Gender-specific patterns of aboveground allocation, canopy conductance and water use in a dominant riparian tree species: *Acer negundo*

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Summary *Acer negundo* Sarg. (box elder) is a dioecious tree species that dominates riparian systems at mid elevations throughout the southwest and Intermountain West of the United States. Previous studies have shown that female *A. negundo* trees occur at higher frequencies along stream margins, whereas males occur at higher frequencies in drier microsites. To better understand the adaptive significance of sex ratio biases and their impact on the ecohydrology of riparian ecosystems, we examined whole-plant water relations and hydraulic properties of mature male and female *A. negundo* trees occurring within 1 m of a perennial stream channel. We hypothesized that (1) females would have significantly greater canopy water fluxes than males (particularly during periods of seed production: May–June), and (2) xylem in females is more hydraulically efficient but more vulnerable to cavitation than xylem in males. Mean sap flux density (J_s) during the early growing season (May and June) was 43% higher in female trees than in male trees ($n = 6$ and 7 trees respectively, $P < 0.0001$). Mean J_s in July and August remained 17% higher in females than in males ($P = 0.0009$). Mean canopy stomatal conductance per unit leaf area ($g_{s,leaf}$) in May and June was on average 140% higher in females than in males ($P < 0.0001$). Mean $g_{s,leaf}$ in July and August remained 69% higher in female trees than in male trees ($P < 0.0001$). Canopy stomatal conductance scaled to basal area was 90 and 31% higher in females relative to males during May–June and July–August, respectively ($P < 0.0001$ during both periods). Conversely, there were no apparent differences in either branch hydraulic conductance or branch xylem cavitation vulnerability between genders. These results improve our capacity to describe the adaptive forces that shape the spatial distribution of male and female trees in dioecious species, and their consequences for ecohydrological processes in riparian ecosystems.

Keywords: dioecy, hydraulic architecture, sap flux, xylem cavitation.

Introduction

Theory suggests that the sexes of dioecious plants have evolved specialized traits to maximize growth, survival and reproduction of each gender. Several studies have demonstrated that divergent physiological traits between genders are consistent with differences in habitat preference that arise so that each sex can meet different resource requirements (Freeman et al. 1976, 1980, Bierzychudek and Eckhart 1988, Dawson and Bliss 1989, Dawson and Ehleringer 1993, Ward et al. 2002). Females have a higher resource requirement for reproduction than males across many dioecious taxa, and therefore often specialize in high resource habitats. In water-limited environments, for example, female plants typically occur in higher densities than males in wet microsites thereby maximizing carbon gain and minimizing drought stress (Dawson and Bliss 1989, Dawson and Ehleringer 1993). Sex ratios tend to be male biased in less favorable habitats, likely because of greater female mortality (Bierzychudek and Eckhart 1988, Dawson and Ehleringer 1993).

The occurrence of sex ratio biases by habitat in dioecious plants implies that sexes display strong morphological and physiological adaptations to environmental gradients. Unfortunately, there is limited information on the occurrence of sexual dimorphism among most dioecious species, including those that display sex ratio biases. One exception is the dominant North American riparian tree species *Acer negundo* Sarg. (box elder). In the Intermountain West of the United States, *A. negundo* exhibits a strong sex ratio bias along soil water gradients, with the ratio of male to female individuals averaging about 1.6 away from stream margins versus 0.7 near stream margins (Dawson and Ehleringer 1993, Ward et al. 2002). At the leaf level, *A. negundo* is sexually divergent in ways that are consistent with the observed patterns of habitat preference. Male *A. negundo* trees are consistently more conservative in their water use compared with female trees (Dawson and Ehleringer 1993, Dawson et al. 2004). Females are apparently

less likely than males to close their stomata even when they experience lowered leaf water potentials. As a result, leaf-level photosynthesis and transpiration are typically lower in males than in females, whereas the ratio of assimilation to transpiration (i.e., water-use efficiency) is substantially higher in males than in females. Divergent patterns of leaf-level physiology may be strongest in wet habitats where females apparently could maintain a competitive carbon-balance advantage over co-occurring males. At the whole-plant level, however, the physiological mechanisms that underlie the observed sex ratio patterns are not well understood.

Gender differences in leaf functional traits across water availability gradients may be associated with differences in xylem conductance. Plants may regulate the efficiency of xylem water transport through adjustments in xylem structure (Sperry and Tyree 1988, Hacke et al. 2000). Consequently, the higher the xylem transport efficiency the more water can flow to the canopy, and the greater the potential capacity for net carbon uptake. However, there may be a biophysical tradeoff between xylem transport efficiency and safety from cavitation and subsequent loss in canopy hydraulic conductance (Carlquist 1988, Tyree et al. 1994, Hacke et al. 2001, 2006). If so, the observed patterns of spatial segregation between the sexes of *A. negundo* may reflect differences in xylem function.

Alternatively, gender-specific water use patterns may be expressed through differences in hydraulic architecture, specifically the ratio of leaf area per unit conducting sapwood area or leaf area per unit absorbing root surface area. Plants that are adapted to wet environments generally have larger canopies and greater leaf area to sapwood area ratios (A_l:A_s) (Waring et al 1982, White et al. 1998) or lower absorbing root area to leaf area ratios (A_r:A_l) compared with plants adapted to more xeric environments (Sperry and Hacke 2002). Fast-growing plants with large sunlit canopies have a competitive advantage in productive habitats, such as along stream margins, where sunlight becomes limiting for plant growth and survival. Female *A. negundo* trees occurring along stream margins have more expansive canopies than co-occurring males (Dawson et al 1993, Ward et al. 2002). However, it is unclear whether gender differences in leaf-level traits and canopy structure translate into differences in aboveground hydraulic architecture and whole-plant water use that may result in gender differences in productivity and habitat dominance.

We measured stem sap flux, canopy conductance, branch xylem function and aboveground architecture of mature male and female *A. negundo* trees occurring in northern Utah, USA. We focused on trees that occurred in high resource locations, within 1 m of a perennial stream channel, so that plant water availability remained seasonally stable. Our goal was to characterize seasonal patterns of whole-plant water fluxes along streamside habitats to gain further insight into the adaptive significance of sexual dimorphism in dominant riparian vegetation. We hypothesized that females express greater whole-plant water use and contain xylem or hydraulic architecture, or both that is more efficient in water transport than males. If so, changes in the population structure of dioecious riparian vege-

tation may have profound effects on watershed-scale carbon, water and nutrient cycling.

