Effects of Stand Thinning on Water Relations, Growth, and Condition of Three Tree Species in a Riparian Restoration Planting

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ABSTRACT. A dense riparian planting was installed on the reconstructed floodplain of the Guadalupe River in San Jose in 1994. Soil investigations conducted 3 years after planting revealed that trees did not root to the depth of groundwater at the site, which was confined beneath a thick clay layer present at a depth of about 3 ft. Many trees in the planting developed water stress-related health problems. We initiated a study to determine whether reducing tree density would reduce water stress and improve tree condition in the planting. In February 1999, established trees were removed from two plots within the planting to reduce stand densities from about 250 to 124 woody plants/acre. We monitored soil moisture and tree water status, growth, and condition for three species in thinned and nonthinned plots between July 1999 and September 2000. The species showed different responses to site conditions and the thinning treatment. For cottonwood (*Populus fremontii*), reducing intertree competition improved water status and shoot growth, and reduced attacks by wood-boring beetles. Nevertheless, thinning did not entirely eliminate water stress in cottonwood and tree condition continued to deteriorate in both thinned and nonthinned plots. Thinning did not substantially improve growth or water status of box elder (*Acer negundo*), which showed the highest levels of water stress overall. Thinning had only minor effects on red willow (*Salix laevigata*), which maintained the best water status overall. Red willow may not have responded to thinning because these trees were meeting their water needs by extracting moisture from the clay subsoil.

INTRODUCTION

A major recontouring and revegetation project was undertaken along the portion of the Guadalupe River that passes through downtown San Jose, California. The purpose of this project was to provide flood protection, recreation opportunities, as well as wildlife habitat. The City of San Jose, the Redevelopment Agency of the City of San Jose, the Santa Clara Valley Water District (SCVWD), and the Army Corps of Engineers were participants in this complex project, which involved converting land from residential and commercial uses into landscaped parkland and natural areas.

The project superimposes parkland and habitat areas over an expanded, regraded flood-control channel for the river. Grading extended well into a layer of heavy clay subsoil. To provide a more favorable substrate for plant growth, the grading plan included provisions to save suitable silt loam topsoil and place a 3 ft deep layer of this topsoil over the graded base. The portions of the regraded flood control channel nearest the river are being revegetated with a variety of native riparian species.

As part of the first phase of the revegetation effort, a dense, multispecies riparian planting was installed on a portion of the reconstructed floodplain in 1994. Parts of this earliest planting were removed by floodwater scouring the winter after planting, but 2 acres of the original planting (called phase 1A) still exist. The planting was established using container-grown stock that was drip-irrigated for several years. Although plants had grown to form a fairly dense stand, the performance and condition of various woody plants in the phase 1A area was problematic.

Health problems that developed for new plantings included branch dieback and heavy infestations of wood-boring insects, both typically related to water stress. SCVWD conducted soil investigations that revealed that a water table was present at a depth of about 12 to 16 ft below the ground surface. Because of this shallow water table, the clay subsoil remains moist throughout the growing season. However, the clay's low rate of hydraulic conductivity may limit the amount of water that can be extracted from it by plant roots. We examined root growth in a number of soil trenches and observed that tree roots generally did not penetrate into this dense clay subsoil to any great degree. From these observations, we surmised that the riparian tree species in the planting did not have access to a permanent water table and that these trees could become drought-stressed after the available water in the surface soil horizon was exhausted.

Water use calculations based on various assumptions about soil and plant characteristics indicated that tree stocking densities were higher than could be sustained by available soil moisture resources (Swiecki and Bernhardt 1997). Thinning of an overly dense stand can improve the water status of remaining plants by reducing competition for limited soil moisture reserves. However, determining a sustainable stand density for this site was complicated by its variability. The depth of the topsoil layer, depth to groundwater, species composition, and irregular contributions of irrigation runoff from adjacent landscape plantings varied across the planting. These factors can influence the amount of thinning needed to alleviate water stress in the planting. We conducted this study to empirically determine if reducing tree density would reduce water stress and thereby improve tree health in the planting.

No single measurement can reliably indicate levels of water stress in all species because chronic water stress affects a variety of interacting physiological processes. For example, when plant water stress develops slowly over the growing season, cell expansion is restricted and plant growth is reduced. As a result, a plant may produce fewer and/or smaller leaves. By maintaining a lower total leaf area, this plant will reduce its total water use. This could allow the plant maintain a relatively high water potential even under conditions where soil moisture is limited. Hence, water potential measurements alone would not show the degree to which the plant is being affected by water stress.

Knowing that plant growth interacts dynamically with stomatal conductance and stem water potential, we measured a number of parameters, including soil moisture, stomatal conductance, stem water potential, plant growth, and plant condition to determine how three riparian tree species responded to a stand thinning treatment. We previously presented our results to SCVWD through two technical reports (Swiecki and Bernhardt 1999, 2000).

METHODS

Thinning Treatments

SCVWD staff arranged for the thinning of the plots before this study was initiated. The planting was divided into 4 sections of roughly similar size and alternate sections were thinned in February 1999. Approximately half of the woody plants were removed from the thinned sections, leaving about 124 woody plants per acre, compared with about 250 woody plants per acre in the nonthinned plots. SCVWD staff preferentially selected trees with heavy borer infestations, large amounts of dieback, and/or poor structural qualities for removal. Seventy percent of the removed trees were *Salix* species. Attempts were made to thin to a relatively uniform stand density, but as discussed below, woody plant densities vary widely between different points within both thinned and nonthinned sections.

SELECTION OF STUDY TREES

Our observations were limited to three of the most common species in the planting: Fremont cottonwood (*Populus fremontii*), red willow (*Salix laevigata*), and box elder (*Acer negundo*). We selected 20 *P. fremontii,* 14 *S. laevigata* and 14 *A. negundo* trees for detailed observations in June and July 1999. Trees were observed through September 2000. We selected equal numbers of trees in thinned and nonthinned plots. Our primary criteria in selecting study trees was to obtain trees that would maximize the contrast between the thinned and nonthinned areas, i.e., we preferentially selected trees from dense portions of the nonthinned areas and from relatively open portions of thinned areas. We avoided trees that were near the edges of the planting or the boundary between the thinning treatments and attempted to obtain trees that were spatially distributed throughout the thinned and nonthinned areas.

