

# Gender specific patterns of carbon uptake and water use in a dominant riparian tree species exposed to a warming climate

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## Abstract

Air temperatures in the arid western United States are predicted to increase over the next century. These increases will likely impact the distribution of plant species, particularly dioecious species that show a spatial segregation of the sexes across broad resource gradients. On the basis of spatial segregation patterns, we hypothesized that temperature increases will have a greater negative impact on female plants compared with co-occurring male plants of dioecious species. This hypothesis was tested by examining the whole-plant carbon and water relations of 10-year-old female ( $n = 18$ ) and male ( $n = 13$ ) *Acer negundo* Sarg. trees grown in a common garden in Salt Lake City, UT. The trees were established from cuttings collected where the growing season temperature averaged about 6.5 °C cooler than at the common garden. During May and June, stem sap flux ( $J_s$ ) was similar between genders, but averaged 25% higher in males during the warmer months of July and August. Daytime canopy stomatal conductance ( $g_s$ ) per unit leaf area was 12% higher in females in May : June, but was 11% higher in males in July : August. We combined measurements of sap flux-scaled transpiration with measurements of tree allometry and  $\delta^{13}\text{C}$  of leaf soluble sugars to estimate whole-tree carbon assimilation ( $A_{\text{tree}}$ ) and water use efficiency (WUE) ( $A_{\text{tree}} : E_{\text{tree}}$ ).  $A_{\text{tree}}$  was similar between genders until late August when  $A_{\text{tree}}$  was 32% higher in male trees.  $A_{\text{tree}} : E_{\text{tree}}$  was on average 7% higher in females than in males during the growing season. Patterns of  $J_s$ ,  $g_s$ ,  $A_{\text{tree}}$  and  $A_{\text{tree}} : E_{\text{tree}}$  in the present study were in contrast to those previously reported for *A. negundo* genders under native growing season temperatures. Results suggest that the spatial segregation of the sexes could shift under global warming such that female plants lose their dominance in high-resource habitats, and males increase their dominance in relatively lower-resource habitats.

**Keywords:** *Acer negundo*, canopy stomatal conductance, climate change, dioecy, riparian ecosystems, sap flux,  $\delta^{13}\text{C}$

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## Introduction

Climate change is expected to bring substantially warmer air temperatures to the arid western United States over the next century (Karl *et al.*, 2009). These temperature increases have the potential to exert strong selection pressures on plants, such that many species will undergo considerable shifts in population structure and distribution. Populations occurring in the warm extremes of current species ranges are most vulnerable to temperature change, particularly where populations are adapted to a relatively narrow range of temperature regimes (O'Neill *et al.*, 2008; Grady *et al.*, 2011). The ability of a species to cope with shifting environmental conditions will determine its long-term distribution and survival in the face of climate change, and other global change processes (Parmesan, 2006).

Dioecious species-plants in which male and female flowers are found on separate individuals—may be

particularly vulnerable to the effects of climate change (Tognetti, 2012). Many dioecious plant species display spatial segregation of the sexes associated with micro-habitat differences in resource availability (Dawson & Bliss, 1989; Iglesias & Bell, 1989; Dawson & Ehleringer, 1993; Ward *et al.*, 2002; Hultine *et al.*, 2007a). For most of these dioecious species, sexes are distributed such that females are more common in high-resource microsites and males are more common in low-resource microsites (within close proximity for reproduction to be successful) (Freeman *et al.*, 1976; Dawson & Bliss, 1989; Dawson & Ehleringer, 1993). The spatial segregation of the sexes likely reflects adaptation to different costs associated with reproduction because females generally require more resources such as water and nutrients for reproduction than males (Freeman *et al.*, 1976; Bierzychudek & Eckhart, 1988; Dawson & Geber, 1999).

Differences in resource demand often result in physiological differences in resource acquisition capacity and resource use efficiency between sexes. Female plants generally maximize resource acquisition

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capacity, thereby allowing individuals to specialize (and outcompete others) in high-resource micro-environments (Hultine *et al.*, 2007a). Specifically, under favourable conditions, females generally have a higher stomatal conductance ( $g_s$ ), higher net carbon assimilation ( $A$ ), and lower water use efficiency (WUE) ( $A/g_s$ ) than males (Dawson & Bliss, 1989; Dawson & Ehleringer, 1993; Dawson *et al.*, 2004; Hultine *et al.*, 2007b, 2008a). Conversely, males tend to maximize resource use efficiency, allowing them to survive in less favourable microhabitats, or during periods when resources are limited (Dawson & Geber, 1999; Hultine *et al.*, 2007a).

As differential resource acquisition capacity may be adaptive, increases in growing season temperature may have a larger relative impact on females than males in regions that are already arid (i.e. where higher temperatures are likely to increase stress). Warmer temperatures generally increase the leaf to air vapour pressure deficit ( $v_{pd}$ ) and subsequent demand for water. Whether or not these changes result in greater plant water stress depends, in part on stomatal sensitivity to increases in either  $v_{pd}$  or internal water potential gradients (Monteith, 1995; Bunce, 1996; Tardieu & Simonneau, 1998). In many cases, plants that operate with a higher maximum  $g_s$  are more sensitive to water stress (Oren *et al.*, 1999; Ewers *et al.*, 2005). This is a result of the coupling of  $g_s$  with plant hydraulic conductance and the inevitable tradeoff between xylem conducting efficiency and cavitation resistance to water stress (Zimmermann, 1983; Tyree *et al.*, 1994; Hacke *et al.*, 2001; Wheeler *et al.*, 2005). Differences in resource acquisition efficiency between genders could also be a function of females having a higher carboxylation capacity than males (Dawson & Ehleringer, 1993), due in part to the higher carbon cost of female reproduction (Dawson & Geber, 1999). Differences in carboxylation capacity rather than stomatal sensitivity would mean that warmer temperatures and higher subsequent  $v_{pd}$  may impact female and male plants equally, unless carboxylation capacity is coordinated directly with plant hydraulic function (Katul *et al.*, 2003).

Among the most well-studied dioecious plant species is *Acer negundo* Sarg. (box elder), which is a common tree species of mid-elevation riparian zones throughout the western United States. As with many other dioecious species, *A. negundo* shows a spatial segregation between the sexes such that the ratio of female to male individuals is ca. 1.50 along perennial stream margins, where soil water and other resources are abundant (Ward *et al.*, 2002). Likewise, there is a large body of evidence showing that the female-skewed sex ratio along stream margins corresponds with females displaying higher vegetative growth (Dawson & Ehlerin-

ger, 1993), higher rates of radial stem growth (Ward *et al.*, 2002), higher rates of leaf and canopy gas exchange (Dawson & Ehleringer, 1993; Dawson *et al.*, 2004; Hultine *et al.*, 2008a), and higher carbon isotope discrimination (Dawson & Ehleringer, 1993; Ward *et al.*, 2002; Dawson *et al.*, 2004). Despite these consistent patterns, it is unknown whether expected climate warming will shift the relative physiological performances of male and female *A. negundo* trees, independent of changes in water availability that are difficult to predict with regional climate change models.