Materials and methods

Site description

Research was conducted during the 2005 growing season in Red Butte Canyon Research Natural Area, east of Salt Lake City, Utah, USA. The Red Butte Canyon drainage covers an area of about 20.8 km^2, and contains a well-defined riparian area that has a free-flowing perennial stream. 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. Our field site was established in a 4.3 ha meadow in Parley's Fork about 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 meadow contained 13 mature streamside (< 1 m from stream channel) *A. negundo* trees that were suitable for study: seven males with diameters ranging from 0.188 to 0.469 m, with a mean diameter of 0.258 m, and six female trees with diameters ranging from 0.177 to 0.429 m, with a mean diameter of 0.298 m. All the trees were dominant, with open canopies that received sunlight throughout the day. Leaf flush in these trees generally occurs in late April or early May and senescence usually begins in early September.

Meteorological measurements

Relative humidity, air temperature, photosynthetic active radiation, and wind speed and direction were measured continuously at Parley's Fork throughout the growing season. Relative humidity and air temperature were measured with a Vaisala HMP 45 AC humidity and temperature probe (Vaisala, Woburn, MA), placed about 2 m above the ground surface. Photosynthetic active radiation (Q) was measured with an LI-190SZ quantum sensor (Li-Cor, Lincoln, NE). Wind speed (u) and direction were measured with a Met One 034B-L wind set (Met One Instruments, Grants Pass, OR). Micrometeorological data were measured every 30 s and stored as 10-min means with a CR10X-2M data logger (Campbell Scientific, Logan, UT). Measurements of relative humidity and air temperature were used to calculate atmospheric vapor pressure deficit (D).

Leaf water potential measurements

Leaf water potential measurements were performed on trees that were instrumented with sap flux sensors. Leaf water potential was measured with a Scholander-type pressure cham-

ber (PMS Instruments, Corvallis, OR) in mid June, July and August before sap flux measurements ended. A single shoot tip from each of the six trees was cut with a sharp razor blade and water potential measured at predawn (Ψ_{pd}) between 0200 and 0400 h, and at midday (Ψ_{md}) between 1100 and 1300 h.

Sap flux, canopy conductance and leaf area measurements

Sap flux density (J_s; g H_2O m^{-2} sapwood s^{-1}) was measured with Granier-type sensors (Granier 1987, 1996). Each sensor consisted of a pair of 20-mm long, 2-mm diameter stainless steel probes inserted about 15 cm apart along the hydroactive xylem (i.e., sapwood). The upper probe 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). A single sensor was randomly placed axially in the main stem of each tree (seven male and six female trees) at about 1.5 m above ground. This sample size has been shown to result in a coefficient of variation of about 15% in previous studies of diffuse-porous species (Oren et al. 1999). Data were logged every 30 s and stored as 10 min means with a Campbell CR10X-2M data logger. Sap flux measurements were conducted during the 2005 growing season from May 28 to June 29 and from July 22 to August 28.

Daily sap flux density (kg m^{-2} day^{-1}) was calculated to evaluate the relationships between mean daytime D and mean daytime Q. Mean daytime D was normalized by day length: day length/24 h (D_z) to correct for the effect of day length on transpiration (Oren et al. 1999). Day length was defined as the period when Q was greater or equal to 10 μmol m^{-2} s^{-1}.

Whole-plant hydraulic conductance (g_t) was calculated by dividing J_s by the difference between Ψ_{pd} and Ψ_{md}. Here we assume that Ψ_{pd} is equal to soil water potential, although disequilibrium may occur between these variables (Donovan et al. 1999). In this case, g_t would be overestimated, but mean relative differences between genders would likely be unaffected.

Canopy conductance (g_c) was calculated from sap flux measurements by a simplified form of the Penman–Monteith equation (Monteith and Unsworth 1990):

$$g_c = \frac{\gamma \lambda}{\rho c_p D} \frac{J_s A_s}{A_l} \quad (1)$$

where γ is the psychrometric constant (kPa K^{-1}), λ is latent heat of vaporization (J kg^{-1}), ρ is density of moist air (kg m^{-3}) and c_p is the specific heat of air at constant pressure (J kg^{-1} K^{-1}). Sapwood area (A_s) was calculated for each tree by evaluating the relationship between sapwood area and basal area (A_b). Two cores were taken from each tree instrumented with sap flux sensors. Sapwood area was obtained by first determining the inside bark diameter, then determining the depth of hydroactive xylem of each core by its translucence, and then subtracting the sapwood area from the total stem cross-sectional area (i.e., basal area). Sapwood area to stem basal area relationships were determined with the power function:

$$A_s = b_1 (A_b)^{b_2} \quad (2)$$

where b_1 and b_2 are fitting parameters.

Leaf area (A_l) was estimated by finding an allometric relationship between A_l and branch diameter, and by measuring the diameter of all leaf-bearing branches extending from the main stem of each tree measured for J_s. Allometric relationships were calculated for each gender by collecting leaves from branches from other streamside *A. negundo* trees in Red Butte Canyon ranging in diameter from 20 to 150 mm; covering the range of branch diameters measured on the sap flux trees measured for J_s. Thirteen branches were collected per gender, the leaves were removed and specific leaf area (SLA; m^2 g^{-1}) was measured on a subset of leaves. Total one-sided leaf area per branch was estimated by multiplying SLA by the total mass of leaves from each branch. The relationship between A_l and branch diameter was determined with the power function given in Equation 2.

Relative seasonal changes in leaf area were estimated by measuring leaf area index (LAI) in June, July and August with a Li-Cor, LAI 2000 plant canopy analyzer. A single value of LAI was calculated by averaging the individual estimates of LAI at five points under the canopy of each tree.