For comparative purposes, we also made certain measurements on five naturally-occurring riparian trees growing along the banks of the Guadalupe River channel which was located about 100 to 250 ft from the edge of the study area. They included one *A. negundo* (mature, somewhat decadent tree 10 inch DBH), two *S. laevigata* (multistemmed, maximum DBH 1.7 and 3 inches), and two *P. fremontii* (3.8 and 6 inches DBH). A sixth riverbank tree (a medium-sized *A. negundo*) was used for stem water potential measurements in September 2000. We selected trees that were growing close enough to the river channel that at least some of their roots were likely to be in contact with the saturated zone along the riverbank.

TREE NEIGHBORHOOD COMPETITION

The density and species composition of plant neighborhoods around individual study trees varied widely between trees in both thinned and nonthinned plots. Because thinning treatment alone does not satisfactorily characterize the level of intertree competition various study trees were likely to experience, we calculated a competition index (CI) to quantify intertree competition.

We used a CI that is based on an influence zone around each tree (Bella 1971) which has a diameter equal to twice the maximum canopy diameter of the tree. The influence zone is an approximation of the extent of the tree root system. In calculating CI, a tree is considered a competitor of a given study tree if its influence zone overlaps that of the study tree. Competition for soil moisture is more directly related to total leaf area or leaf area index (LAI = leaf area/area canopy cover) than to basal area or DBH. Therefore, we estimated total foliated canopy, which is proportional to LAI (Peper and McPherson 1998), to describe the relative sizes of the subject and competitor trees. To account for differences in LAI between different species, we calculated a canopy density correction factor for each species based on the percent foliated area of tree silhouette images (Peper and McPherson 1998).

CI_i (the competition index for a given study tree i) was calculated as follows:

$$CI_i = \sum_{j=1}^{n} \left(\frac{O_{ij}}{Z_i} \times \frac{adjCV_j}{adjCV_i} \right)$$

(Equation 1)

where:

j = competitor tree

O_{ij} = area of overlap of influence zones for study tree i and competitor tree j

Z_i = area of influence zone of subject tree = π × (2 × maximum crown radius)^2

n = number of competitors = trees for which distance$_{ij}$ < (influence zone radius$_i$ + influence zone radius$_j$)

adjCV = adjusted crown volume estimate = crown volume estimate × species canopy density correction factor

Calculated CI values for the study trees are based on data from 249 competitor trees that we measured between July 17 and August 14, 1999.

TREE CONDITION AND GROWTH DATA

At the start of the study and at the end of the 1999 and 2000 growing seasons we rated the condition of each study tree and collected data on several parameters related to tree growth. We visually estimated the amount of foliar chlorosis, necrosis, shoot dieback, and canopy defoliation using the following scale: 0=Symptom not seen; 1= < 2.5% of tree affected or symptomatic; 2= 2.5 - 20% of tree affected or symptomatic; 3= 20 - 50% of tree affected or symptomatic; 4- 50 - 80% of tree affected or symptomatic; 5- 80 - 97.5% of tree affected or symptomatic; 6- > 97.5% of tree affected or symptomatic.

Shoot growth measurements on *S. laevigata* and *P. fremontii* were based on 3 shoots per tree clipped from the outer (unshaded) portion of the canopy with a pole pruner. *S. laevigata* shoots were typically sampled from the upper portion of the canopy whereas *P. fremontii* shoots were collected to a maximum height of about 17 ft. We looked for bud scale scars on each sampled shoot to ensure that the entire current season's growth was included. Because *A. negundo* trees had relatively few shoots overall, we nondestructively measured 3 shoots per tree in the field.

STOMATAL CONDUCTANCE MEASUREMENTS

Most plants respond to acute drought stress by closing their stomata. To assess the degree of stomatal closure in study trees, we used a Li-Cor LI-1600 steady-state porometer (Li-Cor, Inc. Lincoln, NE), which measures the rate at which water vapor diffuses from intact attached leaves. We measured diffusive resistance of the lower (abaxial) leaf surface of at least 4 sunlit leaves per tree at monthly intervals from July to September 1999 and May to September 2000. Measurements were made on a subset of the study trees and on the naturally-occurring riverbank trees noted above.

Factors other than plant water status, such as low light intensity, can decrease the stomatal conductance of individual leaves. To reduce the variability associated with factors other than drought stress, we used the maximum stomatal conductance measured from sampled leaves on a given plant in statistical analyses, rather than the average of the readings for the plant. To reduce variation related to changes in temperature, humidity, and light intensity over the observation period, readings for each species were made in a single time block, alternating between trees in thinned and non-thinned plots.

STEM WATER POTENTIAL MEASUREMENTS

On September 16, 2000, we collected data on midday stem water potential to complement our data on stomatal conductance and soil water potentials. Midday stem water potential (SWP) measures water stress during the period when photosynthesis and transpiration are highest (McCutchan and Shackel 1992). We measured SWP on the 20 trees that were used for porometer readings plus three additional *A. negundo* (thinned, nonthinned, and riverbank) and two additional *S. laevigata* (thinned and nonthinned) trees.

Midday SWP readings were made following the methods outlined by Shackel (2000) using a pump-up pressure chamber (PMS Instrument Company, Corvallis, OR). On each tree, two healthy leaves (*P. fremontii*), terminal leaflets (*A. negundo*), or shoot tips with several leaves (*S. laevigata*) located near the main trunk were sealed in a plastic bag and overbagged with a larger opaque reflective plastic bag. Leaves or shoot tips were allowed to equilibrate to the water potential of the subtending stem for at least two hours. Leaves remained in the inner plastic bags when placed in the pressure bomb for SWP determinations.