We compared the ecophysiological responses of female and male *A. negundo* trees growing at an unusually warm site to contrast with previously reported results for *A. negundo* at a native, cooler site. We utilized an artificial stream system, built specifically to address long-term investigations of riparian ecological processes, to address ecophysiological responses of male and female *A. negundo* trees to anthropogenic climate change. *A. negundo* trees were previously established at the artificial stream system from cuttings collected from a population adapted to much cooler growing season temperatures than those experienced at the artificial stream. We measured stem sap flux, tree allometry, and leaf chemistry and morphology to characterize seasonal patterns of whole plant carbon and water fluxes of female and male trees. We hypothesized that male *A. negundo* trees would express higher rates of resource uptake and growth than female *A. negundo* trees despite the fact that under native temperature conditions, streamside females substantially outperform co-occurring males. Results will shed light on the potential impact of climate change on the population structure of dominant dioecious plant species.

## Materials and methods

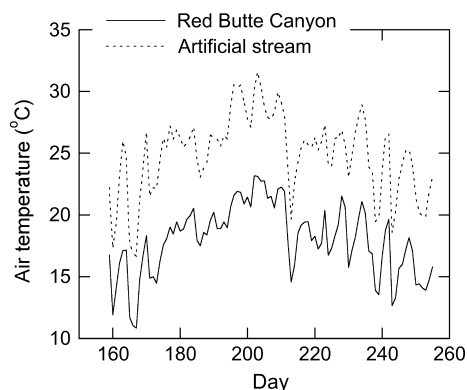
### Site description and artificial stream system design

The artificial stream system was constructed near the mouth of Red Butte Canyon and near Red Butte Creek on the University of Utah campus (40°45'39"N, 111°49'49"W, 1481 m) and has been previously described in detail by Hultine *et al.* (2008b). The site consists of a 100 m by 40 m open field of loamy soil. The upper 2 m of topsoil had been transported to the site a decade earlier, and therefore contained no soil horizons. *A. negundo* cuttings collected from streamside trees in Parleys Fork in the near-by Red Butte Canyon Research Natural Area (RBC) were potted in a glasshouse in 1997, and were allowed to take root. The cuttings were taken from trees in a single population/location in RBC (40°47'21"N 111°47'47"W, 1761 m) to minimize genetic variation. The population in RBC has been extensively studied for gender difference in ecophysiology and productivity (Dawson & Ehleringer, 1993; Dawson *et al.*, 2004; Hultine *et al.*, 2007b, 2008a), and occurred at a loca-

tion that is on average 6.5–7.0 °C cooler during the growing season than at the artificial stream system (Fig. 1) (Ehleringer *et al.*, 1992). The temperature difference between the source population in RBC and the artificial stream system is comparable to the predicted increase in mean temperature in the southwestern US. over the next century (Karl *et al.*, 2009). A total of 36 cuttings were transplanted at the growth site in 1998 in a six by six grid with a 3 m spacing between trees. A total of 33 cuttings successfully established, including 13 males and 20 females, and have reached reproductive maturity (the remaining three trees died shortly after transplanting).

Artificial streams were constructed to bring free-flowing water to within one metre of each tree. Four streams of ca. 1 m width and ca. 0.2–0.25 m depth were constructed with a small backhoe. Water was fed by running 0.75" (1.905 cm) diameter PVC pipe along the centre for the entire length of the streams. The PVC configuration incorporated a T-junction at the inflow where the streams separated, and were rejoined where the streams converged near the outflow so that garden was fed water from a single irrigation unit. Water was delivered from the PVC piping to the streams from 360° adjustable bubblers. The outflow consisted of two 50 l catch basins that drained into a large lowland area near Red Butte Creek.

Irrigation supply into the stream system was controlled and monitored through an intricate plumbing manifold (Hultine *et al.*, 2008b). Manual control valves at the manifold allowed for adjustment of the water supply from 0 to 32 l min<sup>-1</sup>. Although the system can easily be operated to adjust streamflow to mirror phases of snowmelt/runoff, stormflow, and baseflow, we operated the system at a constant flow rate of 16–18 l min<sup>-1</sup>. The experiments for this study were conducted in 2007, however, the streams were operated in 2005, 2006 and 2007 from late April before leaf flush (late May in 2005) until early November, well after leaf senescence commenced. This allowed the tree roots to



**Fig. 1** Mean daily temperature during the 2006 growing season in Red Butte Canyon (1760 m elev.) and at the artificial stream and riparian system at the University of Utah in Salt Lake City, UT (1480 m elev.). The Red Butte Canyon weather station was located in an open meadow adjacent to where *Acer negundo* stem cuttings were originally collected to establish the common garden, and artificial stream system at the University of Utah.

equilibrate and maximize contact with the artificial stream aquifer for almost two full years before experiments commenced. Volumetric streamflow was monitored with two Dwyer, SFI-801-3/4-A711 flow metre/transmitters (Dwyer Instruments, Michigan City, IN, USA). Each flow metre was individually calibrated against a Sensus SR 2 magnetic drive water metre (Sensus Metering Systems, Raleigh, NC, USA) at flow rates between 10 and 60 l min<sup>-1</sup>. After calibration, the flow metres were installed into the plumbing manifold and connected to a Campbell CR23X datalogger (Campbell Scientific, Logan, UT, USA). Data were logged every 30 s and stored as 30 min averages.

#### Meteorological measurements

Relative humidity, air temperature, photosynthetic active radiation, and wind speed were measured continuously from a micrometeorological station located 50 m from the experimental stream system. Relative humidity and air temperature were measured with a Vaisala HMP 45 AC humidity and temperature probe (Vaisala, Woburn, MA, USA), placed ca. 3 m above the ground surface. Photosynthetic active radiation ( $Q$ , see Table 1 for list of abbreviations) was measured with a Li-Cor LI-190SZ quantum sensor (Li-Cor, Lincoln, NE, USA). Wind speed ( $u$ ) and direction were measured with a Met One 034B-L wind set (Met One Instruments, Grants Pass, OR, USA). Micrometeorological data were measured every 30 s and stored as 10 min averages with a Campbell CR10X-2M data logger (Campbell Scientific). Measurements of relative humidity and air temperature were used to calculate atmospheric  $vpd$ .

#### Sap flux, canopy conductance, and leaf area measurements

Granier-type heat dissipation sensors (Granier, 1987, 1996) were used to measure sap flux density ( $J_s$ , g H<sub>2</sub>O m<sup>-2</sup> sapwood s<sup>-1</sup>). Each sensor consisted of a pair of 20 mm long, 2 mm diameter stainless steel probes inserted ca. 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 non-uniformity in sap flux around the stem. The upper probe (i.e. toward the canopy) was supplied with constant power of 200 mW, and the temperature difference between the heated (powered) probe and the lower, unheated reference probe was converted to sap flux density according to the equation:

$$J_s = \beta_1 K^{\beta_2} \quad (1)$$

where  $\beta_1$  and  $\beta_2$  are fitting parameters, and  $K$  is calculated from:

$$K = \frac{\Delta T_0}{\Delta T} - 1 \quad (2)$$

where  $\Delta T$  is the temperature difference between the heated and unheated probes,  $\Delta T_0$  is the temperature difference obtained under zero flow conditions. We assumed that zero flow only occurred during periods when  $vpd$  was at or near zero. A single sensor was randomly placed axially in the main