To calculate g_c from measurements of J_s, A_s and A_l, two important assumptions must first be met. First, sap flux measured in the stem is equal to the rate of water leaving the canopy via transpiration. In other words, the depletion and replenishment of stem water storage is small. Second, conductance of leaf boundary layer (g_{bl}) is large relative to canopy stomatal conductance (g_s). To test the first assumption, lag times between J_s and D of 0–2 h were evaluated for each gender. The highest correlations were found between zero and 0.5 h, and we therefore assumed that stem capacitance had a negligible influence on the relationship between J_s and D. The second assumption, that g_{bl} is greater than g_s is not always true for broad-leaved canopies such as *A. negundo* (Meinzer et al. 1997). We therefore calculated g_{bl} to compare with calculated values of g_s (shown below) for both genders. Boundary layer conductance was calculated according to Jones (1992):

$$g_{bl} = 306.7 \sqrt{\frac{u_c}{d_l}} \quad (3)$$

where d_l is the characteristic leaf dimension (Jones 1992) and u_c is mean canopy wind speed. Mean u_c (m s^{-1}) was estimated from measurements of u recorded at 3 m above ground in an open meadow and by multiplying u_v by u, where u_v is the canopy frictional velocity (m s^{-1}). Canopy frictional velocity was solved according to Campbell and Norman (1998):

$$u_v = \frac{0.4u}{\ln\left(\dfrac{z-d}{z_m}\right)} \quad (4)$$

where z is the approximate canopy height, in this case 15 m,

d is the zero plane displacement (m), z_m is roughness length (m) (Campbell and Norman 1998) and 0.4 is the von Karman constant. Canopy stomatal conductance was calculated as:

$$\frac{1}{g_s} = \frac{1}{g_c} - \frac{1}{g_{bl}} \quad (5)$$

The sensitivity of transpiration to changes in g_{bl} was evaluated based on the dimensionless decoupling coefficient (Ω) described by Jarvis and McNaughton (1986) and later modified by Martin (1989) that takes radiative coupling between leaves and the atmosphere into account:

$$\Omega = \frac{\varepsilon + 2 + \dfrac{g_r}{g_{bl}}}{\varepsilon + 2 + \dfrac{g_{bl} + g_r}{g_s} + \dfrac{g_r}{g_{bl}}} \quad (6)$$

where ε is the change in latent heat to the change in sensible heat of saturated air and g_r is the long-wave radiative transfer conductance. By definition, Ω approaches its upper limit (1.0) as stomatal control over transpiration becomes progressively weaker.

In some cases, J_s 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 the heartwood:sapwood transition. To evaluate the potential importance of radial trends in sap flux on our estimates of canopy conductance, we performed a sensitivity analysis of the potential decline in J_s relative to sapwood depth. First, we assumed that J_s remained uniform with depth as shown with other diffuse-porous riparian species (Lambs and Muller 2002). Then we reduced J_s in the region of the sapwood not measured by our probes by 50 and 100%. Changes in transpiration associated with potential declines in J_s at mean sapwood depth were determined separately for male and female trees at our field site. This allowed us to apply a sensitivity analysis of g_c.

Xylem cavitation measurements and specific conductivities

Vulnerability curves were measured in six current-year branch segments per gender to quantify the response of hydraulic conductivity to negative xylem pressure. Segments, 70 to 100 cm in length, were collected from sun-exposed branches in July. Leaves from each segment were immediately removed and the segments and leaves were transported to the lab in a sealed plastic bag containing a moist paper towel to avoid desiccation. In the lab, all segments were recut under water and trimmed with a sharp razor blade to a standard length of 14 cm. The segments were flushed with filtered (2 μm) 20 mM KCl at 0.1 MPa to remove all native embolisms. Flushed stems were centrifuged in a custom-built rotor (Pockman et al. 1995, Alder et al. 1997) to progressively more negative pressures. The hydraulic conductivity (K) was measured between each centrifugation by fitting the segment with tubing filled with filtered KCl solution, and applying a gravity-induced pressure gradient across the stem. The pressure gradient allowed the solution to flow through the stem and into a reservoir standing on an electronic balance. The flow rate was divided by the pressure gradient to obtain a conductivity value. A Weibull function (Neufeld et al. 1992) was fitted to the conductivity versus negative pressure relationship for each segment and the pressure inducing 50% (P_{50}) and 95% (P_{95}) loss in conductivities was calculated.

Loss of conductivity via cavitation was expressed on a sapwood specific area and leaf specific area basis. Sapwood specific conductivity (K_a) was determined by dividing K by the cross-sectional sapwood area of each segment. Cross-sectional sapwood area was assumed to equal all the area beneath the bark, unless heartwood was evident on visual examination. Cross-sectional area was measured with calipers. Leaf specific conductivity (K_l) was calculated by dividing K by the one-sided leaf area supplied by the stem segment.

Wood density

Wood density is a widely recognized determinant of xylem water transport properties and whole-plant water relations. Wood density was therefore measured on stem cores and branch segments from each gender. Segments, 25-mm long, were cut from fresh stem cores and current-year branches. An additional longitudinal cut was made on branch segments and the pith and bark were removed with a razor blade. Fresh volume of each segment was determined by Archimedes' principle. Displacement mass was measured to the nearest 0.01 g and was converted to sample volume by the formula: displacement mass/0.998, where 0.998 mg mm^{-3} is the density of water at 20 °C. Segments were then oven-dried at 90 °C for 48 h, and their dry mass measured. Wood density was calculated as dry mass per volume. We analyzed two cores and one branch segment per tree ($n = 12$ male and 12 female trees).

Statistics

Regression analysis was performed to relate J_s and g_s of each gender to D and Q. Gender and microsite differences were analyzed by analysis of covariance (ANCOVA). Mean gender differences in J_s, g_s and leaf water potentials during discrete measurement periods were analyzed by a Student's t test. Differences in the seasonal course of J_s, g_s and leaf water potentials were assessed by repeated measures analysis of variance (MANOVA) where multiple measurements (three measurement periods per tree) on a given plant constituted the repeated variables (Potvin et al. 1990). In each analysis, the main effect of gender was tested as a between-subjects effect. Gender differences in P_{50} and P_{95} were analyzed with a Student's t test.

Results

Aboveground biomass allocation

The predicted A_l from branch diameter (BD) was $0.195(\text{BD})^{1.93}$ ($R^2 = 0.89$) for female trees and $0.415(\text{BD})^{1.60}$ ($R^2 = 0.87$) for male trees. Canopy LAI did not change significantly throughout the growing season in either male or female trees. There-

fore, leaf area values determined from leaf and branch allometry were used for the entire measurement period. Male trees had a 30% higher leaf area to sapwood area ratio (A_l:A_s) than female trees: 0.229 versus 0.176 $m^2 cm^{-2}$ (Table 1), although the differences were not statistically significant ($P = 0.21$). Conversely, the mean sapwood area to basal area ratio (A_s:A_b) was 33% greater in female trees relative to co-occurring males ($t = 0.0006$; Table 1), indicating female trees had more hydroactive xylem area per unit stem area than co-occurring male trees. The amount of leaf area per unit basal area (A_l:A_b) was similar between genders (0.97 and 0.91 for male and female trees, respectively; Table 1).

