

Effect of gender on sap-flux-scaled transpiration in a dominant riparian tree species: Box elder (*Acer negundo*)

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[1] *Acer negundo* is a dioecious riparian tree species with a spatial segregation of the sexes along soil moisture gradients. Females are typically more common in wet sites along streams (typically F/M \approx 1.6), whereas males are more common in drier sites away from streams (typically F/M \approx 0.6). Spatial segregation between sexes may develop because of the higher reproductive cost in females compared to males. If so, female *Acer negundo* trees would be under stronger selection to maximize resource uptake, and would therefore likely occur at greater frequencies in high resources sites (i.e., along streambanks), and increase rates of resource acquisition (i.e., water and nutrients). The spatial segregation of the sexes leads to the hypothesis that male and female individuals have varying influence on ecosystem evapotranspiration. To address this, stem sap flux was measured on mature streamside (\leq 1 m from stream channel) and nonstreamside ($>$ 1 m from stream channel) male and female *Acer negundo* trees occurring in Red Butte Canyon near Salt Lake City, Utah, during the 2004 growing season. Despite having similar predawn and midday water potentials, sap flux density was 76% higher in streamside female trees than in males ($P < 0.0001$), while sap flux density was 19% greater in nonstreamside female trees compared to males ($P < 0.0001$). Mean daily sap flux density of all *A. negundo* populations was highly correlated with mean daily vapor pressure deficit ($P < 0.0001$). Mean daily sap flux density of all *A. negundo* populations was highly correlated with mean daily photosynthetic active radiation ($P < 0.0001$). Mean daily sap flux density of all *A. negundo* populations was highly correlated with mean daily transpiration flux from dominant riparian vegetation away from streambanks (estimated from scaled sap flux measurements of all dominant riparian tree species in Red Butte Canyon). Male and female *A. negundo* trees contributed 31 and 46% respectively of the estimated 8.0 mm d⁻¹ transpiration flux from dominant riparian vegetation adjacent to the stream channel. Results from this investigation show that the population structure of dioecious riparian trees has direct consequences on ecosystem ET, particularly along stream margins. Shifts in population structure therefore, may have profound impacts on several ecohydrological processes including stream discharge, biogeochemical cycling, and ecosystem productivity.

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1. Introduction

[2] Plants take up and transpire large amounts of water to the extent that globally, they recycle about half of the more than 100,000 km³ of precipitation that falls on land each year [Jackson *et al.*, 2000]. In arid and semiarid regions such as the western United States, the ratio of plant transpiration to precipitation is low relative to the global mean, except in riparian zones where precipitation is

funneled through surface and subsurface pathways to a well-defined stream channel where adjacent woody plants have access to groundwater for a significant part of the year. Given that water transport through plants is proportional to growth rate and production [Enquist, 2002; Huxman *et al.*, 2005], it is not surprising that riparian zones are among the most productive ecosystems throughout much of the arid and semiarid west.

[3] There is strong evidence that human activities are having impacts on the function and structure of riparian ecosystems on a global scale [Chapin *et al.*, 1997; Vitousek *et al.*, 1997; Jackson *et al.*, 2001]. In the intermountain west and southwestern United States, water diversions, impoundments, and groundwater pumping, coupled with climate change have had substantial impacts on the population structure, productivity and functioning of riparian ecosys-

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tems [Stromberg *et al.*, 1991; Stromberg, 1993; Patten, 1998; Horton *et al.*, 2001]. In particular, hydrologists and ecologists have paid close attention to the impacts global change may have on the population structure of dominant riparian tree species given their considerable biological controls over hydrologic fluxes and habitat quality [Stromberg, 1993; Busch and Smith, 1995; Horton *et al.*, 2001].

[4] Box elder (*Acer negundo* Sarg.) is a dominant tree species that occurs in low- to mid-elevation riparian and floodplain habitats throughout most of the intermountain west and southwestern United States [Sargent, 1965]. *Acer negundo* is dioecious and demonstrates fine-scale spatial segregation among sexes; females preferentially occupy resource rich streamside locations and males predominate on drier margins of riparian ecosystems [Freeman *et al.*, 1976; Dawson and Ehleringer, 1993; Ward *et al.*, 2002]. Differences in habitat preference have likely evolved owing to different resource demands associated with male versus female sexual reproduction [Dawson and Ehleringer, 1993; Dawson *et al.*, 2004]. The cost of reproduction is typically greater for females than for males. Females therefore would be under stronger selection to increase resource uptake. One way to increase resource gain is to specialize in habitats that are highly productive, such as riparian stream margins.

[5] Differences in habitat preference may be associated with differences in physiological responses to water availability [Dawson and Bliss, 1989; Dawson and Ehleringer, 1993]. At the leaf level, male *A. negundo* trees are typically more conservative in their water use and appear better suited to avoid drought stress compared to females [Dawson and Ehleringer, 1993]. Leaf stomata of males are more sensitive to changes in vapor pressure deficit (*vpd*), and to fluctuations in soil water potential, while females are less likely to close their stomates in response to leaf water deficits regardless of habitat [Dawson and Ehleringer, 1993]. As a result, leaf transpiration is typically lower in males than in females. Differences in stomatal behavior between genders may correspond with differences in hydraulic architecture [Tyree and Sperry, 1988; Alder *et al.*, 1996]. If there is a tradeoff between hydraulic efficiency and drought tolerance [Tyree *et al.*, 1994; Pockman and Sperry, 2000; Maherli *et al.*, 2004], then the hydraulic properties that enhance water uptake (and presumably carbon gain) in females along streamside habitats may induce higher rates of drought-induced mortality in more unpredictable, nonstreamside habitats. However, information is lacking on whole plant water relations of male and female *A. negundo* trees. If gender-specific differences in leaf-level water fluxes scale to the watershed, then changes in the population structure of *A. negundo* (i.e., the ratio of male to female individuals) could have significant consequences on ecohydrology and ecosystem productivity.

[6] In this paper, we report results of an investigation on patterns of sap-flux-scaled transpiration between male and female *A. negundo* trees occurring along streamside (within 1 m of a perennial stream) and nonstreamside habitats. We assumed that streamside trees have had access to stable water sources throughout their life history, and potentially have direct influence on stream discharge. Conversely, plants occurring in nonstreamside habitats are exposed to occasional intra-annual and interannual periods of drought [Dawson and Ehleringer, 1993; Ward *et al.*, 2002], there-

fore requiring physiological modifications in hydraulic architecture in order to minimize leaf water deficits. Given the greater resource constraints imposed on females, we hypothesized that mature female *A. negundo* trees along streamside habitats would have a significantly greater water yield than male trees and that these differences scale from individual plant to the watershed. Alternatively, we hypothesized that mature male *A. negundo* trees in nonstreamside habitats would have equal or greater water fluxes than female trees at the watershed scale.