MEASUREMENT OF SOIL WATER STATUS

Gypsum block soil moisture sensors (Soilmoisture block model 5201L06, Soilmoisture Equipment Corp., Goleta, CA) were installed on 8/19/99. Sensors were installed in pairs at two different depths at 16 sites located adjacent to the trees from which porometer data were collected. At each site, one sensor was placed at a depth of 18-21 inches (shallow placement) and the other near the bottom of the silt loam soil horizon at 27-36 inches (deep placement). A quart of water was added to each hole to soften the soil enough to allow the pre-soaked sensors to be pressed into the soil.

DATA ANALYSIS

We used JMP® Statistical Discovery Software (SAS Institute Inc., Cary, NC) to perform statistical analyses of the data. Some variables, including CI, were transformed prior to analysis by taking the natural logarithm (ln) of each value to normalize the data for parametric statistical tests. We used analysis of variance to test the significance of thinning treatment effects and analysis of covariance and linear regression to test for the significance of continuous variables. We used repeated measures analysis of variance and covariance for models involving repeated observations on individual trees. Unless otherwise stated, we refer to effects or differences as significant only if they are statistically significant at $P \leq 0.05$.

RESULTS

Stand Characteristics and Intertree Competition

The thinning treatment significantly increased the average distance between study trees and their nearest competitor, from an average of 7.5 ft in nonthinned plots to 10 ft in thinned plots. Thinning also significantly reduced the average number of competitors per tree, from 12.2 to 7.1. Because the size of a study tree's influence zone increases with increasing canopy diameter, at a given stand density a large tree has more competitors than a small tree. Hence, the relatively large *P. fremontii* trees had significantly more competitors on average (11.3) than the smaller *A. negundo* (7.9) and *S. laevigata* (9.1) trees.

CI was significantly affected by both thinning treatment and species. The three species have widely differing average CI values largely because of the effect of canopy volume on CI. A large tree is a stronger competitor for a small tree than the reverse. Because *P. fremontii* trees are both the largest of the study tree species (Table 1) and the most common species, *P. fremontii* CI values were generally much lower than *A. negundo* and *S. laevigata* CI values (Table 1).

Although CI was significantly greater in nonthinned plots than in thinned plots, CI values of trees in thinned and nonthinned plots overlapped considerably. In some cases, trees in thinned plots had higher CI levels than trees of the same species in nonthinned plots. To account for this variability, we constructed two sets of statistical models: one set using thinning treatment as a predictor and the other using ln CI as a predictor. Because these two predictor variables are highly correlated, they were not included in the same analyses.

TABLE 1. Tree size characteristics of study trees in June 1999.

Species	Mean diameter of largest main stem (inches)	Mean height (ft)	Mean canopy volume[1] (ft^3)	Mean competition index (range)
Acer negundo	1.8	13.4	475	11.8 (0.8 - 33.2)
Populus fremontii	6.5	34	2890	1.2 (0.2 - 2.3)
Salix laevigata	2.7	16.5	1023	3.9 (0.5 - 10.4)

[1] Canopy volume was calculated from canopy measurements using the formula of the regular geometric solid (e.g., ellipsoid) closest to the canopy shape of each individual. Volume was then adjusted downward using the visually estimated shape filling factor (e.g., ×0.5 for a half ellipsoid).

SOIL MOISTURE DEPLETION

Low (i.e., highly negative) soil matric potential values indicate that low amounts of soil moisture are available for plant growth. Most water available to plants is held at matric potentials of more than about -0.4 MPa. By September 1999, soil moisture readings indicated that almost all plant available water was depleted from the upper 3 ft of the soil profile (Figure 1). Soils remained very dry until well into January 2000 (Figure 1). Small amounts of rain falling before January (<2 inches) had little impact on soil moisture, but flooding events that occurred in February saturated the soil profile.

Soil moisture, especially in the upper portion of the soil profile, was depleted relatively early in the growing season. Shallow sensors in both thinned and nonthinned plots dried to below -0.4 MPa by mid May (Figure 1), and deep sensors dried to below -0.4 MPa by mid June. A repeated measures analysis of variance for the interval from 5/12/00 through 9/28/00 showed significant effects of sensor depth, thinning treatment, and date on soil matric potentials. These same three factors were also significant in an analysis of September 1999 data. Soils in the nonthinned plots were drier than those in the thinned plots (Figure 1), presumably because competition for soil moisture was greater in the nonthinned plots. Shallow soil horizons were also significantly drier overall than deeper soil horizons.

STOMATAL CONDUCTANCE

Average monthly leaf conductance measurements are shown in Figure 2. In both years, overall conductance readings were highest for *S. laevigata* and lowest for *A. negundo,* with *P. fremontii* intermediate. The average readings for each species were similar in both years. For individual trees, 1999 stomatal conductance readings were highly correlated with 2000 conductance readings (adjusted R^2=0.787, $P<0.0001$).

In both years, stomatal conductances generally declined as surface soil moisture levels declined (Figure 1) and cumulative reference evapotranspiration (ETo) increased (Figure 3). Stomatal closure appears to coincide with increasing levels of plant water stress over the growing season. Judging by the peaks in conductance readings taken during the 2000 growing season, we infer that *A. negundo* trees began to experience water stress by June, *P. fremontii* by July, and *S. laevigata* by August (Figure 2). Readings did not begin early enough in the 1999 growing season to show the onset of water stress in that year.

Plants may experience increased levels of water stress in response to reduced amounts of available soil moisture and/or high evapotranspiration demand (daily ETo). Because daily ETo values were nearly identical on July and August reading dates in each year (Figure 3), we attribute the decline in average stomatal conductances over these periods to drying of the surface soil (Figure 1) in response to increasing cumulative ETo. However, average conductance values for *P. fremontii* and the thinned *S. laevigata* were higher on 9/16/00 than on 8/19/00 (Figure 2), even though surface soil horizons continued to dry during this period. Presumably, the higher conductances on 9/16/00 reflect the fact that daily ETo was lower on

9/16/00 than on 8/19/00 (3.81 mm compared to 5.08 mm, Figure 3). When considered together with ETo and soil moisture data, the stomatal conductance data indicate that the trees' ability to extract water from the clay subsoil is quite limited at best, and that all species are dependent to varying degrees on moisture present in the fill soil that comprises the shallow portion of the soil profile.