Sap flux measurements

In habitats where soil water is nonlimiting (i.e., along streamsides), patterns of plant water use result largely from atmospheric drivers such as vapor pressure deficit and sunlight. The relationship between J_s and D_z was nonlinear, and was therefore fitted with an exponential saturation model:

$$J_s = b_1(1 - e^{-b_2 D_z}) \quad (7)$$

where b_1 and b_2 are fitting parameters. Early in the growing season (May 28 to June 29), the model explained 86 and 88% of the variability in J_s in male and female trees, respectively (Figure 1a). From July 22 to August 28 (late growing season), the model explained 62 and 78% of the variability in J_s in male and female trees, respectively (Figure 1b). Sap flux density was significantly higher in females than in males during the early growing season (Figure 1a). On average, compared with males, J_s was 43% higher in females in May and June, and remained 17% higher in July and August (Figure 1).

Differences in the response of J_s to climate drivers D and Q between male and female populations were tested by analysis of covariance. In May and June, J_s was highly correlated with D ($F = 84.45$, $P < 0.0001$) and moderately correlated with Q ($F = 10.62$, $P = 0.0012$), whereas in July and August, J_s remained moderately correlated with D ($F = 11.23$, $P = 0.0009$), but Q had no apparent effect on J_s ($P = 0.52$; Table 2). The interaction between D and Q had no effect on J_s during either period of the growing season (Table 2). There were significant gender differences in the response of J_s to the model parameters during both periods of the growing season (Table 2). Dif-
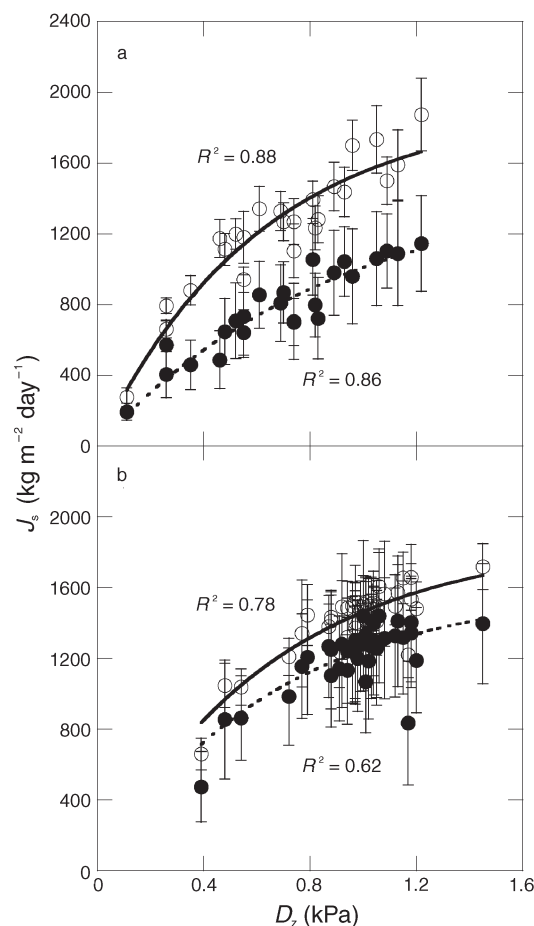

Figure 1. Relationship between mean stem sap flux density (J_s) and mean daytime vapor pressure deficit normalized for day length (D_z) in mature streamside male (●) and female (○) *Acer negundo* trees. Data were collected from (a) May 28 to June 29 and (b) July 22 to August 28, 2005 near Salt Lake City, UT. Error bars represent ± 1 standard error of the mean.

ferences were particularly strong during the early growing season ($F = 87.00$, $P < 0.0001$), and are clearly visible in Figure 1a.

Canopy stomatal conductance

We used nonlinear regression techniques to fit g_s to D according to Oren et al. (1999) and Wullschleger et al. (2002):

Table 1. Mean (± standard error) leaf area to sapwood area ratio (A_l:A_s; $m^2 m^{-2}$), sapwood area to basal area ratio (A_s:A_b; $m^2 m^{-2}$) and leaf area to basal area ratio (A_l:A_b; $m^2 m^{-2}$) of mature male and female *Acer negundo* trees in Red Butte Canyon, near Salt Lake City, UT. Probability values (P) of gender differences in aboveground allocation are shown.

Gender	A_l:A_s	A_s:A_b	A_l:A_b
Male	2285 (271)	0.397 (0.023)	969 (147)
Female	1758 (283)	0.529 (0.012)	905 (142)
P	0.21	0.0006	0.76

Table 2. Probability values from analysis of covariance (ANCOVA) of sap flux density (J_s) against mean daytime vapor pressure deficit, normalized for day length (D_z; kPa) total daily photosynthetic active radiation (Q; mol $m^{-2} s^{-1}$) and gender in mature male and female *Acer negundo* trees occurring in Red Butte Canyon near Salt Lake City, UT.

	D_z	Q	$D_z \times Q$	Gender
May–June	< 0.0001	0.0012	0.26	< 0.0001
July–August	0.0009	0.52	0.97	0.0100

$$g_s = b - m \ln D \tag{8}$$

where b is the intercept (i.e., the value of g_s at $D = 1$ kPa in a log–linear relationship), and m describes the stomatal sensitivity to D (i.e., the slope of the regression fit).

In May and June, mean daily g_s, normalized for leaf area ($g_{s,leaf}$) was highly correlated with $\ln D$ in both male and female trees ($R^2 = 0.78$ and 0.85 for male and female trees, respectively; Figure 2a). Differences in $g_{s,leaf}$ between genders over the measured range of $\ln D$ were highly significant ($F = 157.2$, $P < 0.0001$), with females having a 140% higher $g_{s,leaf}$ than males. There was no interaction between gender and $\ln D$ ($F = 2.23$, $P = 0.14$). In July and August, $g_{s,leaf}$ was again well correlated with mean daytime D ($R^2 = 0.61$ and 0.78 for male and female trees, respectively; Figure 2c). Female trees had 69% higher $g_{s,leaf}$ than male trees and gender differences were again highly significant ($F = 92.5$, $P < 0.0001$). The interaction term gender $\times \ln D$ was correlated with $g_{s,leaf}$ ($F = 3.95$, $P = 0.0474$), suggesting that the slopes of the responses to $\ln D$ were gender specific.