**Table 1** List of abbreviations with common units

Abbreviation	Definition	Units
Meteorological variables		
<i>v<sub>pd</sub></i>	Vapour pressure deficit	kPa
<i>Q</i>	Photosynthetic active radiation	$\mu\text{mol m}^{-2} \text{s}^{-1}$
<i>u</i>	Open air wind speed	$\text{m s}^{-1}$
<i>u<sub>c</sub></i>	Canopy wind speed	$\text{m s}^{-1}$
<i>u<sub>v</sub></i>	Canopy frictional velocity	$\text{m s}^{-1}$
<i>d</i>	Zero plane displacement	m
<i>z<sub>m</sub></i>	Roughness length	m
<i>d<sub>l</sub></i>	Characteristic leaf dimension	m
Fluxes and conductances		
<i>J<sub>s</sub></i>	Sap flux density	$\text{g m}^{-2} \text{s}^{-1}$
<i>g<sub>c</sub></i>	Canopy conductance	$\text{mmol m}^{-2} \text{s}^{-1} \text{kPa}$
<i>g<sub>s</sub></i>	Canopy stomatal conductance	$\text{mmol m}^{-2} \text{s}^{-1} \text{kPa}$
<i>g<sub>sref</sub></i>	Canopy stomatal conductance at <i>v<sub>pd</sub></i> = 1 kPa	$\text{mmol m}^{-2} \text{s}^{-1} \text{kPa}$
<i>g<sub>bl</sub></i>	Boundary layer conductance	$\text{mmol m}^{-2} \text{s}^{-1} \text{kPa}$
<i>g<sub>r</sub></i>	Long-wave radiative transfer conductance	$\text{mmol m}^{-2} \text{s}^{-1} \text{kPa}$
$\gamma$	Psychrometric constant	$\text{kPa K}^{-1}$
$\lambda$	Latent heat of vaporization	$\text{J kg}^{-1}$
$\rho$	Density of moist air	$\text{kg m}^{-3}$
<i>C<sub>p</sub></i>	Specific heat of air	$\text{J kg}^{-1} \text{K}^{-1}$
$\varepsilon$	Change in latent per change in sensible heat	Dimensionless
$\Omega$	Canopy decoupling coefficient	Dimensionless
$\delta^{13}\text{C}$	Carbon isotope ratio of leaf soluble carbohydrates	%
$\delta^{13}\text{C}_a$	Carbon isotope ratio of free air	%
<i>A</i> , <i>A<sub>tree</sub></i>	Leaf/whole-tree photosynthetic rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$ , $\text{g tree}^{-1}$
<i>E<sub>tree</sub></i>	Whole-tree transpiration rate	$\text{kg tree}^{-1}$
<i>c<sub>a</sub></i>	Canopy CO <sub>2</sub> concentration	$\mu\text{l l}^{-1}$
<i>c<sub>i</sub></i>	Intercellular CO <sub>2</sub> concentration	$\mu\text{l l}^{-1}$
Plant measurements and allometry		
<i>A<sub>l</sub></i>	Leaf area	$\text{m}^2$
<i>A<sub>b</sub></i>	Basal area	$\text{cm}^2$
<i>A<sub>s</sub></i>	Sapwood area	$\text{cm}^2$
<i>D<sub>b</sub></i>	Basal diameter	$\text{cm}^2$
<i>R<sub>c</sub></i>	Canopy radius	m
<i>z</i>	Canopy height	m

stem of 18 female (two female trees were not instrumented) and all 13 male trees, at ca. 1.5 m above the ground. Temperature differences of all sensors were logged every 30 s and

stored as 30 min averages with a Campbell CR10X-2M data logger (Campbell Scientific). Sap flux measurements were conducted during the 2007 growing season from May 14 (day 134) to August 31 (day 243).

Mean daytime sap flux density was calculated to correlate with mean daytime *Q* and mean daytime *v<sub>pd</sub>*. Daytime was defined by the period when *Q* was greater or equal to  $10 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Hultine *et al.*, 2007b). Sap flux measurements were separated into two distinctive periods of the growing season: May : June when mean daytime *v<sub>pd</sub>* averaged 2.45 kPa and July : August when mean daytime *v<sub>pd</sub>* averaged 3.13 kPa.

Canopy conductance (*g<sub>c</sub>*,  $\text{mmol m}^{-2}$  (leaf area)  $\text{s}^{-1} \text{kPa}^{-1}$ ) was calculated from sap flux measurements using a simplified form of the Penman–Monteith equation that had no radiation driven component (i.e. assumes perfect canopy–atmospheric coupling) (Monteith & Unsworth, 1990):

$$g_c = \frac{\gamma * \lambda}{\rho * c_p * v_{pd}} * \frac{J_s * A_s}{A_l} \quad (3)$$

where  $\gamma$  is the psychrometric constant ( $\text{kPa K}^{-1}$ ),  $\lambda$  is the latent heat of vaporization ( $\text{J kg}^{-1}$ ),  $\rho$  is the density of moist air ( $\text{kg m}^{-3}$ ),  $c_p$  is the specific heat of air at constant pressure ( $\text{J kg}^{-1} \text{K}^{-1}$ ),  $A_s$  is conducting sapwood area ( $\text{m}^2$ ) and  $A_l$  is leaf area ( $\text{m}^2$ ). Because sapwood area measurements are highly destructive on young trees, sapwood area ( $A_s$ ) was estimated from gender-specific sapwood area to basal area ( $A_s : A_b$ ) relationships reported by Hultine *et al.* (2008a) from tree cores collected on streamside male and female *A. negundo* trees in RBC. Basal area was determined from basal diameter ( $D_b$ ) measurements conducted at the onset of the growing season on April 16 (day 106) and before leaf out the following spring with a diameter tape near the base of each tree. As  $D_b$  increased during the growing season, we used a linear interpolation to estimate  $A_s$  for any given day between May 14 (day 134) and August 31 (day 243). Sapwood depth was estimated by gender specific relationships between stem diameter and sapwood depth measured from tree cores collected on streamside male and female *A. negundo* trees in RBC (unpublished results). From these relationships, we estimated that sapwood depth ranged from 20 to 32 mm in female trees, and 27 to 32 mm in male trees. Therefore, we did not apply a correction for narrow sapwood (Clearwater *et al.*, 1999) as our sap flux sensors did not appear to extend beyond the depth of hydroactive xylem.