On average, trees in thinned plots had higher stomatal conductances than those in nonthinned plots, but readings from trees in thinned and nonthinned plots showed considerable overlap within species. In a repeated measures analysis of variance on stomatal conductance readings in both years, ln CI was more highly significant (P=0.035) than thinning treatment (P=0.050), suggesting that CI was a better predictor of water stress than the thinning treatment. Conductances also varied significantly between species in these analyses. Cumulative ETo and daily ETo were also significantly correlated with stomatal conductance in other statistical models.

Overall, these analyses indicate that across all species, dates, and daily ETo levels, stomatal conductances (and hence transpiration rates) are lower for trees that have higher levels of competition. This is consistent with the hypothesis that soil moisture reserves at the site are limited. In the early part of the summer, trees are probably competing primarily for soil moisture in the surface fill soil. However, differences in stomatal conductances between thinning treatments persist to the end of the season, especially for *P. fremontii* and *S. laevigata.* Because available soil moisture in the surface fill soil was depleted by that time, we infer that trees may also compete to some degree for the limited amount of water available from the clay subsoil.

Only a few natural trees growing along the river near the study area were suitable for measuring stomatal conductances and the sample size was too small to include these trees in statistical analyses. Stomatal conductances of the single natural *A. negundo* we monitored were near the overall average for *A. negundo* in the planting. Late season (August-September) stomatal conductances of the two riverbank *P. fremontii* trees were equal to or greater than those of trees in the thinned plots. One of the two riverbank *S. laevigata* trees we monitored maintained stomatal conductances well above all other study trees (mean conductance 540 mmol/s/m^2). Conductance readings for the other riverbank *S. laevigata* were near the species average through July but remained high late in the season (mean August-September conductance 450 mmol/s/m^2). Hence, with the possible exception of the *A. negundo,* riverbank trees generally showed stomatal conductances similar to or higher than the least-stressed study trees.

STEM WATER POTENTIAL

We measured midday stem water potentials (SWP) on 9/16/00, concurrent with our final stomatal conductance measurements. Average SWP by species and thinning treatment is shown in Figure 4. Although SWP was correlated with both thinning treatment (P=0.090) and ln CI (P=0.032), ln CI was a better predictor of SWP. Trees with lower levels of competition (low CI) had higher stem water potentials (i.e., lower water stress) than trees in more competitive neighborhoods (high CI). SWP also varied significantly between species (Figure 4). SWP readings were positively correlated with stomatal conductance across all species (Figure 5). This provides further evidence that reduced stomatal conductance in study trees indicates increasing water stress.

It is difficult to judge the significance of stem water potentials of natural riverbank trees due to the small number of trees involved (two for each species), although some conclusions can be drawn about the specific trees that were measured. Stem water potentials of the riverbank *A. negundo* averaged -0.2 MPa, which indicates that these trees were less stressed than any of the *A. negundo* study trees. Average stem water potentials for riverbank *S. laevigata* (-0.7 MPa) were close to the overall average for *S. laevigata* in the planting. Given that these riverbank trees also had greater stomatal conductances than the study trees, we can conclude that the riverbank *S. laevigata* were less stressed than trees in the planting. The average stem water potential for the riverbank *P. fremontii* was -0.725 MPa, similar to the average for the thinned study *P. fremontii* trees. Because conductance readings for the riverbank *P. fremontii* were also comparable to the thinned study trees, it appears that thinned trees and riverbank trees had similar levels of water stress.

TREE GROWTH

Trunk Diameter

Stem diameter growth reflects a number of growth processes that may be affected by water stress. Over the period of our study, June 1999 to September 2000 (1.5 growing seasons), trunk diameter increased measurably in all three species. Across all species, trunk diameter increase was negatively correlated with ln CI, showing that growth was reduced as CI increased (Figure 6).

Shoot Growth

P. fremontii* and *S. laevigata. Because of similarities in their stem growth patterns, we analyzed shoot growth of *P. fremontii* (Figure 7) and *S. laevigata* (both in the family Salicaceae) together. We used repeated measures analyses of variance to examine the effects of year, species, and either ln CI or thinning treatment on shoot growth, number of internodes, and average internode length. Analyses for all three growth variables indicated that shoot growth was significantly greater in 1999 than in 2000 and was also significantly greater for *S. laevigata* than for *P. fremontii.* Ln CI was a better predictor of shoot growth than was thinning treatment. All shoot growth variables in the analyses were negatively correlated with ln CI, meaning that trees with greater levels of competition produced both fewer and shorter internodes. However, this effect was more pronounced for *P. fremontii* than for *S. laevigata*. In separate models for each species, ln CI is significant for all three shoot growth variables for *P. fremontii* but not for *S. laevigata*. For P fremontii, relationships between shoot growth variables and CI (nontransformed) were also significant (Figure 7).

For the two *P. fremontii* riverbank trees used for stomatal conductance readings, average shoot and internode lengths and internode counts were well within the range of values seen among in *P. fremontii* trees in the planting. In contrast, the riverbank *S. laevigata* had more internodes and generally longer shoots and internodes than trees in the planting. This is consistent with other data showing that the riverbank *S. laevigata* were less water-stressed than trees in the planting.

Acer negundo. We analyzed stem data for *A. negundo* separately because its shoot growth pattern differs greatly from that of the other two species. As seen in the other species, shoot growth and internode production were significantly reduced in 2000 compared to 1999. The number of internodes produced in 1999 was negatively correlated with ln CI (R^2=0.20, P=0.062), but no significant correlations between shoot growth and ln CI were seen in the 2000 data.