Mean daily canopy stomatal conductance normalized for basal area ($g_{s,bas}$) was well correlated with $\ln D$ in May and June ($R^2 = 0.78$ and 0.86 for males and females, respectively; Figure 2b). Gender differences in $g_{s,bas}$ were highly significant ($F = 171.6$, $P < 0.0001$), with females having 90% higher mean $g_{s,bas}$ than males during May and June. There was a significant interaction between gender and $\ln D$ ($F = 7.36$, $P = 0.007$). The relationships between $g_{s,bas}$ and $\ln D$ in July and August were slightly less robust than in May and June ($R^2 =$

0.52 and 0.72 in male and female trees, respectively). Nevertheless, there was still a large difference between genders in $g_{s,bas}$ ($F = 43.5$, $P < 0.0001$), with females showing a 31% higher $g_{s,bas}$ than males. There was no interaction between gender and $\ln D$ in July and August ($F = 0.60$, $P = 0.44$).

Seasonal patterns of plant water relations

Seasonal patterns of plant water relations were investigated during three discrete periods of the growing season: mid-June (Day 166), mid-July (Day 205), and mid-August (Day 237). Mean daytime D on these days ranged from 1.15 kPa on Day 166 to 1.75 kPa on Day 237 (Figure 3). However, all three days were nearly cloudless resulting in almost identical total daily Q (Figure 3).

Mean Ψ_{pd} was highest in June, but never fell below -0.55 MPa in either male or female trees (Figure 4a), suggesting that neither gender was subjected to significant soil water limitations during the growing season. Mean Ψ_{md} was highest in June and was about -1.50 MPa for both genders. For males, Ψ_{md} reached a low of -2.25 MPa in August, and a low of -2.00 MPa in females in July and August (Figure 4a). There were no seasonal differences between genders for either Ψ_{pd} or Ψ_{md} (Table 3). Leaf water potential measurements were combined with midday measurements of J_s to g_t. Sap flux density measured between 1100 and 1300 h did not differ between genders over the growing season ($P = 0.27$; Table 3), although J_s was higher in females in June ($F = 5.32$, $P = 0.0416$; Figure 4b). Consequently, there were only marginal seasonal dif-
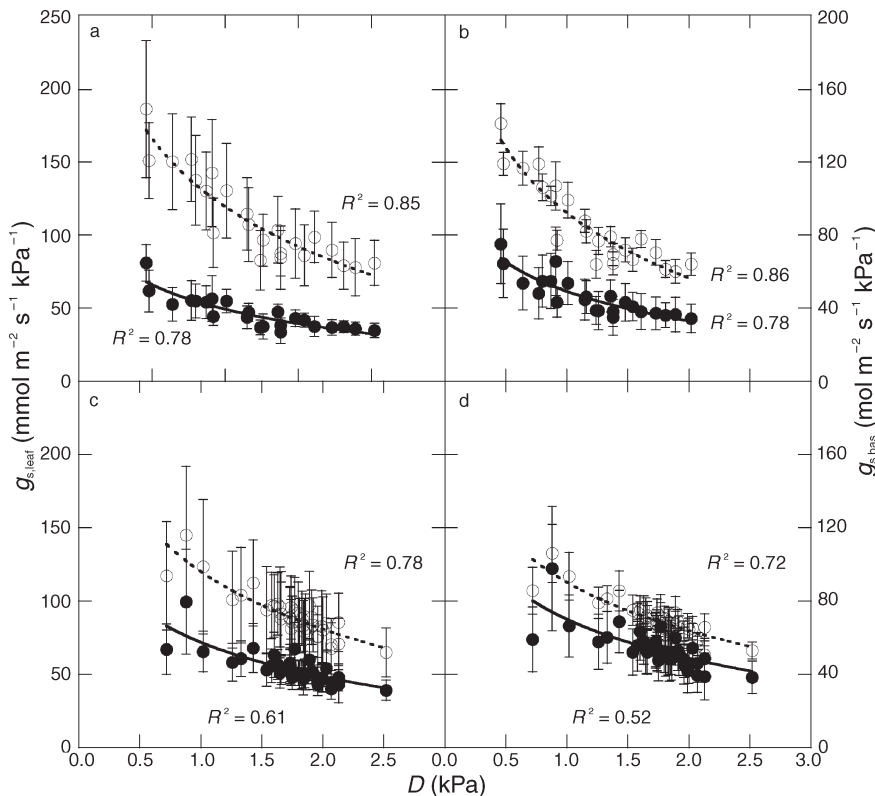

Figure 2. Relationship between mean canopy stomatal conductance (g_s) and mean daytime vapor pressure deficit (D) in mature streamside male (●) and female (○) *Acer negundo* trees near Salt Lake City, UT. Canopy stomatal conductance per unit leaf area ($g_{s,leaf}$) measured from (a) May 28 to June 29 and (b) July 22 to August 28, 2005. Canopy stomatal conductance per unit basal area ($g_{s,bas}$) measured from (c) May 28 to June 29 and (d) July 22 to August 28. Error bars represent ± 1 standard error of the mean.
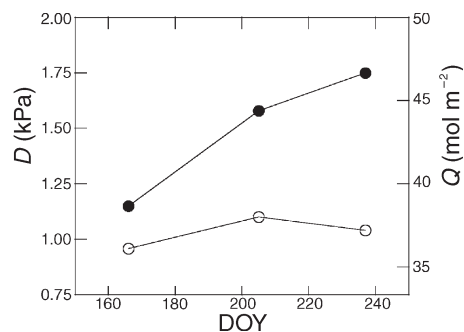
Figure 3. Mean daytime vapor pressure deficit (D) and total daily photosynthetic active radiation (Q) for days in which leaf water potentials were measured. Days include June 15, (day of year (DOY) 166), July 24 (DOY 205) and August 25 (DOY 237), 2005.

ferences in g_t between genders ($P = 0.09$; Table 3), although g_t in June was 56% higher in females than in males ($F = 5.4944$, $P = 0.0389$; Figure 4c). In females, g_t showed a seasonal decline, whereas in males, g_t was constant throughout the season (Figure 4c).

In many cases, broadleaf canopies such as *A. negundo* are not well coupled to the atmosphere. Therefore, it may be inappropriate to assume that g_c closely approximates g_s. Consequently g_{bl}, and subsequent g_s, were calculated with Equation 5. Representative values of g_{bl}, g_c, g_s and Ω for days on which leaf Ψ was measured are shown in Table 4. Canopy decoupling on these days was low ranging from 0.09 to 0.12 in males and 0.16 to 0.25 in females, indicating that g_c did not vary substantially from g_s.