2. Methods

2.1. Site Description

[7] Research was conducted in Red Butte Canyon Research Natural Area, east of Salt Lake City, Utah. The Red Butte Canyon drainage covers an approximately 20.8 km² area, and contains a well defined riparian area that has a free-flowing perennial stream. Volumetric flow rate of the stream is continuously monitored by a USGS stream gauge near the mouth of the watershed. Climate in Red Butte Canyon is characterized by hot, dry summers and long, cold winters. Mean annual precipitation ranges from about 500 mm at lower elevations to about 900 mm at higher elevations [Ehleringer *et al.*, 1992], with precipitation primarily falling in winter and spring. Two sites were established in the canyon for whole plant water relation studies on *Acer negundo* trees and other dominant riparian trees. The first site was established in a 4.3 ha meadow in Parley's Fork approximately 200 m above the confluence with the main channel (111°79'W', 40°79'N, 1820 m elevation), and has previously been described [Dawson and Ehleringer, 1991, 1993]. A small perennial stream runs through the meadow and the overstory is dominated by a mixed age stand of *A. negundo* trees intermixed with *Acer grandidentatum* Nutt. and *Betula occidentalis* Hook. trees. The meadow is characterized by loamy, moderately permeable, well-drained soils [Ehleringer *et al.*, 1992]. The site was ideal for investigating water relations in *A. negundo* given its easy access to trees occurring in streamside and nonstreamside locations. A second site was selected along the main channel of the research area (111°77'W', 40°80'N, 1900 m elevation) to compare water relations of other riparian tree species that typically dominate midelevation riparian areas of the Intermountain West with *A. negundo*. The overstory at the upper site was dominated by mixed age stands of *A. negundo*, *A. grandidentatum*, *B. occidentalis*, and *Populus angustifolia* James. The site is characterized by a thick understory comprising various perennial and annual herbaceous plants, forbs, and grasses. Soils at the upper site comprised poorly drained, highly stratified mixed alluvium [Ehleringer *et al.*, 1992].

2.2. Xylem Water Potential Measurements

[8] Xylem water potential measurements were performed on six male and female *A. negundo* trees at streamside and nonstreamside locations (24 trees) that were instrumented with sap flux sensors. Measurements were also conducted on six *A. grandidentatum*, *B. occidentalis*, and *P. angustifolia* trees that were instrumented with sap flux sensors. Xylem water potential was measured using a Scholander-type pressure chamber (PMS Instruments, Corvallis, Oregon) in

mid-July and again in early September before sap flux measurements commenced. A single shoot tip from each of the six trees was cut with a sharp razor blade and measured at predawn (Ψ_{pd}) between 0200 and 0400 h, and at midday (Ψ_{md}) between 1100 and 1300 h.

2.3. Meteorological Measurements

[9] Relative humidity, air temperature, and photosynthetic active radiation were measured continuously at Parley's Fork and the upper canyon throughout the experiment from 3 m towers. Relative humidity and air temperature were measured with a Vaisala HMP 45 AC humidity and temperature probe (Vaisala, Woburn, Massachusetts), placed approximately 2 m above the ground surface. Photosynthetically active radiation (Q) was measured with a Li-Cor LI-190SZ quantum sensor (Li-Cor, Lincoln, Nebraska). Micrometeorological data were measured every 30 s and stored as 10 min averages with Campbell CR10X-2M data loggers (Campbell Scientific, Logan, Utah). Measurements of relative humidity and air temperature were used to calculate atmospheric vapor pressure deficit (vpd).

2.4. Sap Flux Measurements

[10] Granier-type sensors [Granier, 1987, 1996] were constructed in the laboratory to measure sap flux density (J_s , $\text{g H}_2\text{O m}^{-2}$ sapwood s^{-1}). Each sensor consisted of a pair of 20-mm-long, 2-mm-diameter stainless steel probes inserted approximately 15 cm apart along the axis of the hydroactive xylem (i.e., sapwood). Azimuth direction of each sensor was randomly selected to eliminate potential biases due to nonuniformity in sap flux around the stem. The upper probe (i.e., toward the canopy) was supplied with constant heat of 200 mW, and the temperature difference between the heated probe and the lower, unheated reference probe was converted to sap flux density according to Granier [1987, 1996],

$$J_s = 0.0119 \left(\frac{\Delta T_0}{\Delta T} - 1 \right)^{1.23}, \quad (1)$$

where ΔT is the temperature difference between the heated and unheated probes and ΔT_0 is the temperature difference obtained under zero flow conditions. We assumed that zero flow only occurred at night when vpd was at or near zero.

[11] A single sensor was inserted in each tree at approximately 1.5 m above the ground. At Parley's Fork, sap flux was measured in seven streamside *A. negundo* male trees with diameters ranging from 18.8 to 46.9 cm, with a mean diameter of 25.8 cm, six streamside female trees (dia. range: 17.7–42.9 cm, mean: 29.8 cm), eight nonstreamside male trees (dia. range: 5.5–21.2 cm, mean: 12.3 cm), and nine nonstreamside female trees (dia. range: 8.4–25.9 cm, mean: 16.4 cm). Trees were classified as streamside if they occurred 1 m or less from the stream channel. In addition, a single sap flux sensor was inserted into 10 *A. grandidentatum* (dia. range: 6.9–26.7 cm, mean: 19.0 cm), *B. occidentalis* (dia. range: 7.7–14.2 cm, mean: 10.8 cm), and *P. angustifolia* (dia. range: 10.5–23.5 cm, mean: 18.5 cm) trees at the upper field site. We did not test for differences in J_s between streamside and nonstreamside trees at the upper site, and assumed that fluxes from these

species did not vary significantly between microsites. All the trees selected for sap flux studies were reproductively mature, and were dominant with canopies that received sunlight throughout daylight hours. Temperature differences of all sensors were logged every 30 s and stored as 10 min averages with Campbell CR10X-2M data loggers (Campbell Scientific, Logan, Utah). Sap flux measurements were conducted during the 2004 from 16 July until leaf senescence.

[12] Daily sap flux density (J_s , $\text{g cm}^{-2} \text{d}^{-1}$) was calculated in order to correlate with mean daytime vpd and mean daytime Q . Mean daytime vpd was normalized by day length: daylength/24 hours (vpd_z) in order to correct for the effect of day length on transpiration [Oren *et al.*, 1991]. Day length was defined by the period when Q was greater or equal to $10 \mu\text{mol m}^{-2} \text{s}^{-1}$.

2.5. Sap Flux Scaling

[13] Sap flux densities of each gender, location, and species were scaled to the watershed level by first determining the relationship between stem diameter (D) at 1.5 m above the ground and sapwood area. Two cores were taken from nine to 10 individuals per gender, location, and species covering a wide range in size. Sapwood area (A_s) was obtained by first determining the inside bark diameter, then determining the depth of hydroactive xylem by measuring the length of translucence of each core [Pataki *et al.*, 2000], then subtracting the sapwood area from the total stem cross-sectional area. Sapwood area to stem diameter relationships were determined using a power function given in equation (2),

$$A_s = \beta_1 * D^{\beta_2}, \quad (2)$$

where β_1 and β_2 are fitting parameters.

[14] Stand transpiration within the riparian area was estimated by multiplying the mean daily sap flux densities by the total sapwood area within the riparian area. To estimate the sapwood area, six 50 m \times 50 m (2500 m^2) plots were established at six locations within the canyon's riparian area between 1660 and 1900 m elevation. In each plot, the diameter of every stem greater than 2 cm diameter was estimated at approximately 1.5 m above the ground, and the species was identified. The gender of all *A. negundo* trees was also identified, and trees occurring within one m of the stream channel were noted.

