d	1.8 (0.0) a	1.4 (0.0) c	1.7 (0.0) b
Xylem pressure potential (MPa)				
Site: df = 3, MS = 30.3, F = 6.7, P-value = 0.0003				
	−1.9 (0.0) c	−1.8 (0.0) bc	−1.7 (0.0) ab	−1.7 (0.0) a

being studied for energy plantations (Schulte et al. 1987) and for wood and fiber production (Ceulemans and Impens 1980, 1987), identifying genotypes in natural populations with drought-adaptive traits would be extremely beneficial (Bassman and Zwier 1991). We know that plants coming from arid environments generally are better adapted for survival under low water conditions (Gurevitch et al. 1986); therefore, genotypes from these populations might be useful for introduction to plantations under arid and low watering regimes.

Water availability, as reflected in soil and groundwater parameters, differed significantly among separate, cottonwood-dominated sites in the Rio Grande basin. At the northern site at Abiquiu, there were high levels of salt in both the soil and groundwater, presumably reducing the water available to *P. deltoides* trees at this site. High salinity and nitrogen levels at Abiquiu may be due to the extensive agricultural fields that are directly adjacent to the forest. Leaching and runoff of salts and fertilizer into the cottonwood forest from agricultural fields could cause elevated salinity

and nitrogen levels at this site; abandoned agricultural fields can be extremely saline (Hendrickx et al. 1992). The Bernardo site also had high salt levels, but these may be due to increased abundance of salt cedar. Salt cedar was much more abundant at Bernardo than at the other 3 sites; and, as Busch and Smith (1995) have shown, salt cedar, because of its high salt content in leaf litter, tends to salinize soil. Corrales showed a relative deficiency in soil nitrogen and very low soil salinity, both of which might be a result of its extremely sandy soil texture. These environmental differences, both in soil and groundwater, may be factors contributing to the physiological and morphological variation we found among these populations.

Large variation in many physiological traits and leaf morphological traits related to water use was evident among the New Mexico populations and appears to be somewhat influenced by environmental differences among populations. With high soil and groundwater salinity levels at Abiquiu, we expected cottonwoods there to be water stressed. That is precisely

TABLE 3. Pearson correlations between average water-use efficiency (mmol C · mol H_2O^{-1}) and the environmental characteristics of soil salinity and distance to river. Correlations are within a single population (Abiquiu, $N = 28$; Corrales, $N = 30$; Bernardo, $N = 27$; San Antonio, $N = 30$).

Population	Salinity (dSiemens · cm^{-1})	Distance to river (m)
Abiquiu	−0.523*	−0.272
Corrales	0.146	0.284
Bernardo	0.088	0.080
San Antonio	0.019	−0.005

*$P \leq 0.05$

what we found, with Abiquiu cottonwoods experiencing higher transpiration levels and lower midday water potentials than cottonwoods at the other sites. In fact, midday water potentials of −1.8 MPa suggest that cavitation stress may be high in these trees because cavitation is known to occur in *Populus* at water potentials of −1.7 MPa (Tyree et al. 1994). The negative correlation of water-use efficiency and soil salinity at Abiquiu appears to support the conclusion that environment is influencing cottonwood physiology to some extent.

Environmental differences among cottonwood populations related to the geography of the Rio Grande basin are indicated by the north–south trends in physiological and morphological variation. The 2 middle sites, Bernardo and Corrales, are separated by 60 miles and are isolated from the other 2 sites by natural constrictions in the river north of Corrales and south of Bernardo. Hence, these 2 middle populations may be more environmentally similar. This is certainly true for our measurements of soil nitrogen and nitrogen:phosphorus ratio. Further, we found that transpiration, water potential, and chlorophyll content did not differ between these 2 sites. Nonetheless, there are important environmental parameters, such as soil salinity, which did differ between them and may explain tree-response differences in other physiological traits (e.g., water-use efficiency) and morphological traits (e.g., specific leaf weight). We found a strong geographic trend in stomatal conductance that was greatest at Abiquiu and decreased to the south. Geographic trends in physiological traits are not uncommon. For example, Dang et al. (1994) found that photosynthesis, midday water potentials, and transpiration in red alders (*Alnus rubra*) have a geographic trend increasing

from southeast to northwest in British Columbia, Canada.