TREE CONDITION

We rated leaf chlorosis and necrosis and canopy defoliation and dieback of all study trees in September 1999 and 2000. In both years, general chlorosis (yellowing) of the foliage was the most prominent symptom seen in *A. negundo.* Many leaves also exhibited a necrotic scorching symptom that appeared to be related to drought stress and/or excessive heating of the foliage. Such symptoms were evident as early as June in 2000, and tended to develop first in leaves that were located in full sun. September condition ratings for *A. negundo* were not related to thinning treatment or CI and were comparable in both years.

Foliar chlorosis was also the most common symptom seen in *P. fremontii,* but the pattern of chlorosis differed substantially from that seen in *A. negundo*. In *P. fremontii,* chlorosis typically affected entire branches. These chlorotic leaves were associated with acute water stress in affected branches; chlorotic leaves of affected branches consistently had very low stomatal conductances. *P. fremontii* defoliation and chlorosis ratings were significantly higher in 2000 than in 1999. Chlorosis affected at least 20% of tree canopy in 5 of the 20 *P. fremontii* study trees in September 1999. In September 2000, 10 of the 20 trees had at least 20% chlorosis in the canopy. The high prevalence of chlorotic branches among *P. fremontii* study trees suggests that these trees were under significant water stress, but may have maintained higher stomatal conductances and SWP by effectively reducing leaf area through branch senescence.

P. fremontii condition ratings from September 1999 and 2000 were not significantly correlated with CI, although some ratings differed by thinning treatment. Levels of shoot dieback were greater in nonthinned plots than in the thinned plots in both 1999 and 2000. *P.*

fremontii trees in nonthinned plots also had significantly more borer strikes on the lower portion of the trunk than trees in thinned plots in both years. The number of borer strikes in 1999 was significantly higher than in 2000 for trees in both thinned and nonthinned plots.

Ratings for dieback, defoliation, and leaf rust in *S. laevigata* were significantly greater in September 2000 than in September 1999. Neither ln CI nor thinning treatment was significantly related to any of the *S. laevigata* condition ratings. However, defoliation seen in some *S. laevigata* study trees in June may have been associated with water stress. Natural riverbank *S. laevigata* showed no defoliation even in September.

CONCLUSIONS

A. negundo apparently experienced the greatest level of drought stress among the three species studied. SWP and stomatal conductance readings were lower than those of *P. fremontii* and *S. laevigata*. *A. negundo* leaf conductances observed here were also lower than midsummer readings previously reported for *A. negundo* growing in riparian or floodplain conditions (Donovan and Ehleringer 1991, Foster 1992, Foster and Smith 1991). After accounting for differences between SWP and leaf water potentials, it also appears that *A. negundo* trees in this study had much lower water potentials than those reported by Foster (1992) for *A. negundo* growing over a shallow water table.

We infer that *A. negundo* study trees were largely dependent on water stored in the surface soil and did not obtain appreciable amounts of water from the clay subsoil. They responded to summer drought conditions by closing their stomata to limit transpiration. Over the short term at least, the thinning treatment did not reduce depletion of the surface soil moisture enough to substantially benefit *A. negundo*. Thinning had little effect on growth and no demonstrable effect on condition of *A. negundo*.

In contrast to *A. negundo*, stomatal conductances of *S. laevigata* remained relatively high throughout the summer, and were the highest of the three species. Peak stomatal conductance occurred in mid-July, when the upper 3 ft of the soil profile was already quite dry (Figure 1). *S. laevigata* also had the highest stem water potential of the three species in the planting (Figure 4). We surmise that *S. laevigata* study trees were able to extract at least moderate amounts of water from the moist clay subsoil. Nonetheless, it appears that riverbank trees, which presumably had access to a free water table, maintained better water status than *S. laevigata* trees in the planting. The thinning treatment had some effect on growth but no detectable effect on condition of *S. laevigata*.

P. fremontii developed only intermediate levels of stress, presumably because it made use of water in the clay subsoil as well as water stored in the surface fill soil. To maintain a favorable water balance as water in the surface soil was depleted, *P. fremontii* trees closed stomata and apparently sacrificed branches to reduce leaf area. Early senescence of branches or "branch sacrifice", is thought to be due to water stress-induced xylem cavitation (Rood et al 2000, Tyree et al 1994). By rapidly reducing leaf area, this pattern of branch senescence and subsequent dieback allows the remaining portions of the tree to maintain a higher water potential. It appears that *P. fremontii* study trees did not extract enough water from the clay subsoil to support the amount of transpiring leaf area that they had produced early in the season. Of the three study trees, *P. fremontii* showed the greatest positive response to reduced intertree competition. *P. fremontii* trees with reduced competition had improved growth and water status. Trees in thinned plots also had reduced levels of dieback and fewer borer strikes, both of which could be directly related to improved water status.

Our study suggests that the reconstructed floodplain does not provide a soil moisture regime that is optimal for phreatophytic riparian species, presumably because tree roots are unable to penetrate the dense clay subsoil and reach the water table. Certain species, including *P. fremontii* and *S. laevigata,* apparently extract some water from the clay subsoil. However, even these species are still largely dependent on the water that is stored in the surface fill soil horizon, and show progressively greater levels of water stress as moisture in this layer is depleted. Thinning of the stand reduced the rate at which moisture in the fill soil was depleted and improved water relations in *P. fremontii*, but even trees in thinned plots showed stress by the end of the season.

Although many of the riparian species used in the planting may persist at this location indefinitely, we believe that the condition of many of the plants is likely to deteriorate over time because of the limited soil water supply. Water stress is likely to be more severe in low rainfall years in which soil moisture in the fill soil layer is inadequately recharged. Although thinning may reduce water stress in some species, our study shows that a given level of stand thinning will not benefit all tree species equally.