[15] Biomass zones were established within the canyon to allow for changes in species composition, total biomass, and climate that occurs with changes in elevation. Each zone extended from the center of each plot to the midway point along the riparian corridor to the nearest plot: (distance between Plot_{*i*} and Plot_{*i-1*})/2. A total of eight biomass zones were established; six zones spanned the length of the riparian area of the main channel, and two zones that spanned the two main forks of the canyon: Knowlton's and Parley's.

[16] Aerial photographs were used to determine the area and length of each biomass zone. The riparian corridor was identified by its dense canopy cover that was easily distinguishable on the photographs. The area and length of each zone was calculated using the public domain NIH Image J (National Institute of Health, <http://rsb.info.nih.gov/ij>).

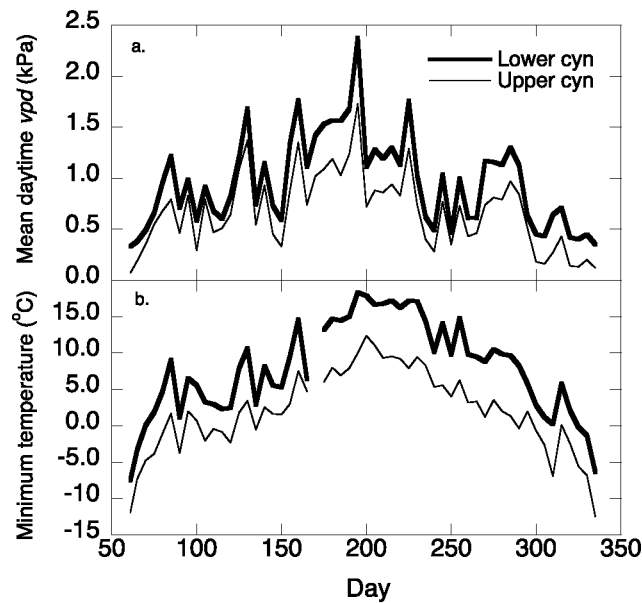


Figure 1. Mean daily vapor pressure deficit (vpd) and minimum daily air temperature near the top (1900 m) and mouth (1660 m) of Red Butte Canyon watershed. Vapor pressure deficit and minimum air temperature were used to estimate daily evapotranspiration and length of growing season of dominant riparian vegetation within the Red Butte Canyon watershed.

Total sapwood area in each zone (A_{sz}) was calculated for each gender and species as

$$A_{sz} = A_{sp} * (A_{gz}/A_{gp}), \quad (3)$$

where the subscripts sp, gz, and gp represent the plot sapwood area (of individual genders and species), total ground area of each biomass zone, and plot ground area respectively. The total sapwood area along stream margins (i.e., ≤ 1 m from stream) was estimated by multiplying the length of each zone by 2 m to account for both sides of the channel. Total sapwood area within the stream margin of each zone was calculated using equation (3). Because the stream channel could not be identified on the aerial photographs (owing to the dense canopy cover), the stream channel was assumed to have a straight course through each zone. However, because the channel does meander somewhat, it is likely that the total ground area and sapwood area along the stream margin were slightly underestimated.

[17] To estimate daily ET of each zone, measurements of J_s were correlated with vpd , and multiplied by A_s . Mean daytime vpd was estimated for each zone by calculating vpd from air temperature and humidity data collected at the mouth of the watershed (elevation 1660 m) and from data collected at the upper canyon site (Figure 1a). This allowed for interpolation of daytime vpd for each biomass zone except for Knowlton's Fork, which was slightly higher in the canyon than the upper canyon site. In this case, we used climate data from the upper canyon to estimate ET patterns. Total growing season ET was estimated by summing the daily ET of each zone by the number of growing season days. The length of the growing season in each zone was estimated by the number of days between first and last frost

during the growing season. Days were considered frost-free when the minimum temperature was above -1°C . The daily minimum temperature of each zone was estimated by interpolation from data collected at the mouth of the watershed and at the upper canyon site (Figure 1b), yielding a range of growing season days between 159 at the mouth of the watershed to 128 in the upper canyon. The relative contribution by each gender and species to canopy ET at the watershed scale was determined by summing the ET flux of each biomass zone over the growing season.

[18] In some cases sap flux density varies considerably with sapwood depth [Granier *et al.*, 1994; Schäfer *et al.*, 2000; Ewers *et al.*, 2002; Ford *et al.*, 2004], and often declines from the outer 20 mm of sapwood (i.e., the length of our sap flux probes). To address this problem, we performed a sensitivity analysis of the potential decline in J_s relative to sapwood depth. First, we assumed that sap flux density remained uniform with depth as shown with some other diffuse porous species [Lamb and Muller, 2002]. Then we reduced J_s in the region of sapwood not covered by our probes by 50% and 100%. Changes in transpiration due to potential declines in J_s were determined for different diameter classes in all tree populations. This allowed us to apply a sensitivity analysis of canopy ET at the watershed scale.

2.6. Statistical Analysis

[19] Regression analysis was performed to relate J_s of each species, gender and location to vpd and Q . Gender and microsite differences were analyzed using analysis of covariance (ANCOVA). JMP 5.1 (SAS Institute Inc, Cary, North Carolina) was used for all statistical analysis, with $P \leq 0.05$ as the significance level.

3. Results

3.1. Predawn Xylem Water Potential Measurements

[20] Predawn xylem water potential (Ψ_{pd}) measured in mid-July was about $-0.5 (\pm 0.0)$ MPa in both streamside and nonstreamside *A. negundo* populations. In early September, mean Ψ_{pd} in streamside trees was $-0.7 (\pm 0.0)$ MPa, while mean Ψ_{pd} in nonstreamside trees dropped to $-0.9 (\pm 0.0)$ MPa. There were no differences detected between genders in either streamside or nonstreamside populations in either July or September. Mean midday xylem water potentials (Ψ_{md}) in mid-July were about $-2.0 (\pm 0.1)$ MPa in all *A. negundo* populations. In September, mean Ψ_{md} was slightly higher in streamside populations (-2.1 ± 0.1 MPa) than nonstreamside populations (-2.2 ± 0.1 MPa). Again there were no differences between genders at either microsite. At the upper site, mean Ψ_{pd} ranged from -0.3 to -0.4 MPa for all species in July, and ranged from -0.5 to -0.6 MPa in all species in September. Midday leaf water potential in July ranged from $-1.5 (\pm 0.1)$ MPa for *B. occidentalis* to $-1.8 (\pm 0.3)$ MPa for *A. grandidentatum*. In September, Ψ_{md} ranged from $-1.5 (\pm 0.1)$ MPa for *P. angustifolia* to $2.3 (\pm 0.2)$ MPa for *A. grandidentatum*.