Mean $g_{s,leaf}$ was higher in females relative to males throughout the year ($P = 0.0437$; Table 5, Figure 5a). Differences were most apparent in June when $g_{s,leaf}$ was 161% higher in females than in males (Figure 5a). Likewise, $g_{s,bas}$ was considerably lower in male trees than in female trees ($P = 0.08$; Table 5) with the largest differences again being detected in June (Figure 5b).

Branch xylem cavitation vulnerability, specific conductivities and wood density

Gender differences in canopy fluxes and aboveground allocation patterns did not appear to be caused by differences in xylem function. Mean maximum sapwood area specific conductivity (K_a) and leaf specific conductivity (K_l) did not vary between genders (cf. intercepts at 0 MPa in Figures 6a and 6b, respectively). Moreover, percent loss of K_a and K_l from xylem embolism did not vary between genders across the range of xylem pressures in which $K > 0$ (0 to –4 MPa). Mean P_{50} was –2.1 MPa for both genders ($F = 0.01$, $P = 0.93$), and mean P_{95} was –3.6 and –4.1 MPa for male and female branches, respectively, but gender differences were not significant ($F = 2.10$, $P = 0.18$).

Mean stem wood density was 0.47 mg mm^{-3} (SE $\pm$ 0.01) in streamside male trees and 0.44 $\pm$ 0.01 mg mm^{-3} in streamside female trees. Mean differences between genders were marginally significant ($F = 4.00$, $P = 0.059$). Mean branch wood den-
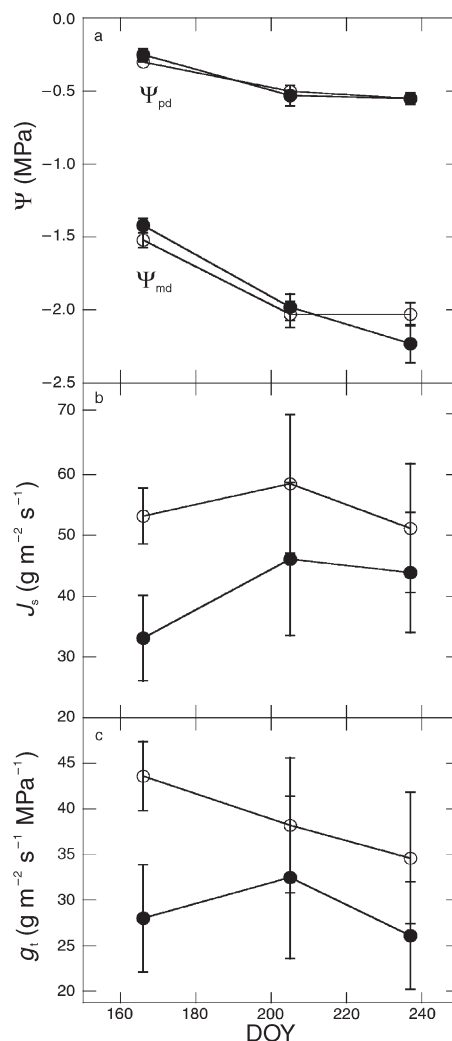

Figure 4. Leaf water potential (Ψ), stem sap flux density (J_s) and total whole-plant hydraulic conductance (g_t) of mature streamside male (●) and female (○) *Acer negundo* trees on June 15, (day of year (DOY) 166), July 24 (DOY 205) and August 25 (DOY 237), 2005. (a) Predawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potentials measured between 0200 and 0400 h, and between 1100 and 1300 h respectively. (b) Mean stem sap flux density measured during daylight hours ($Q > 10$ μmol m^{-2} s^{-1}). (c) Mean total whole-plant conductance, calculated as midday J_s, measured between 1100 and 1300 h divided by the difference between Ψ_{md} and Ψ_{pd}. Error bars represent $\pm$ 1 standard error of the mean.

sity did not vary between genders ($F = 0.02$, $P = 0.88$), and was 0.49 $\pm$ 0.02 mg mm^{-3} for all branch segments.

Discussion

We observed significant differences in aboveground hydraulic architecture that resulted in large differences in water fluxes between the genders of streamside *A. negundo* trees occurring in northern Utah. Mature female trees maintained much higher water use and canopy stomatal conductance per unit leaf area and basal area than mature male trees. Gender differences in

Table 3. Probability values from repeated measures (MANOVA) analysis of predawn leaf water potential (Ψ_{pd}; MPa), midday leaf water potential (Ψ_{md}; MPa), whole-plant hydraulic conductance (g_t; g m^{-2} s^{-1} MPa^{-1}) and sap flux density (J_s; g m^{-2} s^{-1}) of mature streamside male and female *Acer negundo* trees. Whole-plant conductivity was calculated by dividing stem sap flux density by the difference between Ψ_{pd} and Ψ_{md}.

	Ψ_{pd}	Ψ_{md}	g_t	J_s
Gender	0.88	0.82	0.09	0.27
Month	< 0.0001	< 0.0001	0.0095	0.0025
Gender × Month	0.57	0.29	0.80	0.06

Table 5. Probability values from repeated measures (MANOVA) analysis of stomatal conductance per unit leaf area ($g_{s,leaf}$; mmol m^{-2} s^{-1} kPa^{-1}) and stomatal conductance per unit basal area ($g_{s,bas}$; mol m^{-2} s^{-1} kPa^{-1}). Data were collected on June 15, July 24 and August 25, 2005.

	$g_{s,leaf}$	$g_{s,bas}$
Gender	0.0437	0.08
Month	0.17	0.0433
Gender × Month	0.0087	0.0093

resource allocation and resource acquisition likely reflect the 4- to 6-fold higher resource cost of reproduction in female *A. negundo* versus males (Dawson and Ehleringer 1993), and the observed pattern of female biased sex-ratios along stream margins (Dawson and Ehleringer 1993, Ward et al. 2002). Our study together with previous investigations provide insight into the adaptive significance of sex-ratio biases along environmental gradients, and identify the morphological and physiological mechanisms underlying the observed sex ratios. Furthermore, our results highlight the consequences that sex ratio biases in dominant riparian vegetation may have on important ecohydrological processes including ecosystem water balance, stream flow, and carbon and nutrient cycling.