The need to investigate thinning as a remedial treatment at this site arose because the planting plan did not adequately account for the limitations of the site that existed after the extensive grading and recontouring. Tree roots were unable to reach the free water table that is confined under the thick, dense clay layer. However, this clay layer remains moist due to the underlying water table and does provide some plant-available moisture. Species such as valley oak (*Quercus lobata*), that tolerate both summer drought and winter flooding, may be better adapted to this site than phreatophytes like *P. fremontii*. Successful restoration plantings in extensively altered riparian sites such as this need to account for limitations imposed by seasonal soil water regimes that may not be typical of natural riparian systems.

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FIGURE 1.

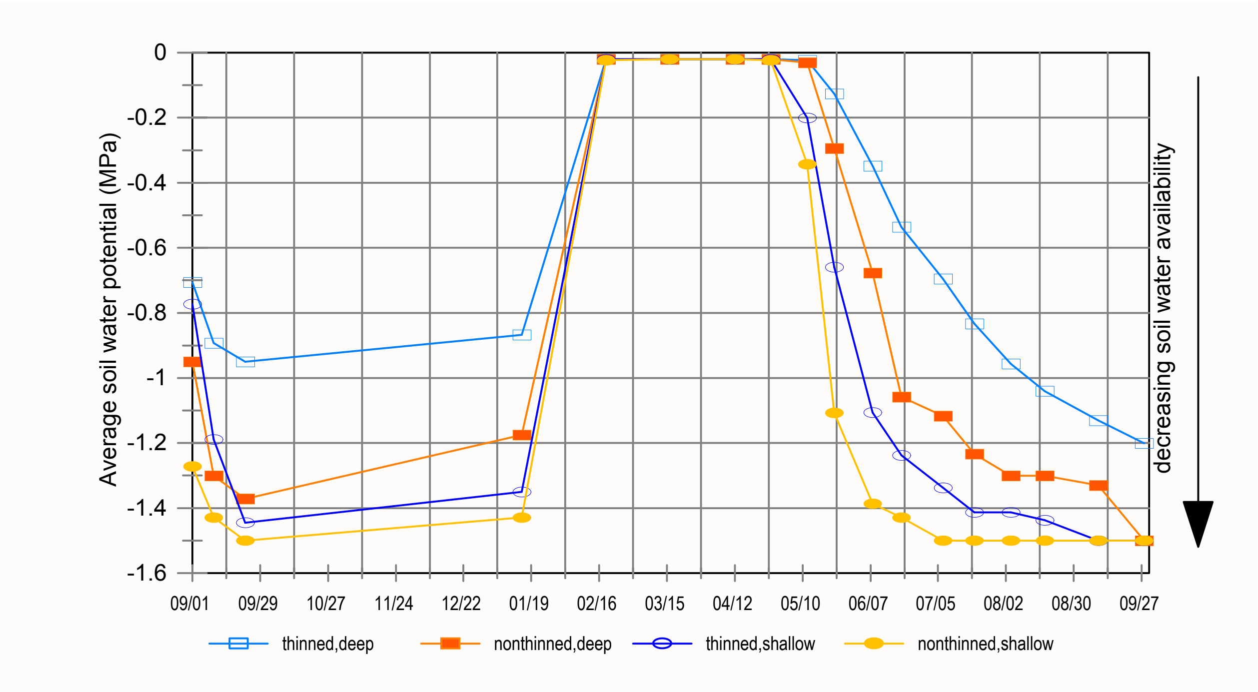


FIGURE 2.

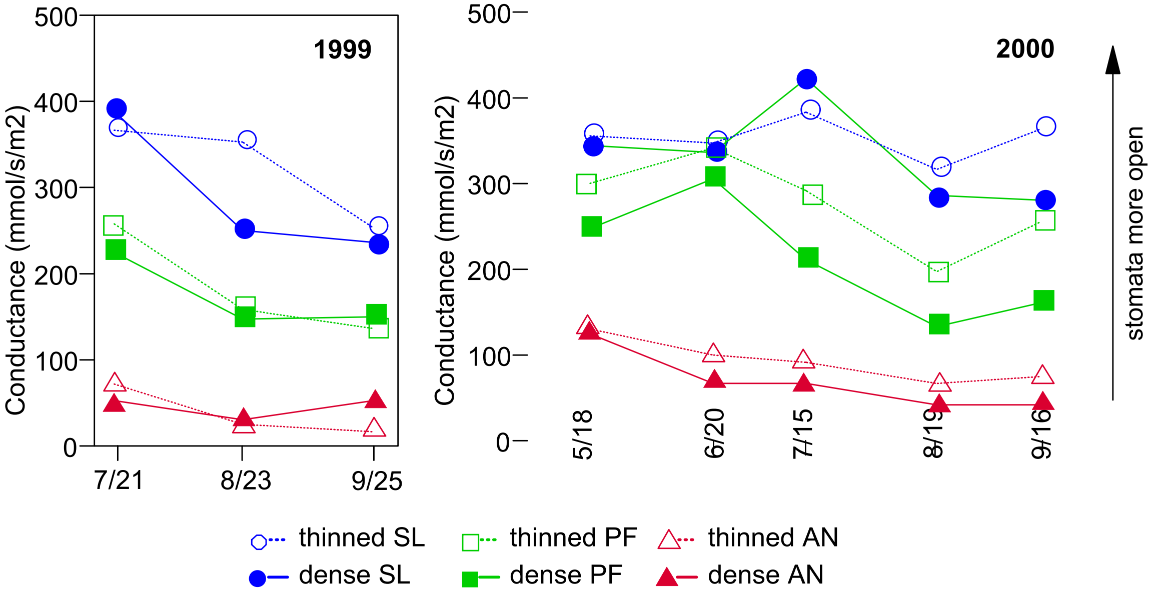


FIGURE 3.