3.2. Sap Flux Density

[21] The relationship between J_s and vpd_z for all *A. negundo* populations is shown in Figure 2, and for other

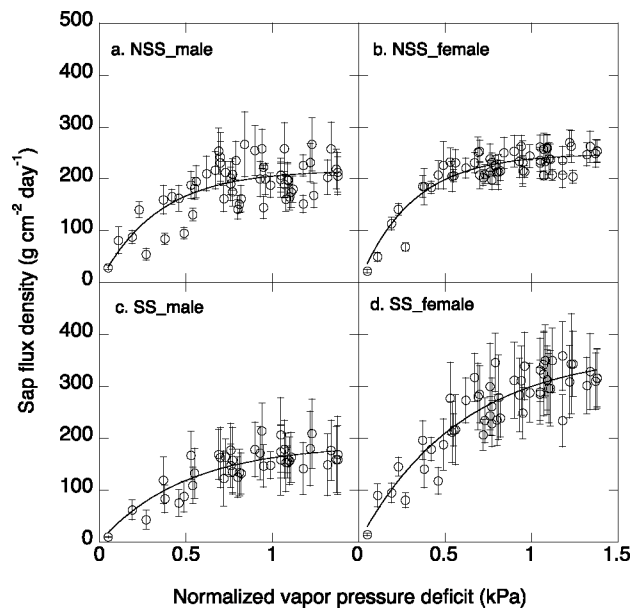


Figure 2. Response of sap flux density (J_s) of mature *Acer negundo* trees to mean daytime vapor pressure deficit, normalized for day length (vpd_z) during the 2004 growing season at Red Butte Canyon near Salt Lake City Utah. (a) Nonstreamside (>1 m from channel) male trees, (b) nonstreamside female trees, (c) streamside (≤ 1 m from channel) male trees, and (d) streamside female trees. Error bars represent ± 1 standard error of the mean. Regression equations are presented in Table 1.

dominant riparian tree species in Figure 3. The relationship between J_s and vpd_z measured was nonlinear in all populations. Thus data were fitted with an exponential saturation model,

$$J_s = b_1(1 - e^{-b_2 vpd_z}), \quad (4)$$

where b_1 and b_2 are fitting parameters. The model explained between 55% (*B. occidentalis*) to 86% (*A. negundo*, nonstreamside, female) of the variability in J_s (Table 1). Model coefficients, presented in Table 1, were therefore used to scale sap flux to stand transpiration (see below). Female *A. negundo* trees occurring along streamside microsites had a noticeably higher sap flux density relative to all other *A. negundo* populations or other riparian tree species (compare Figure 2d with all other plots in Figures 2 and 3). Conversely, male *A. negundo* trees along stream margins had lower fluxes than other *A. negundo* populations, but were similar to both *A. grandidentatum*, and *P. angustifolia* (compare Figure 2c with all other plots in Figures 2 and 3). *B. occidentalis* showed the lowest fluxes of all the populations investigated (Figure 3c). There were no relationships J_s and tree size or azimuth direction in any of the populations we studied.

[22] Differences in the response of J_s to climate drivers vpd_z and Q among *A. negundo* populations were tested using analysis of covariance. Sap flux density was highly correlated with vpd_z in streamside, nonstreamside, and within all populations, which was not surprising given the strong relationship between J_s and vpd_z within individual

populations (see Table 2). There was no relationship between J_s and Q in streamside trees, although there was a fairly robust relationship between J_s and Q in nonstreamside populations and among all *A. negundo* populations (Table 2). The interaction between vpd_z and Q had no effect on J_s among streamside, nonstreamside, and among all populations of *A. negundo*.

[23] There were significant gender differences in the response of J_s to the model parameters in both streamside and nonstreamside populations (Table 2). Differences were particularly strong in streamside populations ($F = 176.0$, $P < 0.0001$), and are clearly visible when Figure 2c is compared with Figure 2d. Representative diurnal patterns of vpd , Q and J_s of male and female streamside *A. negundo* trees are shown in Figure 4. Mean J_s was significantly higher in females than in males throughout daylight hours (Figure 4b), particularly on days where vpd remained relatively high throughout the day, such as on August 16 (day one in Figure 4). Mean J_s over the course of the

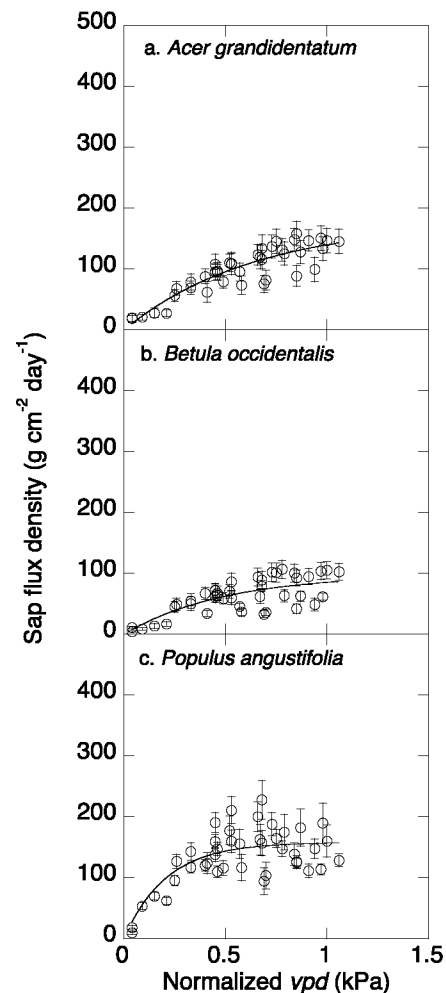


Figure 3. Response of sap flux density (J_s) of dominant riparian tree species to mean daytime vapor pressure deficit, normalized for day length (vpd_z) during the 2004 growing season at Red Butte Canyon near Salt Lake City, Utah. (a) *Acer grandidentatum*, (b) *Betula occidentalis*, and (c) *Populus angustifolia* trees. Error bars represent ± 1 standard error of the mean. Regression equations are presented in Table 1.

Table 1. Regression Coefficients of Sap Flux Density Against Mean Daytime Vapor Pressure Deficit, Normalized for Day Length (vpd_z) for Mature Male and Female *Acer negundo* Trees and Other Dominant Riparian Tree Species Occurring in Red Butte Canyon Near Salt Lake City, Utah^a

Species	b_1	b_2	F	P	R^2
<i>Acer negundo</i>					
NSS_male	216.7	2.945	85.3	<0.0001	0.60
NSS_female	248.5	3.220	347.5	<0.0001	0.86
SS_male	187.5	1.998	68.7	<0.0001	0.62
SS_female	367.9	1.685	230.5	<0.0001	0.81
<i>Acer grandidentatum</i>	177.9	1.545	161.0	<0.0001	0.80
<i>Betula occidentalis</i>	98.6	2.020	49.6	<0.0001	0.55
<i>Populus angustifolia</i>	158.2	4.793	55.2	<0.0001	0.58

^aSap flux density is J_s , in $\text{g cm}^{-2} \text{d}^{-1}$. Model: $J_s = b_1(1 - \exp^{-b_2vpdz})$.

growing season was on average 76% higher in streamside females than in streamside males. Differences in J_s between male and female trees were subtle in nonstreamside populations (compare Figure 2a with Figure 2b), but were 19% higher in nonstreamside females than in nonstreamside males ($F = 36.1$, $P < 0.0001$). When all *A. negundo* populations were compared, females showed a 41% higher J_s over the growing season, and these differences were highly significant ($F = 92.9$, $P < 0.0001$, Table 2).