Leaf area ( $A_l$ ) for each tree was estimated by finding the gender-specific  $A_l$  per leaf node, by finding the gender-specific allometric relationship between the number of leaf nodes and branch diameter, and by measuring the diameter of all leaf-bearing branches extending from the main stem of each tree measured for  $J_s$ . Relationship between  $A_l$  and leaf node were calculated by collecting all the leaves from eight nodes per tree in mid-May, 2007 (the leaves were fully expanded by mid-May). The fresh leaves were scanned with a high-resolution computer scanner, and one-sided leaf area was measured using public domain NIH image program software (<http://rsb.info.nih.gov/nih-image/>). Mean  $A_l$  per node was  $0.0134$  (SE = 0.0007)  $\text{m}^2$  for female trees and  $0.0117$  (SE = 0.0006)  $\text{m}^2$  for males. Allometric relationships between



the number of leaf nodes and branch diameter were calculated by counting the total number of leaf nodes on a subset of branches on each tree ( $n = 2\text{--}5$  branches per tree), ranging in diameter from 7 to 70 mm. The diameter of all leaf-bearing branches was measured with a diameter tape. To estimate changes in leaf area throughout the growing season, leaf node counts and measurements of branch diameters were conducted at the onset of the growing season on April 16, 2007 (day 106) and at the onset of the following growing season on April 29, 2008 (day 120). Allometric relationships between leaf node number and branch diameter in 2007 were  $27.24 \cdot \text{dia} \text{ (cm}^2\text{)}^{1.69}$ ,  $n = 33$  ( $R^2 = 0.92$ ,  $P < 0.0001$ ), and  $25.45 \cdot \text{dia}^{1.86}$ ,  $n = 39$  ( $R^2 = 0.90$ ,  $P < 0.0001$ ) for females and males respectively. While in 2008, relationships were  $21.68 \cdot \text{dia}^{1.83}$ ,  $n = 50$  ( $R^2 = 0.86$ ,  $P < 0.0001$ ), and  $21.13 \cdot \text{dia}^{1.80}$ ,  $n = 47$  ( $R^2 = 0.90$ ,  $P < 0.0001$ ) for females and males respectively. As with  $A_s$ , we used a linear interpolation to estimate  $A_l$  for any given day between May 14 (day 134) and August 31 (day 243). Leaf area index (LAI) was estimated for the onset and conclusion of the growing season by measuring the canopy diameter of each tree from eight points from the tree base to the canopy edge, and by dividing  $A_l$  by canopy area.

To calculate  $g_c$  from measurements of  $J_s$ ,  $A_s$ , and  $A_l$ , two important assumptions must first be met. The first assumption is that sap flux measured in the stem is equal to the rate of water leaving the canopy via transpiration. In other words, the depletion and subsequent replenishment of stem water storage is small. Second, conductance of leaf boundary layer ( $g_{bl}$ ) is large relative to canopy stomatal conductance ( $g_s$ ). With regard to the first assumption lag times between  $J_s$  and  $vpd$  of 0–2 h were previously evaluated for each gender from source population trees in RBC (Hultine *et al.*, 2008a). The highest correlations were found between zero and half hour, and was therefore assumed that stem capacitance had a negligible influence on the relationship between  $J_s$  and  $vpd$  (Hultine *et al.*, 2008a). The second assumption,  $g_{bl} > g_s$  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):

$$g_{bl} = 306.7 * \sqrt{\frac{u_c}{d_l}} \quad (4)$$

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

$$u_v = \frac{u * 0.4}{\ln \frac{z-d}{z_m}} \quad (5)$$

where  $z$  is the approximate canopy height (m), in this case 5 m,  $d$  is the zero plane displacement (m),  $z_m$  is the roughness length (m), and 0.4 is the von Karman constant. Canopy stomatal conductance was calculated from:

$$g_s = \frac{1}{\frac{1}{g_c} - \frac{1}{g_{bl}}} \quad (6)$$

Both  $d$  and  $Z_m$  were estimated from calculations of LAI (Campbell & Norman, 1998). The sensitivity of transpiration to changes in  $g_{bl}$  were evaluated using the dimensionless decoupling coefficient ( $\Omega$ ) described by Jarvis & McNaughton (1986) and later modified by Martin (1989) that takes radiative coupling between leaves and the atmosphere into account:

$$\Omega = \frac{\varepsilon + 2 + \frac{g_r}{g_{bl}}}{\varepsilon + 2 + \frac{g_{bl} + g_r}{g_s} + \frac{g_r}{g_{bl}}} \quad (7)$$

where  $\varepsilon$  is the change of latent heat to the change in sensible heat of saturated air, and  $g_r$  is the long-wave radiative transfer conductance. By definition,  $\Omega$  approaches its upper limit, 1.0 when stomatal control over transpiration grows progressively weaker.

### Leaf $\delta^{13}\text{C}$ , leaf nitrogen, and leaf mass per area analysis

Carbon isotope ratios of soluble carbohydrates were measured on leaves collected on May 20 (Julian day 140), June 13 (day 164), June 30 (day 181), July 30 (day 211), and August 24 (day 236), of the 2007-growing season. These days were selected for leaf collections because they were all nearly cloudless resulting in nearly identical levels of total daily  $Q$ . 10–20 sunlit leaves were collected at dusk from each tree at mid-canopy height. Roughly half of the leaves were prepared for soluble carbohydrate extraction by immediately immersing them in liquid nitrogen to inhibit all metabolic activity. These leaves were transported to the lab in dry ice and placed in a freezer where they were stored at  $-70^\circ\text{C}$ . The remaining leaves were placed in sealed ziplock bags, transported to the lab in dry ice and placed in a freezer for later analysis.

Carbon isotope ratios of soluble leaf carbohydrates ( $\delta^{13}\text{C}$ , ‰) were evaluated to infer short-term gas exchange (photosynthesis and  $g_s$ ) variability over short time periods (24–72 h: Brugnoli *et al.*, 1988; Brugnoli & Farquhar, 1998). We have adopted a method from Brugnoli *et al.* (1988) to extract leaf soluble carbohydrates from bulk leaf material (West *et al.*, 2007). Analytical tests indicate that our extraction method does not induce sample fractionation, and that our approach is reproducible (West *et al.*, 2007). Leaf soluble carbohydrates were extracted in distilled water, followed by a purification procedure according to Brugnoli *et al.* (1988), and then freeze-dried for 72 h. Carbon isotope ratios were determined for leaf soluble carbohydrates using an elemental analyser (Model 1108, Carlo Erba, Milano, Italy) coupled with a Finnigan MAT delta S isotope ratio mass spectrometer (San Jose, CA, USA). Carbon isotope ratios were calculated using  $\delta$  notation:

$$\delta = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) * 1000 \quad (8)$$

where  $R$  is the ratio of the heavy isotope ( $^{13}\text{C}$ ) to the lighter isotope ( $^{12}\text{C}$ ), and the standard was V-PDB. The instrument error (twice the SD) associated with each observation was  $\pm 0.1\%$ .

We combined measurements of  $\delta^{13}\text{C}$  with measurements of  $g_s$  to estimate short-term canopy photosynthetic rates ( $A$ ) (Hu *et al.*, 2010). We assumed that  $\delta^{13}\text{C}$  of leaf soluble carbohydrates only reflected canopy gas exchange parameters of the day in which the leaves were collected at dusk. Photosynthetic rates were estimated by first calculating the carbon isotope discrimination factor ( $\Delta$ ) as:

$$\Delta = \frac{\delta^{13}\text{C}_a - \delta^{13}\text{C}}{1 + \delta^{13}\text{C}} \quad (9)$$

where  $\delta^{13}\text{C}_a$  is the carbon isotopic composition of free air. For  $\delta^{13}\text{C}_a$ , we used values reported by Pataki *et al.* (2006) for the Salt Lake Valley:  $-9.0\%$ . The intercellular  $\text{CO}_2$  concentration ( $c_i$ ) was solved for by calculating the ratio  $c_i : c_a$  according to Farquhar *et al.* (1982):

$$c_i : c_a = \frac{\Delta - a}{b - a} \quad (10)$$

where  $c_a$  is the canopy  $\text{CO}_2$  concentration, assumed to equal that of free air,  $a$  is the fractionation due to diffusion in air (4.4%), and  $b$  is the fractionation due to C3 carboxylation (27%). Because the artificial stream system was constructed in a heavily urbanized area, we used atmospheric  $\text{CO}_2$  data collected at the University of Utah, and available at: <http://co2.utah.edu/>. Mean daytime  $\text{CO}_2$  on days that leaves were collected ranged from 387 to 390  $\mu\text{l l}^{-1}$ .  $A$  was then calculated as:

$$A = (c_a - c_i) * \frac{g_s}{1.6} \quad (11)$$

where 1.6 is the ratio of diffusivities of water and  $\text{CO}_2$  in air.