Morphological variation among sites suggests that some populations are better able than others to respond favorably to water stress conditions. For example, at Corrales, cottonwoods had higher specific leaf weights than did cottonwoods at other sites, indicating that Corrales leaves were smaller but thicker (Busch and Smith 1995). This type of leaf morphology is adaptive in relatively dry habitats. Leaf morphology may explain the ability of Corrales trees to maintain higher water-use efficiencies than trees in the other populations. Geber and Dawson (1990) provided evidence that small-leafed populations in certain plants have high gas exchange rates, low water-use efficiencies, and maximum vegetative yields, all leading to a highly cost-efficient photosynthetic system. This appears to be the case for cottonwoods in Corrales, since they have relatively small leaves and high photosynthetic rates. Other morphological traits, such as stomatal frequency, can be linked to gas exchange characteristics that are positively correlated with photosynthesis (Paul and Eagles 1988). Although we found no significant variation in stomatal density among studied populations, a trend toward high stomatal density was noted in Corrales trees, which may be another factor explaining their high photosynthetic rates.

In addition to the variation among populations, we also found significant variation within populations of *P. deltoides* for several physiological and morphological traits. This is not an uncommon finding since individual plants within populations can respond differently to stress, and recent studies have shown considerable microscale environmental variation within populations. What is important about this intrapopulation variation in physiological response is that it may lead to small-scale genetic variation within populations (Perry and Knowles 1991, Young and Merriam 1994, Loisell et al. 1995). Because our study spanned only a single growth season, long-term predictions about the continued direction of inter- and intrapopulation variation are limited. Long-term monitoring of these populations is necessary as well as determining the genetic basis of the physiological and morphological traits for a full understanding of any possible adaptive responses to environmental stress.

TABLE 4. Variation in leaf morphological characteristics among 4 populations (AB = Abiquiu, CO = Corrales, BE = Bernardo, SA = San Antonio). Mixed-model nested ANOVAs were performed to determine both variation among populations (SITE) and within-population differences (among individuals) (TAG[SITE]) for all traits except stomatal density. A fixed-model ANOVA was performed to determine among-population differences in stomatal density. Means reported with standard error in parentheses; different letters denote significant differences among populations at a 0.05 significance level (Scheffe grouping).

Trait	Source of variation			
	AB	CO	BE	SA
Chlorophyll (μg · cm^{-2})				
Site: df = 3, MS = 217.0, F = 6.4, P-value = 0.0005				
Tag(Site): df = 116, MS = 34.1, F = 2.9, P-value = 0.0001				
	23.6 (0.5) c	26.1 (0.6) b	25.9 (0.5) b	28.1 (0.5) a
Leaf area (cm^2)				
Site: df = 3, MS = 2379.5, F = 27.2, P-value = 0.0001				
Tag(Site): df = 116, MS = 87.8, F = 3.2, P-value = 0.0001				
	24.9 (0.7) b	20.1 (0.5) c	31.7 (0.9) a	29.5 (0.7) a
Specific leaf weight (g · m^{-2})				
Site: df = 3, MS = 22709.7, F = 45.4, P-value = 0.0001				
Tag(Site): df = 116, MS = 501.5, F = 6.6, P-value = 0.0001				
	75.5 (1.6) b	100.0 (2.1) a	71.6 (1.3) c	62.9 (1.1) d
Stomatal density (stomates · mm^{-2})				
Adaxial density				
Site: df = 3, MS = 330.0, F = 2.0, P-value = 0.1287				
	67.2 (2.9) a	79.8 (2.7) a	77.6 (3.4) a	71.6 (2.9) a
Abaxial density				
Site: df = 3, MS = 445.6, F = 2.6, P-value = 0.0656				
	53.4 (2.7) a	68.3 (2.5) a	66.0 (2.7) a	65.1 (2.8) a

LITERATURE CITED

BALDOCCHI, D.D., S.B. VERMA, AND D.E. ANDERSON. 1987. Canopy photosynthesis and water-use efficiency in a deciduous forest. Journal of Applied Ecology 24: 251–260.