3.3. Sap-Flux-Scaled Transpiration

[24] The gender and species specific mean daily evapotranspiration of the Red Butte Canyon riparian area was determined by combining measurements of sap flux density with estimates of total sap wood area (A_s) of each gender and species that dominate the riparian area. In order to estimate total A_s , relationships between diameter and A_s derived from stem cross sections were applied from Table 3, which showed strong correlations for all populations. We used gender/location specific $A_s:D$ relationships for *A. negundo*, although relationships did not vary among populations ($F = 0.4$, $P = 0.73$). Nearly 50% of the sapwood area, and sapwood area to ground area ($A_s:A_g$) of the riparian zone was from *A. grandidentatum*, while almost all the remaining A_s was from male and female *A. negundo* and *B. occidentalis* (Table 4). Conversely, *A. grandidentatum* only contributed about 7% of the 60 m^2 of A_s along the stream margins, while *B. occidentalis*, and male and female *A. negundo* trees contributed 34, 31, and 28% respectively (Table 4).

Table 2. Analysis of Covariance (ANCOVA) of Sap Flux Density (J_s) Against Mean Daytime Vapor Pressure Deficit, Normalized for Day Length (vpd_z), Total Daytime Photosynthetic Active Radiation (Q), Gender, and Location for Mature *Acer negundo* Trees Occurring in Red Butte Canyon Near Salt Lake City, Utah^a

	Nonstreamside	Streamside	All Populations
vpd	<0.0001	<0.0001	<0.0001
Q	0.0079	0.58	0.0263
$vpd*Q$	0.46	0.41	0.92
Gender	<0.0001	<0.0001	
Gender*location			<0.0001

^aModel: $b_1(1 - e^{-b_2vpdz}) + \log Q + [b_1(1 - e^{-b_2vpdz}) * \log Q]$.

[25] Dominant riparian vegetation in Red Butte Canyon transpired an estimated 80,820 m^3 of water during the 2004 growing season, of which 65,734 m^3 was transpired by nonstreamside vegetation, and 15,086 m^3 was transpired by streamside vegetation. Evapotranspiration contributed by streamside vegetation was small because only 5% of the total riparian vegetation occurred within 1 m of the stream channel. However, ET per unit ground area was much higher along the stream channel than in the remaining riparian area (8.0 mm d^{-1} versus 1.7 mm d^{-1}), or compared to the total riparian area where ET was 2.0 mm d^{-1} .

[26] Given its large proportion of A_s , it is not surprising that 44% of canopy ET in the riparian area and 52% of canopy ET in the nonstreamside area derived from *A. grandidentatum* trees (Figure 5). Female *A. negundo* trees contributed 24 and 19% in riparian and nonstreamside areas, respectively, followed by male *A. negundo* (21 and 19%, respectively), *B. occidentalis* (10 and 8%, respectively), and *P. angustifolia* (1 and 2%, respectively). Along stream margins, female *A. negundo* trees contributed 48% of canopy ET compared to 30 and 16% from male *A. negundo* and *B. occidentalis* respectively (Figure 5c).

[27] The relationship between population level ET and vpd is shown for the total riparian area and streamside populations in Figure 6. When vpd reached 3.5 (not uncommon for RBC), riparian area ET reached 1.1 mm d^{-1} in *A. grandidentatum*.

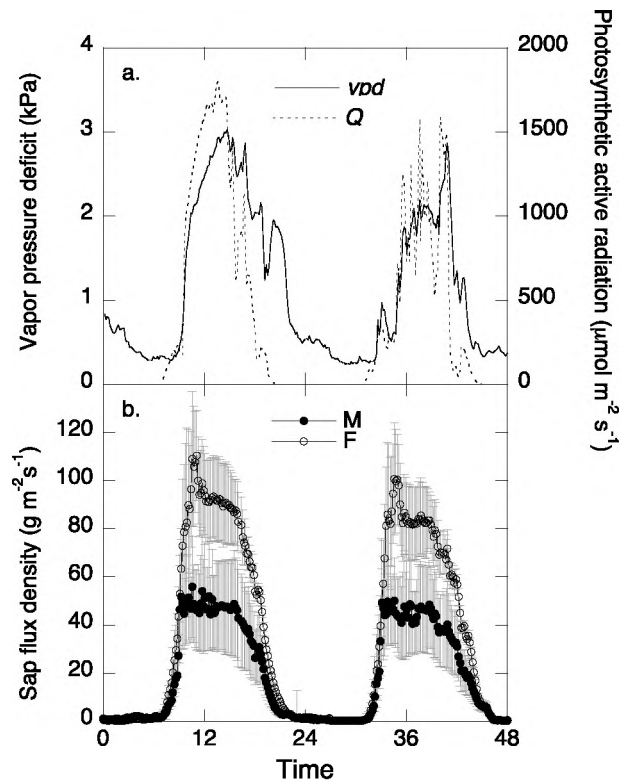


Figure 4. Daily patterns of vapor pressure deficit (vpd), photosynthetic active radiation (Q), and sap flux density (J_s) for mature *Acer negundo* trees on 16 and 17 August 2004 in Red Butte Canyon near Salt Lake City, Utah: (a) vpd (kPa) and Q ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and (b) J_s of streamside (≤ 1 m from channel) male and female trees. Error bars represent ± 1 standard error of the mean.

Table 3. Regression Coefficients for Predictions of Cross-Sectional Sapwood Depth (L_s , cm), and Cross-Sectional Sapwood Area (A_s , cm²) Generated From Tree Diameters (D) Measured 1.5 m Above the Ground, With Sample Size (n) and the Range of Diameters Measured^a

Spp.	D , cm	Sapwood Depth (L_s)			Sapwood Area (A_s)			n
		b_1	b_2	R^2	b_1	b_2	R^2	
<i>Acer negundo</i>								
NSS_male	7.2–37.8	0.828	0.529	0.58	1.232	1.650	0.96	9
NSS_female	6.1–26.9	0.664	0.605	0.51	0.992	1.724	0.96	10
SS_male	6.7–47.0	1.259	0.379	0.10	1.551	1.532	0.76	9
SS_female	5.9–43.5	0.504	0.711	0.53	0.843	1.785	0.94	10
<i>Acer grandidentatum</i>	6.9–29.4	0.986	0.539	0.45	0.997	1.789	0.95	10
<i>Betula occidentalis</i>	4.1–14.1	0.531	0.921	0.96	0.589	2.071	0.99	9
<i>Populus angustifolia</i>	10.5–24.9	0.405	0.886	0.62	0.616	1.988	0.96	10

^aModel: $b_1 * D^{b_2}$.

dentatum, 0.6 mm d⁻¹ for female *A. negundo*, 0.5 mm d⁻¹ for male *A. negundo* and 0.2 mm d⁻¹ from *B. occidentalis* (Figure 6a). Conversely, ET along stream margins was dominated by female *A. negundo*, where maximum ET reached 4.6 mm d⁻¹, followed by male *A. negundo* at 2.6 mm d⁻¹, *B. occidentalis* at 1.5 mm d⁻¹, and *A. grandidentatum* at 0.6 mm d⁻¹ (Figure 6b). *P. angustifolia* is not shown because ET flux was negligible compared to the other populations.