### Bulk leaf traits

Leaf mass per area (LMA), nitrogen per unit mass ( $N_{\text{mass}}$ ), nitrogen per unit leaf area ( $N_{\text{area}}$ ), and  $C_{\text{mass}} : N_{\text{mass}}$  ratios were measured in a second subset of leaves collected on May 20 (day 140), June 30 (day 181), and August 24 (day 236), of the 2007-growing season. Fresh leaves were scanned with a high-resolution computer scanner, and one-sided leaf area was measured using public domain NIH image program software (Image-J). Leaves were then oven-dried for 72 h at 70 °C and weighed to the nearest 0.01 g to obtain LMA ( $\text{g cm}^{-2}$ ). Leaves were ground to a fine powder and analysed for carbon and nitrogen content using an elemental analyser coupled with a Finnigan MAT delta S isotope ratio mass spectrometer (see above). Leaf nitrogen content per unit leaf area was calculated by multiplying  $N_{\text{mass}}$  by LMA. The photosynthetic nitrogen use efficiency (NUE), the rate of carbon assimilation per unit nitrogen (NUE,  $\mu\text{mol mol}^{-1} \text{s}^{-1}$ ), was evaluated by multiplying  $A$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) by  $N_{\text{area}}$  ( $\text{mol m}^{-2}$ ).

### Statistics

In habitats where soil water is not limiting (i.e. along perennial stream margins), patterns of plant water use are largely coupled to atmospheric drivers. Therefore, we modelled  $J_s$  against  $vpd$  and  $Q$ . The relationship between  $J_s$  and atmospheric drivers is non-linear and thus was fitted against  $\ln(vpd)$  and  $\ln(Q)$ . We also used a nonlinear regression model to fit  $g_s$  to  $vpd$

according to Oren *et al.* (1999), Wullschlegel *et al.* (2002), and Hultine *et al.* (2008a):

$$g_s = b - m * \ln vpd \quad (12)$$

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

Regression analysis was performed to relate  $J_s$  and  $g_s$  of each gender to  $vpd$  and  $Q$  after both atmospheric variables were log transformed. Gender differences in  $J_s$  and  $g_s$  in response to  $\ln(vpd)$ ,  $\ln(Q)$ , and the interactions  $\ln(vpd)*\text{gender}$ , and  $\ln(Q)*\text{gender}$  were analysed using analysis of covariance (ANCOVA). Mean gender differences in aboveground productivity and allometry,  $J_s$ ,  $g_s$ ,  $A$ , and bulk leaf traits during individual sampling periods were analysed using a standard parametric Student's  $t$ -test. In cases of unequal variance between female and male populations, a Welch correction was added to the student's  $t$ -test. Differences in  $J_s$ ,  $g_s$ ,  $A$ , and leaf traits on days that we sampled leaves were assessed by repeated measures analysis of variance (MANOVA) where multiple measurements on a given plant constituted the repeated variables (Potvin *et al.*, 1990). In each MANOVA analysis the main effect of gender was tested as a between subjects effect. JMP 8.0 (SAS institute Inc., Cary, NC, USA.) was used for all statistical analysis, with  $P \leq 0.05$  as the significance level.

## Results

### Aboveground productivity and allometry

Changes in mean basal diameter ( $D_b$ ), canopy height ( $z$ ), and canopy radius ( $R_c$ ) during the growing season were similar between genders. Mean  $D_b$  increased 17% and  $z$  increased 2% in both female and male trees, while  $R_c$  increased 13% and 10% in female and male trees respectively (Table 2). Male trees maintained slightly taller canopies and greater  $R_c$  before and after the growing season, while  $D_b$  remained equal between genders (Table 2). Alternatively,  $A_1$  increased by 28% in female trees during the growing season but actually decreased by 4% in male trees (Table 2). Consequently, LAI was 36% higher in female trees at the conclusion of the growing season even though both genders expressed similar LAI values at the onset of the growing season (Table 2). Mean  $A_1 : A_s$  and  $A_1 : A_b$  decreased 3% and 7%, respectively, in female trees during the growing season, while the same allometric variables decreased 24% and 29%, respectively, in male trees (Table 2).

### Sap flux and canopy stomatal conductance

During May and June,  $\ln(vpd)$  explained 46% ( $F = 1217$ ,  $P < 0.0001$ ) and 47% ( $F = 1278$ ,  $P < 0.0001$ ) of the variation in mean daytime  $J_s$  of female and male trees respectively (Fig. 2a). Over the same period,  $\ln(Q)$

**Table 2** Allometric data on female ( $n = 18$  trees) and male ( $n = 13$  trees) *Acer negundo* trees occurring at an artificial stream system in Salt Lake City, UT during the 2007 growing season. Measurements include stem diameter ( $D_s$ ), Sapwood area ( $A_s$ ), tree height ( $z$ ), canopy radius ( $R_c$ ), leaf area ( $A_l$ ), leaf area index (LAI), leaf area to sapwood area ratio ( $A_l : A_s$ ) and leaf area to basal area ratio ( $A_l : A_b$ ). Numbers in parentheses represent the SE of the means.  $P$ -values represent the comparison of means between female and male populations. Numbers in bold represent population differences in mean values between genders ( $P < 0.05$ )

Gender	$D_s$ (cm)	$A_s$ (cm <sup>2</sup> )	$z$ (m)	$R_c$ (m)	$A_l$ (m <sup>2</sup> )	LAI (m <sup>2</sup> m <sup>-2</sup> )	$A_l : A_s$ (m <sup>2</sup> cm <sup>-2</sup> )	$A_l : A_b$ (m <sup>2</sup> cm <sup>-2</sup> )
Spring 2007								
Female	8.8 (0.4)	41.7 (3.0)	3.72 (0.19)	1.44 (0.05)	25.19 (1.69)	3.94 (0.27)	0.64 (0.04)	0.43 (0.03)
Male	8.9 (0.4)	44.9 (3.1)	4.25 (0.12)	1.65 (0.08)	30.79 (4.06)	3.85 (0.65)	0.66 (0.05)	0.46 (0.03)
$P$	0.79	0.57	<b>0.026</b>	<b>0.024</b>	0.22	0.90	0.75	0.47
Fall 2007								
Female	10.3 (0.4)	55.0 (3.8)	4.06 (0.24)	1.63 (0.05)	31.28 (2.49)	3.80 (0.27)	0.59 (0.04)	0.38 (0.03)
Male	10.4 (0.5)	57.0 (4.1)	4.60 (0.15)	1.79 (0.06)	29.17 (4.17)	2.80 (0.26)	0.50 (0.04)	0.33 (0.02)
$P$	0.82	0.73	0.06	<b>0.050</b>	0.65	<b>0.017</b>	0.15	0.17
Relative change from Spring to Fall								
Female	0.17 (0.01)	0.33 (0.03)	0.08 (0.02)	0.13 (0.02)	0.28 (0.11)	-0.04 (0.08)	-0.03 (0.08)	-0.07 (0.08)
Male	0.17 (0.01)	0.27 (0.04)	0.08 (0.02)	0.10 (0.03)	-0.04 (0.04)	-0.18 (0.06)	-0.24 (0.04)	-0.29 (0.04)