BARDEN, J.A., J.M. LOVE, P.J. PORPIGLIA, R.P. MARINI, AND J.D. CALDWELL. 1980. Photosynthesis and dark respiration of apple leaves are not affected by shoot detachment. HortScience 15:595–597.

BASSMAN, J.H., AND J.C. ZWIER. 1991. Gas exchange characteristics of *Populus trichocarpa*, *Populus deltoides* and *Populus trichocarpa* × *P. deltoides* clones. Tree Physiology 8:145–159.

BLACK, C.A., D.D. EVANS, L.E. ENSMINGER, J.L. WHITE, AND F.E. CLARK. 1965. Methods of soil analysis. American Society of Agronomy Inc., Madison, WI. 1572 pp.

BLAKE, T.J., T.J TSCHAPLINSKI, AND A. EASTHAM. 1984. Stomatal control of water use efficiency in poplar clones and hybrids. Canadian Journal of Botany 62:1344–1351.

BUSCH, D.E., AND S.D. SMITH. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. Ecological Monographs 65:347–370.

BUXTON, G.F., D.R. CYR, E.B. DUMBROFF, AND D.P. WEBB. 1985. Physiological responses of three northern conifers to rapid and slow induction of moisture stress. Canadian Journal of Botany 63:1171–1176.

CEULEMANS, R., AND I. IMPENS. 1980. Leaf gas exchange processes and related characteristics of seven poplar clones under laboratory conditions. Canadian Journal of Forest Research 10:429–435.

_____. 1983. Net CO$_2$ exchange rate and shoot growth of young poplar (*Populus*) clones. Journal of Experimental Botany 34:866–870.

_____. 1987. Variations in photosynthetic, anatomical, and enzymatic leaf traits and correlations with growth in recently selected *Populus* hybrids. Canadian Journal of Forest Research 17:273–283.

CHAPIN, F.S., III, AND W.C. OECHEL. 1983. Photosynthesis, respiration, and phosphate absorption by *Carex aquatilis* ecotypes along latitudinal and local environmental gradients. Ecology 64:743–751.

CRAWFORD, C.S., S.C. CULLY, R. LEUTHEUSER, M.S. SIFUENTES, L.H. WHITE, AND J.P. WILBUR. 1993. Middle Rio Grande Ecosystem: Bosque Biological Management Plan. U.S. Department of Interior, Fish and Wildlife Service.

DANG, Q.L., C.Y. XIE, C. YING, AND R.D. GUY. 1994. Genetic variation of ecophysiological traits in red alder (*Alnus rubra* Bong.). Canadian Journal of Forest Research 24:2150–2156.

DICKMANN, D.I. 1971. Photosynthesis and respiration by developing leaves of cottonwood (*Populus deltoides* Bartr.). Botanical Gazette 132:253–259.

DONAHUE, R.A., T.D. DAVIS, C.H. MICHLER, D.E. RIEMENSCHNEIDER, D.R. CARTER, P.E. MARQUARDT, N. SANKHLA, ET AL. 1994. Growth, photosynthesis, and herbicide tolerance of genetically modified poplar. Canadian Journal of Forest Research 24:2377–2383.

DUNLAP, J.M., J.H. BRAATNE, T.M. HINCKLEY, AND R.F. STETTLER. 1993. Intraspecific variation in photosynthetic traits of *Populus trichocarpa.* Canadian Journal of Botany 71:1304–1311.

GEBER, M.A., AND T.E. DAWSON. 1990. Genetic variation in and covariation between leaf gas exchange, morphology, and development in *Polygonum arenastrum*, an annual plant. Oecologia 85:153–158.

GUREVITCH, J., J.A. TEERI, AND A.M. WOOD. 1986. Differentiation among populations of *Sedum wrightii* (Crassulaceae) in response to limited water availability: water relations, CO_2 assimilation, growth and survivorship. Oecologia 70:198–204.

HENDRICKX, J.M.H., B. BAERENDS, Z.I. RAZA, M. SADIG, AND M.A. CHAUDHRY. 1992. Soil salinity assessment by electromagnetic induction of irrigated land. Soil Science Society of America Journal 56:1933–1941.

HOWE, W.H., AND F.L. KNOPF. 1991. On the imminent decline of Rio Grande cottonwoods in central New Mexico. Southwestern Naturalist 36:218–224.