[28] A sensitivity analysis was performed to test for errors in sap-flux-scaled transpiration caused by radial variation in J_s . If we assume that J_s remains constant throughout the radial profile, then differences in transpiration between streamside male and female *A. negundo* increase with tree size. At a mean daytime v_{pd} of 2.0 MPa, a 7.5 cm diameter streamside female tree transpires about 60% more water than a streamside male of the same diameter, while at 45 cm, a streamside female transpires 140% more than a streamside male (Figure 7a). The size-related differences are not caused by size-related changes in J_s , but differences in sapwood depth, and subsequent sapwood area. For example, sapwood depth calculated from the coefficients shown in Table 3 is 53 and 75 mm in 45 cm diameter streamside male and female trees, respectively. If we assume that there is a radial decline in J_s of 50% and 100% from the outer 20 mm to the sapwood:heartwood transition, then differences in transpiration between 45 cm male and female streamside trees decreases to 2.3 and 1.8 times, respectively (Figures 7b and 7c). Differences between nonstreamside male and female trees remain fairly constant regardless of tree size (Figure 7).

[29] Radial declines in sap flux would have a moderate impact on sap-flux-scaled transpiration of the watershed. Predicted sapwood area from the outer 20 mm to the sapwood:heartwood transition at mean stem diameter (Table 4) would encompass 18 to 30% of the total sapwood area of all populations except for *P. angustifolia*, where 72% of its sapwood is beyond the outer 20 mm. Consequently, a 50% decline in J_s in the inner portion of sapwood would reduce streamside ET from 8.0 to 6.9 mm d⁻¹ and total riparian area ET from 2.0 to 1.8 mm d⁻¹. A 100% decline in J_s would reduce streamside and riparian area ET to 5.9 and 1.3 mm d⁻¹, respectively. The proportion of ET contributed by each gender and species would remain essentially unchanged if all species experienced a 50 or 100% decline in J_s .

4. Discussion

[30] The genders of *Acer negundo* displayed large and significant differences in sap flux density and sap-flux-scaled evapotranspiration. Females maintained substantially higher sap flux density and evapotranspiration in streamside locations, and somewhat higher J_s and ET in nonstreamside locations compared to males. Consistent with our results, Dawson and Ehleringer [1993] found that male *A. negundo* trees growing in both wet habitats along streamsides, and along dry habitats away from streamsides displayed lower leaf gas exchange rates, suggesting that the genders of *A. negundo* have adapted disparate physiological constraints over water uptake. From the current investigation, we conclude that physiological differences between genders

Table 4. Mean Tree Diameter (D) at 1.5 m Above the Ground, Mean Modeled Sapwood Depth (L_s), and Cross-Sectional Sapwood Area to Ground Area ($A_s:A_g$) of Dominant Riparian Tree Species in Red Butte Canyon Near Salt Lake City, Utah^a

Spp.	Streamside (≤ 1 m From Channel)				Total Riparian Area			
	Mean D , cm	Mean L_s , cm ²	A_s , m ²	$A_s:A_g$, m ² :m ²	Mean D , cm	Mean L_s , cm ²	A_s , m ²	$A_s:A_g$, m ² :m ²
<i>Acer negundo</i> male	12.6 (1.0)	3.29	18.8	$1.4 * 10^{-3}$	12.0 (0.4)	3.08	59.1	$2.2 * 10^{-4}$
<i>Acer negundo</i> female	13.2 (1.0)	3.16	16.7	$1.3 * 10^{-3}$	13.6 (0.5)	3.22	52.1	$1.9 * 10^{-4}$
<i>Acer grandidentatum</i>	10.9 (1.1)	3.58	4.4	$3.3 * 10^{-4}$	8.9 (0.2)	3.21	161.7	$6.0 * 10^{-4}$
<i>Betula occidentalis</i>	7.5 (0.3)	3.40	20.1	$1.5 * 10^{-3}$	7.4 (0.2)	3.36	60.9	$2.3 * 10^{-4}$
<i>Populus angustifolia</i>	11.2 (2.6)	3.46	0.1	$5.6 * 10^{-5}$	34.2 (4.4)	9.36	6.0	$2.2 * 10^{-5}$
Total	9.8 (0.3)	3.50	60.0	$4.5 * 10^{-3}$	9.8 (0.2)	3.33	339.7	$1.3 * 10^{-3}$

^aNumbers in parentheses are ± 1 standard error of the mean.

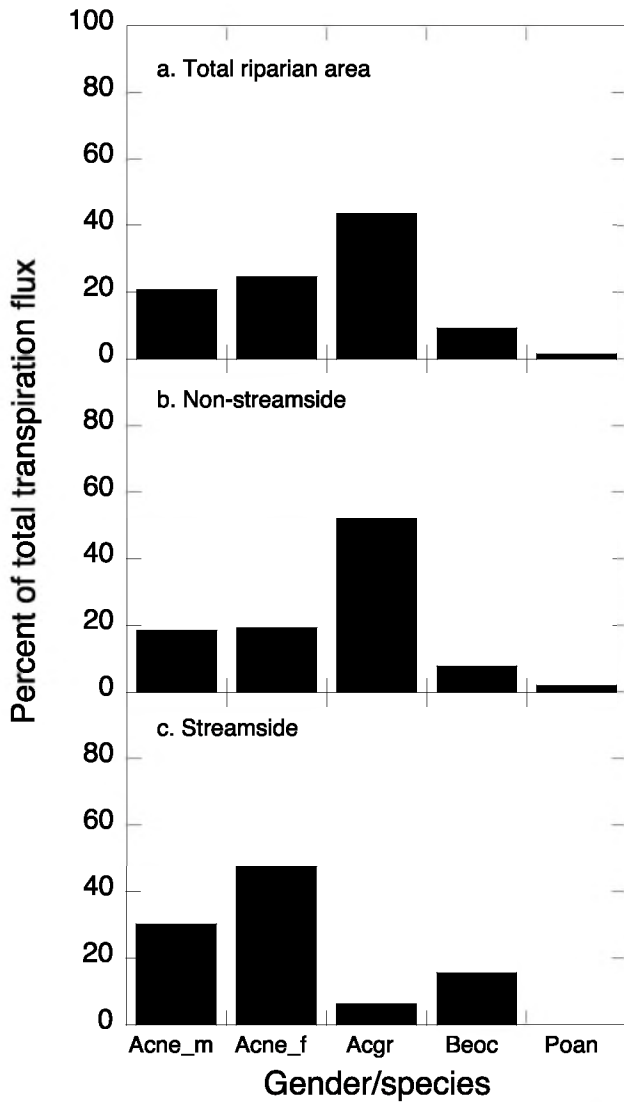


Figure 5. Percent of daily evapotranspiration (mm d^{-1}) of dominant riparian vegetation in Red Butte Canyon during the 2004 growing season. Species include male and female *Acer negundo* (*Acne_m*, and *Acne_f*, respectively), *Acer grandidentatum*, (*Acgr*), *Betula occidentalis* (*Beoc*), and *Populus angustifolia* (*Poan*). (a) Percent mean daily ET of the total riparian area, (b) percent mean daily ET of nonstreamside vegetation ($>1\text{ m}$ from channel), and (c) percent mean daily ET of trees of streamside vegetation ($\leq 1\text{ m}$ from channel).

in leaf-level water use patterns scale to the whole plant, and translate into differences in landscape level water fluxes.