explained 67% ( $F = 2873$ ,  $P < 0.0001$ ) and 75% ( $F = 4353$ ,  $P < 0.0001$ ) of the variation in mean daytime  $J_s$  of female and male trees respectively (Fig. 2b). In July and August,  $\ln(vpd)$  explained 38% ( $F = 1064$ ,  $P < 0.0001$ ) and 34% ( $F = 917$ ,  $P < 0.0001$ ) of the variation in mean daytime  $J_s$  of female and male trees respectively (Fig. 2c), while  $\ln(Q)$  explained 72% ( $F = 4608$ ,  $P < 0.0001$ ) and 82% ( $F = 7726$ ,  $P < 0.0001$ ) of the variation in mean daytime  $J_s$  of female and male trees respectively (Fig. 2d). Mean daily  $J_s$  (i.e. mean  $J_s$  during daylight hours) was virtually equal between female and male trees in May : June, while mean  $J_s$  in July and August was 25% higher in male trees than in female trees (Fig. 3). Differences in  $J_s$  between genders begin to clearly appear in early July, between days 180 and 190 when daytime  $vpd$  was consistently at its highest point during the growing season (Fig. 3).

The response of daytime  $J_s$  to climate drivers  $\ln(vpd)$  and  $\ln(Q)$  was tested in an ANCOVA model.  $J_s$  in May : June was highly correlated with both  $vpd$  ( $F = 882$ ,  $P < 0.0001$ ) and  $Q$  ( $F = 3417$ ,  $P < 0.0001$ ). Gender had no impact on  $J_s$  during this period ( $F = 0.17$ ,  $P = 0.68$ ), although there was considerable interaction between  $vpd$  and gender ( $F = 14.8$ ,  $P < 0.0001$ ) and  $Q$  and gender ( $F = 30.6$ ,  $P < 0.0001$ ). In July : August,  $J_s$  was also highly correlated with  $vpd$  ( $F = 1307$ ,  $P < 0.0001$ ), and  $Q$  ( $F = 5915$ ,  $P < 0.0001$ ), but unlike in May : June, there was also strong gender influence on  $J_s$  ( $F = 1260$ ,  $P < 0.0001$ ). Likewise, the interaction  $Q$ \*gender had a strong effect on  $J_s$  ( $F = 316$ ,  $P < 0.0001$ ) while  $vpd$ \*gender had a weak effect on  $J_s$  ( $F = 4.07$ ,  $P = 0.0438$ ).

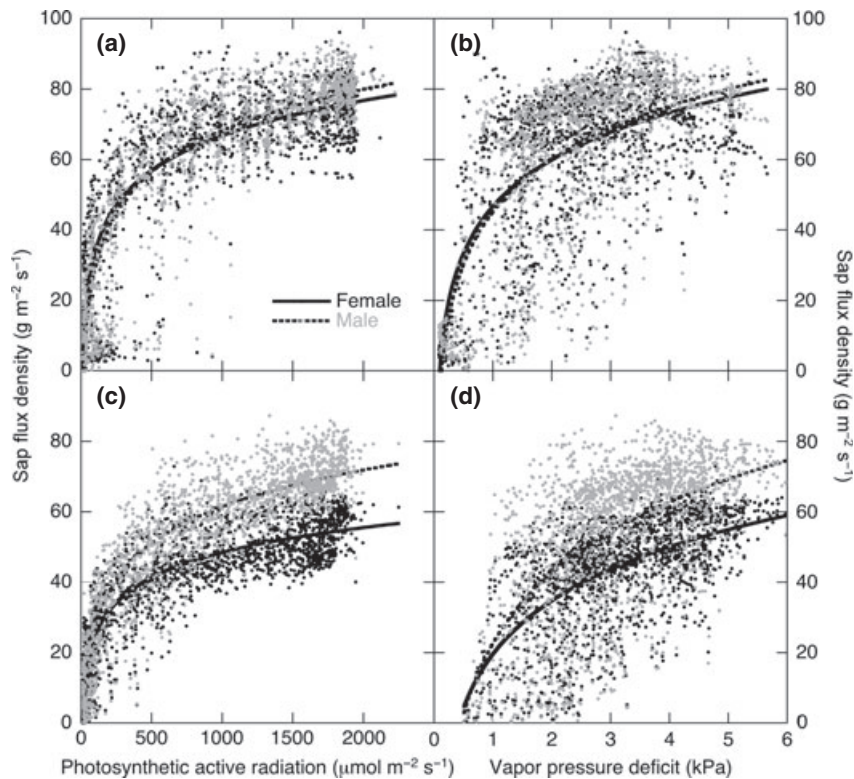
In May and June, mean daily  $g_s$ , per unit leaf area was highly correlated to  $\ln(vpd)$  in both female ( $R^2 = 0.94$ ,  $F = 635$ ,  $P < 0.0001$ ), and male ( $R^2 = 0.96$ ,  $F = 1119$ ,  $P < 0.0001$ ) trees (Fig. 4a). Mean  $g_s$  was on

average 12% higher per day in female trees than male trees, and strong differences were detected in each gender's relationship with mean daytime  $vpd$  ( $F = 45.2$ ,  $P < 0.0001$ ). There was also a significant interaction between  $vpd$  and gender ( $F = 12.9$ ,  $P = 0.0005$ ), suggesting the differences in  $g_s$  between genders were largest when  $vpd$  was relatively low (Fig. 4a). In July and August,  $g_s$  was again highly correlated with  $vpd$  for both female ( $R^2 = 0.71$ ,  $F = 262$ ,  $P < 0.0001$ ) and male ( $R^2 = 0.85$ ,  $F = 583$ ,  $P < 0.0001$ ) trees (Fig. 4b). However, during this period, mean  $g_s$  was ca. 11% higher in males than in females. Significant differences were also detected in each gender's response to  $vpd$  ( $F = 36.0$ ,  $P < 0.0001$ ), along with a weak interaction between  $vpd$  and gender ( $F = 3.77$ ,  $P = 0.0544$ ).