Whole-plant water use and aboveground hydraulic architecture

Gender differences in g_s have previously been identified in streamside *A. negundo* trees from leaf gas exchange studies (Dawson and Ehleringer 1993, Dawson et al. 2004). Mean g_s measured during three separate years in June, July and August was on average 100% higher in female trees than in co-occurring males (Dawson et al. 2004). Similarly, Dawson and Ehleringer (1993) reported that streamside female *A. negundo* trees have 70% higher maximum g_s in July relative to co-occurring males. In our study, whole-plant g_s was calculated by combining measurements of stem sap flux with measurements of A_s:A_l, and A_s:A_b. The whole-plant approach yielded similar differences between genders: mean daytime $g_{s,leaf}$ averaged over June, July and August was 107% higher in female trees than in male trees. Likewise, mean daytime $g_{s,leaf}$ measured in July was 72% higher in females than in males, similar to the

magnitude of gender difference that Dawson and Ehleringer (1993) reported based on leaf gas exchange measurements. Our results demonstrate that previously reported differences in leaf-level g_s between genders scale to the whole plant.

Measurements of g_s were also scaled to basal area (i.e., $g_{s,bas}$). Although basal area measurements are of little use in scaling fluxes to the ecosystem or watershed level, they provide a metric for identifying population differences in aboveground allocation and resource uptake. Both genders had about the same leaf area per unit basal area. Consequently, gender differences in $g_{s,leaf}$ were maintained when scaled to $g_{s,bas}$. Thus, a female *A. negundo* tree would be expected to transpire about 70% more water during the growing season than a co-occurring male tree having a similar basal diameter. The large difference between genders in resource acquisition may explain the observed sex ratio biases in streamside habitats.

Differences in water use between male and female trees were substantially higher in May and June than in July and August (cf. Figures 1, 2, 4 and 6). A possible explanation for the seasonal patterns in resource uptake is the timing of flowering which differs between genders. At our field site, male *A. negundo* trees generally flower in April before leaf flush, whereas female *A. negundo* trees flower from mid May to mid June, well after the onset of leaf emergence. Males therefore draw on stored carbohydrates from previous-years photosynthate. Females, in contrast, likely offset some of the high resource costs of reproduction by drawing on photosynthate accumulated during flowering and subsequent seed development, thereby requiring enhanced resource acquisition early in the growing season. Unfortunately, there is little information on the seasonal course of resource uptake in female versus

Table 4. Wind speed (u; m^2 s^{-1}) measured 3 m above the ground surface in an open meadow and mean (± standard error) boundary layer conductance (g_{bl}; mmol m^{-2} s^{-1}), canopy conductance (g_c; mmol m^{-2} s^{-1}), canopy stomatal conductance (g_s; mmol m^{-2} s^{-1}) per unit leaf area and mean canopy decoupling coefficient (Ω) for mature male and female *Acer negundo* trees. Data were collected on June 15, July 24 and August 25, 2005.

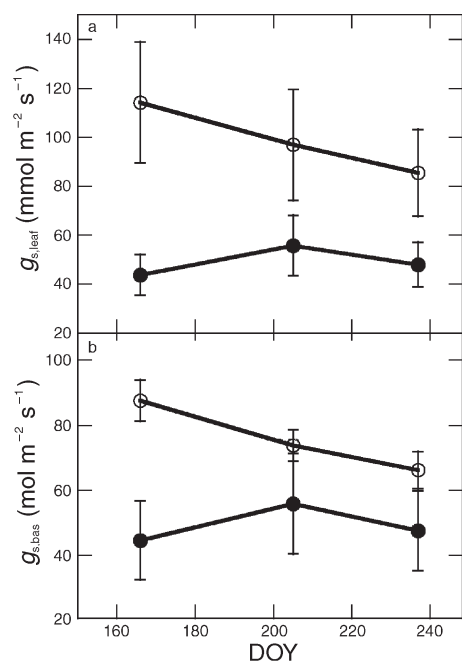|	Daytime u	g_{bl}		g_c		g_s		Ω	
		Male	Female	Male	Female	Male	Female	Male	Female
June	0.99	962	919	41.8 (7.1)	101.1 (19.4)	43.8 (7.7)	114.3 (24.7)	0.10	0.22
July	0.98	954	912	52.3 (10.3)	87.1 (18.1)	55.7 (11.5)	97.0 (22.7)	0.12	0.25
August	1.16	1130	1079	45.9 (7.7)	79.0 (15.3)	48.0 (8.4)	85.6 (17.8)	0.09	0.16

Figure 5. Canopy stomatal conductance (g_s) measured in mature streamside male (●) and female (○) *Acer negundo* trees on days leaf water potentials were measured. Data were collected on June 15 (day of year (DOY) 166), July 24 (DOY 205) and August 25 (DOY 237), 2005. (a) Canopy stomatal conductance calculated per unit leaf area ($g_{s,leaf}$). (b) Canopy stomatal conductance calculated per unit basal area ($g_{s,bas}$). Error bars represent ± 1 standard error of the mean.

Figure 6. (a) Decreases in sapwood specific conductivity (K_a) and (b) leaf specific conductivity (K_l) caused by pressure-induced xylem cavitation. Measurements were conducted on current-year sun-exposed branches collected from mature streamside male (●) and female (○) *Acer negundo* trees during the 2005 growing season. Error bars represent ± 1 standard error of the mean.

male plants that might explain the timing of flowering and fruit set. However, within a single plant, leaves adjacent to female reproductive structures often have higher photosynthetic rates than leaves distant from female reproductive structures (de Jong 1986, Reekie and Bazzaz 1987*a*, 1987*b*, McDowell et al. 2000). Spatial patterns of resource uptake observed in monoecious plants may be analogous to the temporal patterns observed in *A. negundo*, where large gender differences in resource acquisition during the early growing season likely resulted from the strong sink strength of female reproductive structures.