IACOBELLI, A., AND J.H. MCCAUGHEY. 1993. Stomatal conductance in a northern temperate deciduous forest: temporal and spatial patterns. Canadian Journal of Forest Research 23:245–252.

ISEBRANDS, J.G., AND P.R. LARSON. 1973. Anatomical changes during leaf ontogeny in *Populus deltoides.* American Journal of Botany 60:199–208.

JACQUARD, P., AND K. URBANSKA. 1988. Population genetics, whole-plant physiology, and population biology: interactions with ecology. Acta Oecologia 9:3–10.

LAKSO, A.N. 1982. Precautions on the use of excised shoots for photosynthesis and water relations measurements of apple and grape leaves. HortScience 17:368–370.

LAMOREAUX, R.J., W.R. CHANEY, AND K.M. BROWN. 1978. The plastochron index: a review after two decades of use. American Journal of Botany 65:586–593.

LARSON, P.R., AND J.G. ISEBRANDS. 1971. The plastochron index as applied to developmental studies of cottonwood. Canadian Journal of Forest Research 1:1–11.

LEFFLER, A.J., AND A.S. EVANS. 1999. Variation in carbon isotope composition among years in the riparian tree *Populus fremontii.* Oecologia 119:311–319.

LIU, Z., AND D.I. DICKMANN. 1992. Responses of two hybrid *Populus* clones to flooding, drought, and nitrogen availability. I. Morphology and growth. Canadian Journal of Botany 70:2265–2270.

LOISELLE, B.A., V.L. SORK, J. NASON, AND C. GRAHAM. 1995. Spatial genetic structure of a tropical understory shrub, *Psychotria officinalis* (Rubiaceae). American Journal of Botany 82:1420–1425.

MCGEE, A.B., M.R. SCHMIERBACH, AND F.A. BAZZAZ. 1981. Photosynthesis and growth in populations of *Populus deltoides* from contrasting habitats. American Midland Naturalist 105:305–311.

MONJE, O.A., AND B. BUGBEE. 1992. Inherent limitations of nondestructive chlorophyll meters: a comparison of two types of meters. Hortscience 27:69–71.

PAUL, N.K., AND C.F. EAGLES. 1988. Cultivar differences in net photosynthetic rates and their relationship with leaf anatomical characteristics in *Brassica.* Photosynthetica 22:320–327.

PERRY, D.J., AND P. KNOWLES. 1991. Spatial genetic structure within three sugar maple (*Acer saccharum* Marsh.) stands. Heredity 66:137–142.

ROOD, S.B., AND S. HEINZE-MILNE. 1989. Abrupt downstream forest decline following river damming in southern Alberta. Canadian Journal of Botany 67:1744–1749.

ROOD, S.B., AND J.M. MAHONEY. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. Environmental Management 14: 451–464.

ROWLAND, D.L., B. BIAGINI, AND A.S. EVANS. 2000. Variability among five riparian cottonwood (*Populus fremontii* Wats.) populations: an examination of size, density, and spatial distribution. Western North American Naturalist 60:384–393.

SAS INSTITUTE. 1989. SAS Institute Inc., Cary, NC.

SCHOLANDER, P.F., H.T. HAMMEL, E.D. BRADSTREET, AND E.A. HEMMINGSEN. 1965. Sap pressure in vascular plants. Science 148:339–346.

SCHULTE, P.J., T.M. HINCKLEY, AND R.F. STETTLER. 1987. Stomatal responses of *Populus* to leaf water potential. Canadian Journal of Botany 65:255–260.

SLAVIK, B. 1974. Methods of studying plant water relations. Springer-Verlag, New York. 449 pp.

SOKAL, R.R., AND F.J. ROHLF. 1995. Biometry. W.H. Freeman and Company, New York. 887 pp.

SYSTAT. 1996. SYSTAT: statistics. SPSS Inc., Chicago, IL.

TYREE, M.T., K.J. KOLB, S.B. ROOD, AND S. PATIÑO. 1994. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem. Tree Physiology 14:455–466.

YOUNG, A.G., AND H.G. MERRIAM. 1994. Effects of forest fragmentation on the spatial genetic structure of *Acer saccharum* Marsh. (sugar maple) populations. Heredity 72:201–208.