We quantified the sensitivity of  $g_s$  to  $vpd$  by calculating the slope in Eqn 12 (i.e.  $-m$ ) in proportion to an extrapolated maximum value that is in this case the intercept of Eqn 12 ( $g_{sref}$ ) (Monteith, 1995; Oren *et al.*, 1999). In this way stomatal sensitivity to changes in  $vpd$  can be assessed without incurring autocorrelation error. Over the course of the growing season, mean daily  $g_s : g_{sref}$  was highly correlated to  $\ln(vpd)$  in both female ( $R^2 = 0.71$ ,  $F = 260$ ,  $P < 0.0001$ ) and male ( $R^2 = 0.85$ ,  $F = 560$ ,  $P < 0.0001$ ) trees (Fig. 4c). The relationship between mean  $g_s : g_{sref}$  and  $\ln(vpd)$  was gender-dependent ( $F = 7.72$ ,  $P = 0.006$ ) with male trees having a slightly higher mean  $g_s : g_{sref}$  (0.55) than female trees (0.51). There was no interaction between gender and  $\ln(vpd)$  ( $F = 0.55$ ,  $P = 0.46$ ).

#### Seasonal patterns of plant water use and carbon uptake

Seasonal patterns of plant water use and carbon uptake were investigated in detail on 5 days during the growing season: May 20 (Julian day 140), June 13 (day 164),



**Fig. 2** Relationship between mean daytime sap flux density ( $J_s$ ) in female ( $n = 18$ ) and male ( $n = 13$ ) *Acer negundo* trees and environmental drivers: daytime photosynthetic active radiation ( $Q$ ) and daytime vapour pressure deficit ( $vpd$ ). Data were collected every 30 min at an artificial stream and riparian system in Salt Lake City, UT from (a, b) May 14 to June 30, 2007 and (c, d) July 1 to August 31, 2007.

June 30 (day 181), July 30 (day 211), and August 24 (day 236). Although, total daily  $Q$  was nearly identical on all of these days, mean daytime  $vpd$  ranged from 2.44 kPa (day 164) to 3.62 kPa (days 181, 211) (Fig. 5a).

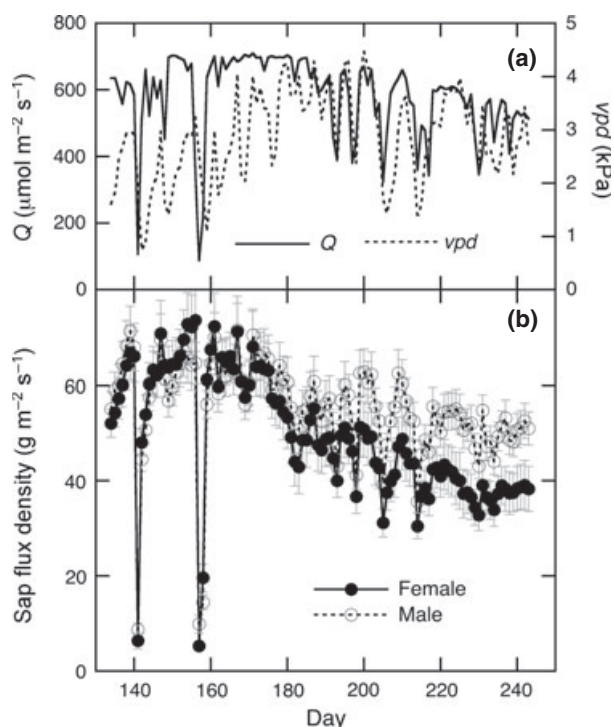
Both female and male trees had canopies that were well coupled to the atmosphere such that the mean canopy  $\Omega$  was never higher than 0.08 for either female or male trees on any day canopy coupling was evaluated (Table 3). Consequently,  $g_s$  closely approximated  $g_c$  throughout the growing season (Table 3). No differences in  $g_s$  between female and male trees were detected over the growing season with a MANOVA model ( $P = 0.47$ , Table 4), although mean  $g_s$  was on average 10% higher in male trees than in female trees (Fig. 5a). Likewise,  $g_s$  of male trees progressively increased relative to female trees throughout the growing season resulting in a significant relationship between  $g_s$  and time\*gender interaction ( $P = 0.0463$ , Table 4). Stomatal conductance was 35% higher in male than in female trees on day 211 ( $F = 3.57$ ,  $P = 0.0688$ , Fig. 5a), and 53% higher in males on day 236 ( $F = 13.65$ ,  $P = 0.0009$ , Fig. 5a).

Carbon isotope ratios ( $\delta^{13}C$ ) were measured in soluble sugars of sun exposed leaves to investigate

short-term patterns of  $c_i : c_a$ . There was no effect of gender ( $P = 0.11$ ), or time\*gender interaction ( $P = 0.25$ ) on  $\delta^{13}C$  during the growing season (Table 4). However,  $\delta^{13}C$  of female trees was consistently higher (less negative) than male trees after day 181 (Fig. 5b). Measurements of  $\delta^{13}C$  were combined with measurements of  $g_s$  to estimate carbon uptake (i.e. Eqn 11). Assimilation throughout the growing season was similar between female and male trees ( $P = 0.15$ , from Repeated Measures, Table 4), except on day 236 when  $A$  was 21% higher in males compared with females ( $F = 5.82$ ,  $P = 0.0224$ , Fig. 5c).

We combined measurements of sap flux-scaled transpiration ( $E_{tree}$ ) with measurements of tree allometry and  $\delta^{13}C$  to estimate whole-tree carbon assimilation ( $A_{tree}$ ) and WUE ( $A_{tree} : E_{tree}$ ). No differences in  $E_{tree}$  between female and male trees were detected with a MANOVA model ( $P = 0.33$ , Table 4), although there was an effect of time\*gender on  $E_{tree}$  ( $P = 0.0347$ ), demonstrating that water use of female trees declined relative to male trees during the growing season (Fig. 6a). In fact,  $E_{tree}$  on day 236 was 47% higher in males compared with females ( $F = 7.41$ ,  $P = 0.0108$ ). Overall, water use was on average 17%

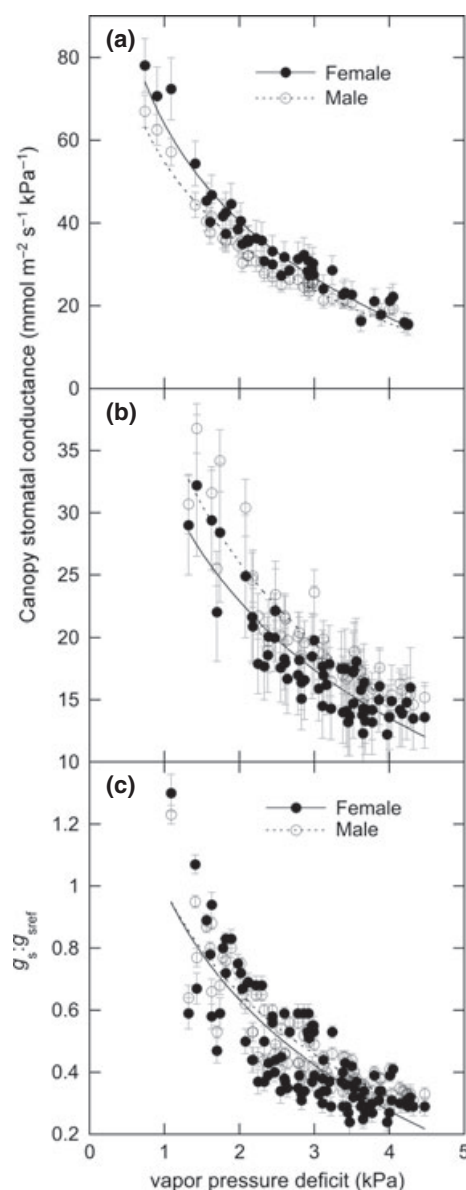




**Fig. 3** Seasonal patterns of (a) daytime photosynthetic active radiation ( $Q$ ) and daytime vapour pressure deficit ( $vpd$ ) and (b) mean daily stem sap flux density ( $J_s$ ) in female ( $n = 18$ ) and male ( $n = 13$ ) *Acer negundo* trees at an artificial stream and riparian system in Salt Lake City, UT. Data were collected from May 14 (day 134) to August 31 (day 243), 2007. Error bars represent  $\pm 1$  SE of the mean.

higher in males relative to females throughout the growing season (Fig. 6a).