Estimates of canopy stomatal conductance depended heavily on sap-flux-scaled estimates of transpiration. Sap flux density is often overestimated in cases where the depth of conducting sapwood is substantially greater than the length of the sap flux probe (Ford et al. 2002). For example, thermal sensors similar to those we used 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). We assumed that J_s remained constant throughout the sapwood profile, as shown for other riparian hardwood species (Lambs and Muller 2002). However, mean sapwood depth ranged from 43.1 mm (SE ± 1.69) in males to 56.3 ± 0.82 mm in females, leaving 48 and 58%, respectively, of the total sapwood area unmeasured by our 20-mm-long probes. If we assume that J_s declined in both genders by 50% from the outer 20 mm to the heartwood:sapwood transition, females
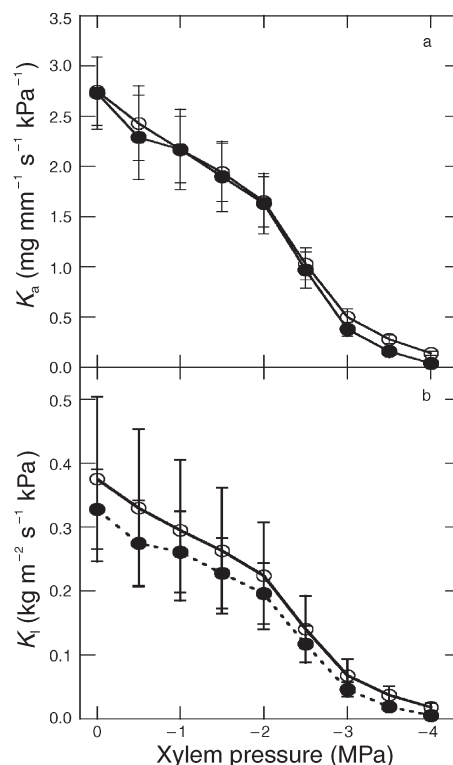
would have maintained a 151% higher $g_{s,leaf}$, than males in June (Table 6). Mean differences in $g_{s,leaf}$ between genders for the whole growing season would have changed only slightly from 104 to 94%. If we assume that J_s ceased completely in both genders from the outer 20 mm to the heartwood:sapwood transition (which is unlikely), females would have maintained a 137% higher $g_{s,leaf}$ than males in June (Table 6). Mean differences in $g_{s,leaf}$ over the whole growing season would decrease to 84%.

Xylem cavitation and hydraulic conductivity

In general, plants with high maximum water fluxes tend to have xylem that is highly efficient at transporting water to the canopy relative to plants with lower maximum fluxes (Pockman and Sperry 2000, Martínez-Vilalta et al. 2002). However, xylem efficiency appears to be accompanied by the tradeoff of reduced safety from xylem cavitation (Carlquest 1988, Tyree et al. 1994, Hacke et al. 2006). Given that female *A. negundo* trees occur at higher frequencies along stream sides and maintained higher J_s than males, we hypothesized that the branches of female plants have a higher maximum K_a and K_l at the possible expense of having less resistance to cavitation. We found no differences between genders in any of the xylem parameters measured. However, g_t was 56% higher in

Table 6. Predicted decrease in canopy stomatal conductance ($g_{s,leaf}$) if sap flux density (J_s) declined from a constant rate throughout the sapwood profile to 50 and 100% from the outer 20 mm of sapwood to the heartwood:sapwood transition. Data are from male and female *Acer negundo* trees occurring in Red Butte Canyon, near Salt Lake City, UT.

	June			July			August		
	Male	Female	% Diff	Male	Female	% Diff	Male	Female	% Diff
Constant J_s	44.0	116.7	165	56.1	98.7	76	48.2	86.7	80
50% Decline	37.6	94.3	151	47.8	80.1	68	41.2	70.8	72
100% Decline	30.8	73.1	137	39.0	62.3	60	33.8	55.4	64

females than in males during early stages of the growing season, suggesting that females were more efficient at delivering water to the canopy during the early part of the growing season. In addition, females showed declines in hydraulic conductance during the season (Figure 4c), suggesting that high stomatal conductance resulted in progressive seasonal cavitation. One possibility is that xylem hydraulic conductivity of the root system or main stem, or both, was substantially higher in female trees than in male trees. Although we have no direct evidence that root or stem hydraulic function differed between genders, wood density of the main stem, an important determinant of plant hydraulic function (Hacke et al. 2001, Meinzer 2003), was 6% lower in female trees than in male trees. Small changes in wood density could be related to large changes in g_t. For example, a 5-fold increase in g_t was correlated with a 30% decrease in wood density in Hawaiian dry forest species (Stratton et al. 2000). Therefore, it is plausible that xylem structure and the function of the main stem differ between genders. Further work is needed to better gauge the hydraulic constraints and long-distance water transport in male and female *A. negundo*.

Dioecy impacts on ecohydrology

Given that female *A. negundo* trees have higher water use rates per unit leaf area and basal area compared with co-occurring male trees, the spatial segregation of the sexes could have important ramifications on several ecohydrologic processes in riparian systems. Trees that occur along stream margins remove water stored in and around stream banks and shallow water tables (Scott 1999). Therefore, females, because of their higher transpiration rates, may have a significantly greater impact on stream discharge and groundwater recharge than males. Female *A. negundo* trees have higher sap flux rates per unit sapwood area than other co-occurring tree species that dominate mid-elevation riparian zones in the intermountain western USA including, *A. grandidentatum*, *Betula occidentalis* and *Populus angustifolia* James (Hultine et al. 2007a). Conversely, male *A. negundo* trees have sap flux rates that are comparable with other co-occurring species (Hultine et al. 2007a). Moreover, if higher water use rates in females trees result in greater carbon acquisition and productivity (Dawson and Ehleringer 1993, Ward et al. 2002), it is plausible that a higher frequency of female versus male trees would have measurable impacts on carbon and nutrient cycles at large spatial and temporal scales.

Alternatively, because of their higher resource demands, global change processes such as land use and climate change may have a larger negative impact on streamside female trees than on male trees. If substantial increases in stream diversions and groundwater extractions are met with greater incidence of drought, rapid shifts in the sex ratio of riparian *A. negundo* will likely occur. Furthermore, the spatial segregation of the sexes has been correlated with resource uptake in other dioecious riparian tree species including *Populus fremontii* S. Watson (Hultine et al. 2007b), suggesting that the fitness of dioecious riparian tree species may be particularly sensitive to global change processes.

In conclusion, we found clear differences in sap-flux-scaled transpiration, canopy stomatal conductance, and carbon uptake between the genders of *A. negundo* occurring along a perennial stream in the Intermountain West of the USA. Females had a substantially greater acquisition of water (and presumably carbon) than males, suggesting that physiological traits in females are selected for in highly competitive streamside habitats. Differences in sap fluxes between genders were most apparent early in the growing season and appeared to coincide with the timing of flowering and seed development in female trees. Disparate patterns of physiology between genders may improve our understanding of the adaptive significance of the observed sex ratios of *A. negundo*, whereby females occur at higher frequencies than males along streamside habitats. Changes in sex ratio patterns may have significant effects on many ecohydrological processes including evapotranspiration, streamflow, and carbon and nutrient cycling. Furthermore, patterns of gender-specific resource acquisition in *A. negundo* may reflect larger scale occurrences of gender effects on ecohydrology given that other dominant riparian tree species are also dioecious, including *Populus* spp. and *Salix* spp.

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