4.1. Sap Flux and ET Scaling

[31] Female *A. negundo* trees occur more frequently along streamsid es than do male trees [Dawson and Ehleringer, 1993; Ward et al., 2002], to the extent that only 40% of all streamside *A. negundo* trees in Utah are male [Ward et al., 2002]. The observed sex ratio bias magnifies the differential contribution of male and female *A. negundo* to streamside ET at the landscape scale. Given that sap flux density is 76% higher in streamside female versus streamside male

trees, and that 60% of all *A. negundo* trees are female, male trees can be expected to contribute only 28% of the total ET flux generated from streamside *A. negundo*, depending on the size distribution of both genders. Spatial segregation of the genders along streamside habitats likely reflects the more conservative water use and slower growth in males [Dawson and Ehleringer, 1993]. Females therefore are likely to out compete males along perennial stream channels where water availability is relatively stable, resulting in a greater total ET flux from streamside canopy vegetation.

[32] Streamside female *A. negundo* trees demonstrated significantly higher maximum sap flux densities than all the other midelevation riparian species we studied including *A. grandidentatum*, *B. occidentalis*, and *P. angustifolia*. Females also had higher maximum fluxes than many tree species that dominate low-elevation riparian zones in western North America including *Salix goodingii* [Schaefer et al., 2000], *Salix exigua* (K. R. Hultine, unpublished data, 2004), and *Eleagnus angustifolia* (S. E. Bush, unpublished data, 2004), while having similar fluxes to *Populus fremontii* [Schaefer et al., 2000; Pataki et al., 2005]. These data suggest that the distribution of male and female *A. negundo* trees relative to other woody species has potential ecohy-

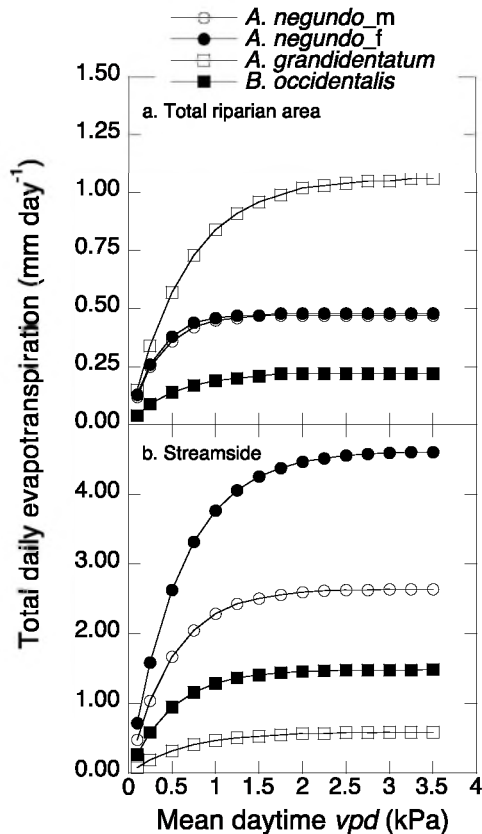


Figure 6. Modeled daily evapotranspiration (ET) of mature male and female *Acer negundo*, *Acer grandidentatum*, and *Betula occidentalis* trees, and of all trees in response to mean daily vapor pressure deficit (*vpd*) during the 2004 growing season at Red Butte Canyon, near Salt Lake City, Utah. (a) Mean daily ET of total riparian area and (b) mean daily ET of streamside vegetation ($\leq 1\text{ m}$ from channel).

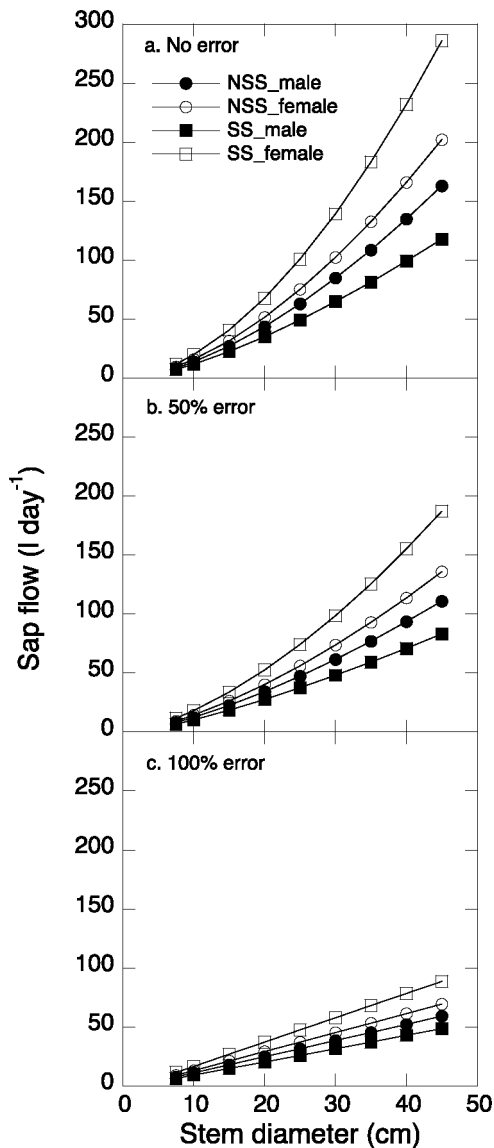


Figure 7. Potential error in sap-flux-scaled transpiration of male and female *A. negundo* trees of various stem diameters at a mean daily vapor pressure deficit (v_{pd}) of 2 kPa. (a) Transpiration if sap flux density (J_s) between 20 mm (length of sap flux probes) and sapwood:heartwood transition remains constant. (b) Transpiration if J_s between 20 mm and sapwood:heartwood transition declines by 50%. (c) Transpiration if J_s between 20 mm and sapwood:heartwood transition declines by 100%.

drological consequences such as evapotranspiration, streamflow, and biogeochemical cycling.

[33] In nonstreamside habitats, normalized sap flux density during the 2004 growing season was 19% higher in female than in male *A. negundo* trees, and the difference in sap flux was significant. However, because 62% of all nonstreamside *A. negundo* trees throughout Utah are male [Ward et al., 2002], an estimated 58% of *A. negundo* ET at the landscape scale was by males (assuming that the size distribution is similar between genders). The proportion of water that is transpired by each gender in nonstreamside

habitats may vary considerably within and among years owing to severe fluctuations in interannual and intra-annual soil water availability. For example, years with above average precipitation apparently increase the water yield from females relative to males [Ward et al., 2002; Dawson et al., 2004]. On the other hand, periodic drought that is common in the arid western United States may produce not only lower ET rates by females, but enhance the rate of drought-induced mortality compared to males, demonstrated by the male biased gender ratios observed in nonstreamside habitats [Dawson and Ehleringer, 1993; Ward et al., 2002; Hultine et al., 2007]. In the present study, slightly above average precipitation fell before and during the 2004 growing season, producing favorable soil moisture conditions throughout the growing season. In fact, predawn leaf water potentials (assumed to approximate soil water potential of the rhizosphere) were similar between streamside and nonstreamside trees in mid-July, and were only slightly lower in early September, suggesting that nonstreamside trees were never exposed to severe soil water deficits throughout the growing season. The slightly higher sap flux rates in female trees in nonstreamside microsites were likely facilitated by the favorable soil water conditions. More work is needed however, to better gauge how each gender responds to year-to-year fluctuations in soil moisture in terms of water balance, growth, and survival.