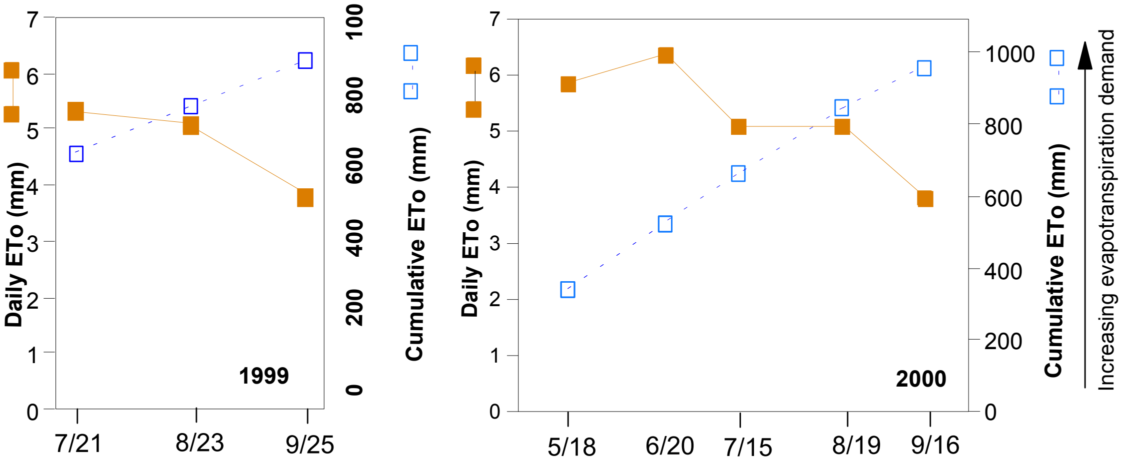


FIGURE 4.

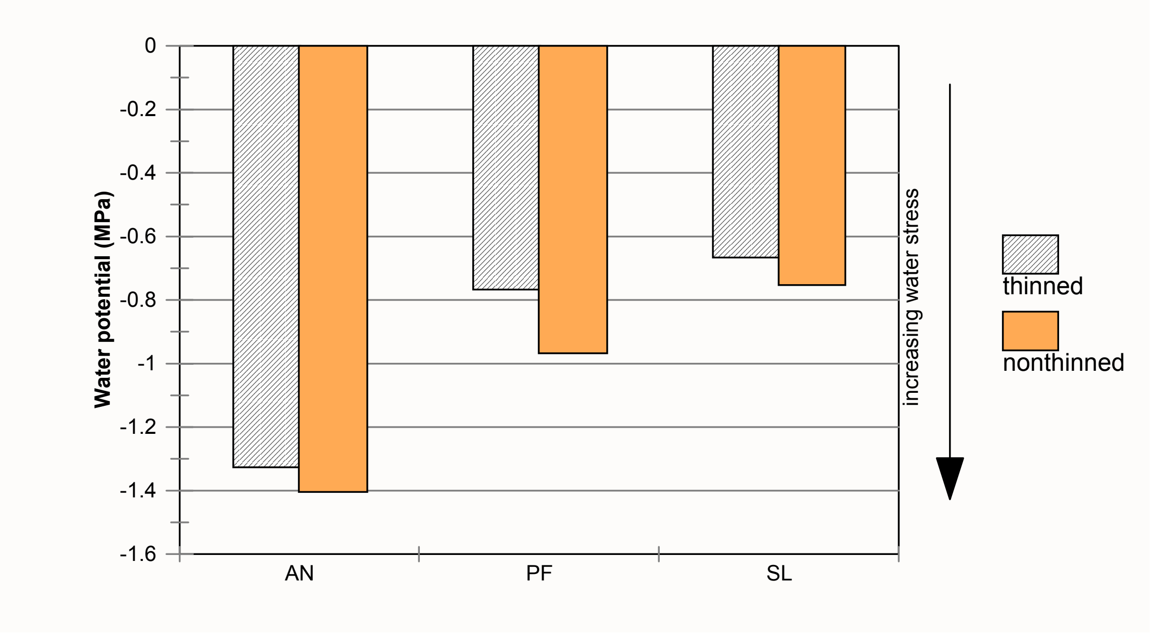


FIGURE 5.

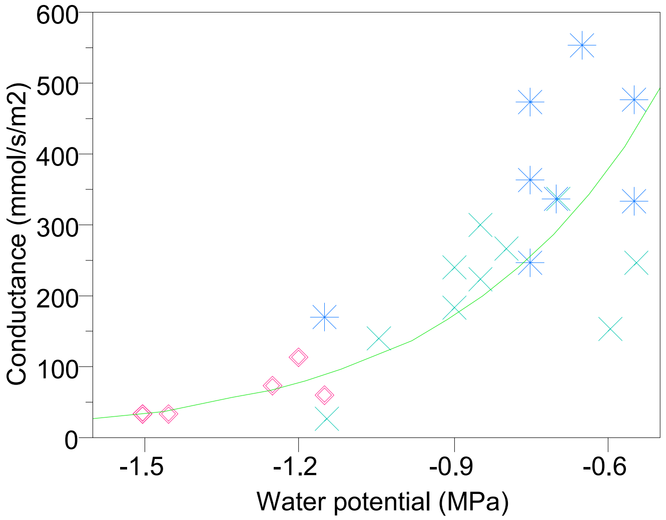


Figure 6.