[34] Generally there is some degree of radial variation in sap flux density that sometimes leads to large errors when scaling sap flux measurements to whole plant or ecosystem ET. Errors can be extreme in cases where the depth of conducting sapwood is substantially greater than the length of the sap flux probe. For example, Granier sensors similar to those used in the present study yielded a 67% mean error in sap flux when measured on trees that had a radial mean sapwood depth six times greater than the length of the sap flux sensors [Ford et al., 2004]. In the present study, modeled sapwood depth at mean diameter of each gender/species was only 1.5 to 2 times greater than the length of our sap flux sensors, leaving between 18 and 30% of the total sapwood unaccounted for in our measurements of J_s . If sap flux ceased entirely beyond 20 mm (not likely), error in our transpiration estimates would have been between 18 and 30%, with the exception was *P. angustifolia* where sapwood depth extended more than 4.5 times beyond the length of our sensors leaving 72% of the sapwood area unmeasured. However, *P. angustifolia* only accounted for 6% of the total sapwood area in the study.

[35] Because sapwood depth was positively correlated with stem diameter, potential error in sap flux scaling increased with stem diameter. This is particularly important when comparing streamside male and female *A. negundo* because large female trees had thicker sapwood than males. Therefore some caution should be taken when scaling the absolute differences in transpiration between genders of the same size.

[36] In general growth and productivity is proportional to water transport through plants [Enquist, 2002]. Results from the present study, and previous studies suggest that female plants have higher rates of growth and productivity than males in wet streamside habitats and during wet years in dry nonstreamside habitats. In a separate study, streamside female *A. negundo* had up to 71% more leaf area and

100% greater gross carbon uptake per unit stem diameter than cooccurring streamside males (K.R. Hultine, unpublished). In a common garden study, radial growth in female *A. negundo* trees was 35% higher relative to male *A. negundo* trees during wet years [Ward et al., 2002]. Moreover, the resource cost of reproduction is 4 to 6 times greater in female compared to male *A. negundo* [Dawson and Ehleringer, 1993]. Therefore large offsets in transpiration between genders likely reflect combined differences in leaf area, radial growth rates and reproductive costs in female versus male trees. Differences in growth rate may play a key role in the population structure of streamside microsites where survival in these highly productive habitats depends, in part, on light capture. Fast growing plants, such as female *A. negundo* are capable of out competing slower growing plants such as male *A. negundo* for sunlight, resulting in a canopy dominated by female trees. Moreover, if we assume that growth is in fact, proportional to water transport, then it is not surprising that *A. negundo* dominates midelevation riparian zones throughout much of North America, given its much higher water yield relative to all other dominant riparian species we investigated.

[37] Alterations in the water cycle due to changes in climate and/or land use change could have considerable consequences on the population structure of *A. negundo* throughout the arid west [Dawson and Ehleringer, 1993; Ward et al., 2002; Dawson et al., 2004]. For example, enhanced interannual and intra-annual variability coupled with warmer temperatures [Intergovernmental Panel on Climate Change, 2001] is expected to reduce snow pack, and subsequent streamflow in the western United States over the coming decades [Mote et al., 2005]. Streamflow reductions will decrease recharge into adjacent soils and shallow aquifers, and reduce the amount of water available for plant uptake of some riparian systems and microhabitats [Stromberg, 1993; Patten, 1998; Weltzin et al., 2003]. Such changes may have a nonlinear consequence on the success of male and female *A. negundo*, given that males are apparently less sensitive to water limitations. Likewise, anthropogenic stream diversions that inhibit episodic flooding and groundwater pumping may disproportionately impact female *A. negundo* trees owing to their susceptibility to drought-induced mortality relative to males [Dawson and Ehleringer, 1993]. At this time it is difficult to predict how the complex interaction between climate and land use change will impact population structure of *A. negundo* trees. Nevertheless, it is apparent that changes in population structure will have important consequences on hydrologic cycling and functioning of riparian and stream communities throughout the arid west.

4.2. Dioecy Impacts on Ecohydrology

[38] Woody vegetation along stream margins alters both surface and subsurface streamflow generation through transpiration [Bosch and Hewlett, 1982; Calder, 1990; Zhang et al., 2001; Huxman et al., 2005]. In the present study, streamside riparian trees during July and August in Red Butte Canyon removed about 260 cubic meters of water per day. Over the same period, stream discharge measured at the mouth of Red Butte Canyon from a USGS gauging station, declined diurnally by about 235 cubic meters per day: about 8% of total discharge. Whether transpiration of streamside

trees had a direct impact on stream discharge is an open question. Diurnal declines in stream flow are often due to diurnal changes in stream and streambed temperatures. In some cases afternoon increases in stream temperature and subsequent increases in streambed hydraulic conductivity could lead to large increases of infiltration and groundwater recharge [Constantz et al., 1994; Hatch et al., 2006]. For example, where streams experience diurnal temperature fluctuations of up to 25°C, groundwater recharge accounts for up to 95% of the total diurnal decline in stream discharge [Constantz et al., 1994]. However, diurnal stream temperature fluctuations of Red Butte Canyon rarely exceed 5°C during the growing season (USGS National Water Information System: <http://waterdata.usgs.gov>). Therefore it is plausible that a major component of diurnal stream flow losses in Red Butte Canyon are due to near-channel ET. If so, a potential consequence of female biased gender ratios is a reduction in stream discharge via the high transpiration rates in streamside female versus streamside male *A. negundo* trees and all other dominant riparian tree species.

[39] Regardless of whether riparian vegetation has direct impacts on stream discharge, the population structure of *A. negundo* has potential indirect consequences on ecohydrology via impacts on biogeochemical cycling. Females, because of their relatively high resource uptake and subsequent growth, add relatively large quantities of plant litter to the soil. The quantity of plant litter returning to the soil has a large impact on the composition of soil carbon and nitrogen pools that control N mineralization rates [Schulze et al., 1991; Martens, 2000]. An abundance of highly decomposable litter and soil organic matter should also set the stage for very high ecosystem respiration fluxes along streamside habitats. Moreover, the population structure of *A. negundo* trees along streamsides may have potentially important ramifications on nutrient and organic carbon fluxes into stream ecosystems, which in turn impacts stream biogeochemistry [Dodds et al., 2004].

5. Conclusions and Implications

[40] Results from this investigation show clear and significant differences in the pattern of water use between genders of *A. negundo*. Although caution must be taken when scaling sap flux measurements from a relatively small population of trees to the watershed level, it is apparent that the genders impact ecosystem water fluxes and biogeochemical cycling quite differently. How the population structure of *A. negundo* and subsequent water balance of riparian ecosystems will respond to global change is an open question. However, establishing a link between eco-physiology and population biology is imperative in order to predict outcomes of large-scale population structure, and its consequence on water, carbon, and nutrient cycling in response to global change scenarios. Current and future work will focus on the physiological parameters that underpin the disparate water use patterns between genders including, xylem anatomy and function, whole plant leaf area sapwood area ratios, and canopy conductance. Patterns of gender-specific water use in *A. negundo* may reflect larger-scale patterns of gender effect on ET fluxes in western North American riparian systems given that other dominant riparian tree species are also dioecious including

Populus and *Salix* spp. Therefore characterizing species assemblages alone may not be adequate for developing fine-scale relationships between riparian ecosystem function with population structure.

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