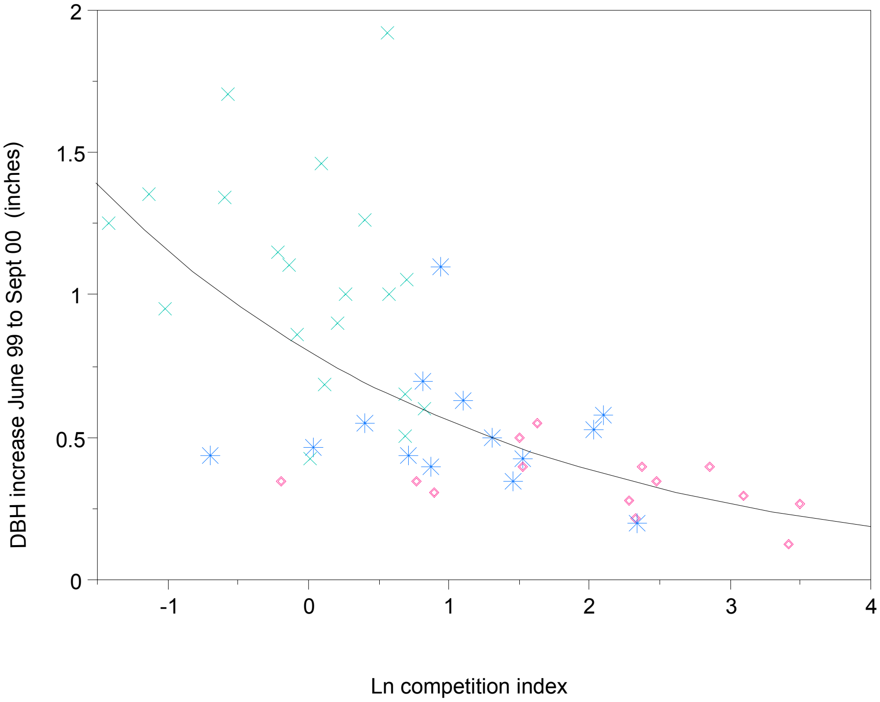
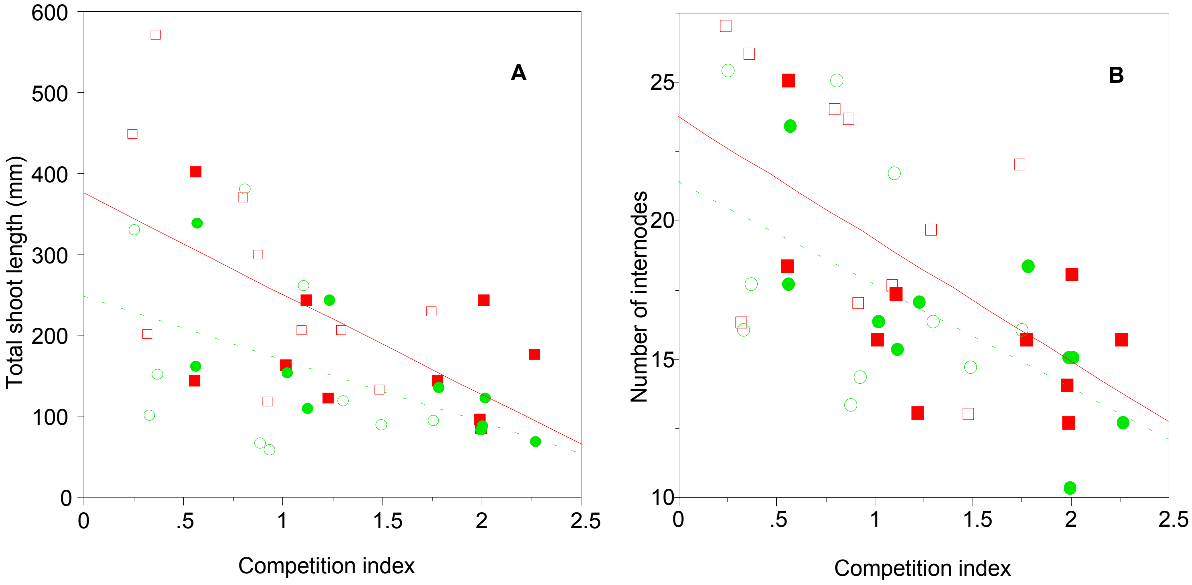


FIGURE 7.



A
Total shoot length (mm)
0
100
200
300
400
500
600
Competition index
0
.5
1
1.5
2
2.5
B
Number of internodes
10
15
20
25
Competition index
0
.5
1
1.5
2
2.5

FIGURE LEGENDS

FIGURE 1. Overall average soil matric water potential (MPa) at deep (27 to 36 inches below ground) and shallow (18 to 21 inches below ground) sensor locations from September 1999 through September 2000 in thinned and nonthinned plots. Note that sensors used in this study cannot measure soil water potentials less than -1.5 MPa. Sample size = 6 to 9 sensors per depth/treatment combination.

FIGURE 2. Average stomatal conductance readings in 1999 and 2000 for selected trees in thinned and nonthinned plots. AN = *Acer negundo* (3 trees/treatment), PF = *Populus fremontii* (4 trees/treatment), SL = *Salix laevigata* (3 trees/treatment).

FIGURE 3. Daily reference evapotranspiration (ETo) (solid squares) and cumulative ETo (open squares) in San Jose in 1999 and 2000 on dates that stomatal conductance was measured in study trees. Data are from CIMIS station 69 in San Jose, about 2.6 miles southwest of the study location.

FIGURE 4. Average midday stem water potential (MPa) measured September 16, 2000. AN = *Acer negundo*, PF = *Populus fremontii*, SL = *Salix laevigata.* Sample size = 4 trees per species/treatment combination.

FIGURE 5. Midday leaf conductance (mmol/s/m^2) versus midday stem water potential (MPa) on September 16, 2000. ◊ = *Acer negundo*, X= *Populus fremontii,* ✳ = *Salix laevigata*. The plotted regression line shown (adjusted R^2=0.754, P=<.0001) is for ln(leaf conductance) vs. water potential.

FIGURE 6. DBH increase (inches) from June 1999 to September 2000 plotted against log competition index (ln CI). ◊ = *Acer negundo*, X= *Populus fremontii*, ✳ = *Salix laevigata*. Plotted regression line is for ln DBH increase vs. ln CI (adjusted R^2=0.504, P<0.0001).

FIGURE 7. *Populus fremontii* current season shoot growth (mm) (A) and number of internodes (B) in 1999 (squares) and 2000 (circles) plotted against competition index. Open symbols represent trees in thinned plots, and solid symbols represent trees in nonthinned plots. Solid and dashed lines show regression lines for 1999 and 2000 data, respectively. Graph A regressions: 1999 R^2=0.231 (P=0.0054), 2000 R^2=0.199 (P=0.0280). Graph B regressions: 1999 R^2=0.326 (P=0.0050); 2000 R^2=0.297 (P=0.0076).