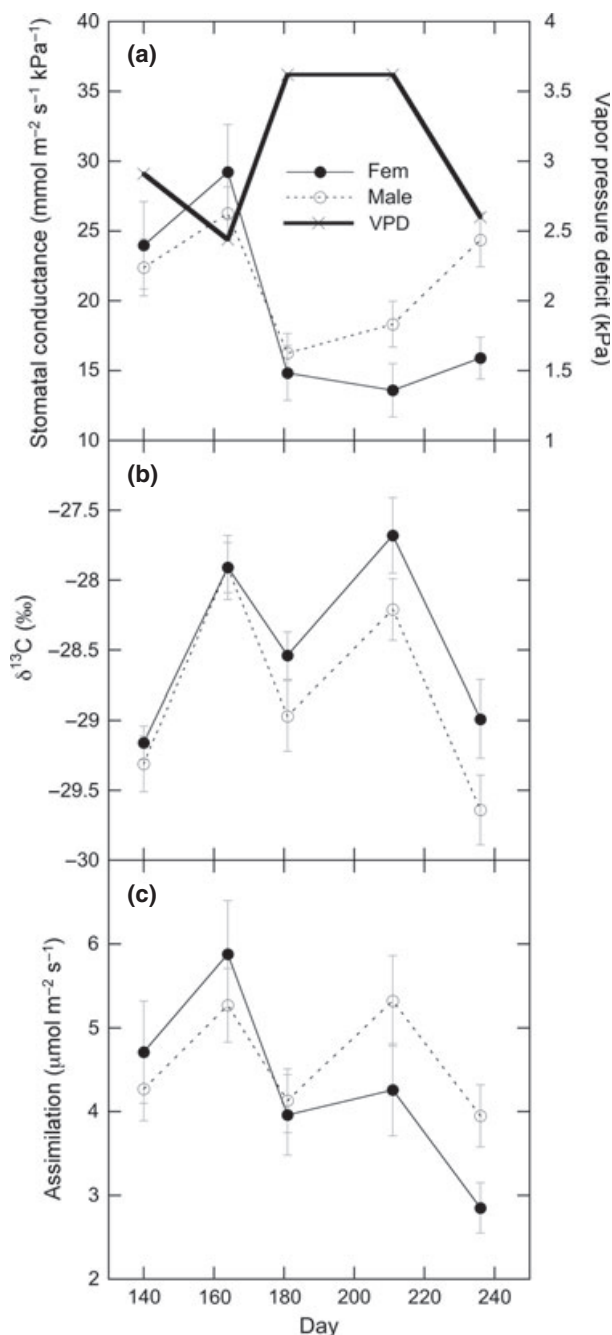
As with  $E_{tree}$ , the Manova model did not detect differences between genders in  $A_{tree}$  over the course of the growing season ( $P = 0.55$ , Table 4). Likewise, there was no effect of time\*gender on  $A_{tree}$  ( $P = 0.82$ , Table 4). Nevertheless,  $A_{tree}$  on day 236 was 32% higher in male trees, although differences on this day were only marginally significant ( $F = 3.00$ ,  $P = 0.0937$ , Fig. 6b). Overall, assimilation was on average 11% higher in males relative to females over the course of the growing season (Fig. 6b). Unlike  $E_{tree}$  and  $A_{tree}$ , the Manova model showed an effect of gender on  $A_{tree} : E_{tree}$  ( $P = 0.0347$ , Fig. 6c; Table 4). There was no effect of time\*gender ( $P = 0.40$ , Table 4), suggesting that differences between genders remained fairly constant throughout the growing season (Fig. 6c). Differences were largest on day 211 ( $F = 6.35$ ,  $P = 0.0175$ ), where mean  $A_{tree} : E_{tree}$  of females was 12% higher than in males (Fig. 6c). Overall, females had a 7% higher  $A_{tree} : E_{tree}$  over the growing season compared with males (Fig. 6c).



**Fig. 4** Relationship between mean daily canopy stomatal conductance per unit leaf area ( $g_s$ ) and mean daytime vapour pressure deficit ( $vpd$ ) in female and male *Acer negundo* trees at an artificial stream and riparian system in Salt Lake City, UT. Data were collected from (a) May 14 to June 30, 2007 and (b) July 1 to August 31, 2007. Panel c shows  $g_s$  of female and male plants, normalized by a reference  $g_s$  ( $g_{sref}$ ), defined at  $vpd = 1$  kPa for data from May 14 to August 31. Error bars represent  $\pm 1$  SE of the mean.

#### Bulk leaf traits

Female *A. negundo* trees consistently displayed a higher LMA, a higher percent leaf N concentration per unit mass ( $N_{mass}$ ), a lower  $C_{mass} : N_{mass}$  ratio, and a higher N per unit leaf area concentrations ( $N_{area}$ ) than male *A.*



**Fig. 5** Physiological traits of leaves collected from female and male *Acer negundo* trees at an artificial stream and riparian system in Salt Lake City, UT. Leaves were collected on May 20 (day 140), June 13 (day 164), June 30 (DOY 181), July 30 (day 211), and August 24 (day 236), 2007. (a) Mean daytime canopy stomatal conductance per unit leaf area ( $g_s$ ) and mean daytime vapour pressure deficit ( $vpd$ ), (b) carbon isotope ratios ( $\delta^{13}\text{C}$ ) of leaf soluble sugars; and (c) carbon assimilation per unit leaf area ( $A$ ) calculated from measurements of  $g_s$  and  $\delta^{13}\text{C}$ . Error bars represent  $\pm 1$  SE of the mean.

*negundo* trees throughout the growing season (Fig. 7). Differences in LMA ranged from 8 to 10% (Fig. 7a), while differences in  $N_{\text{mass}}$  ranged from 10 to 12% (Fig. 7b). Differences in  $C_{\text{mass}} : N_{\text{mass}}$  ranged from 7 to 12% (Fig. 7c), while differences in  $N_{\text{area}}$  ranged from 19 to 22% (Fig. 7d). Photosynthetic NUE decreased dramatically in female trees during the growing season from a high of  $60.8 \mu\text{mol mol}^{-1} \text{s}^{-1}$  on day 140 to a low of  $34.7 \mu\text{mol mol}^{-1} \text{s}^{-1}$  on day 236, while NUE of male trees stayed fairly constant and only ranged from  $64.5 \mu\text{mol mol}^{-1} \text{s}^{-1}$  on day 140 to  $58.5 \mu\text{mol mol}^{-1} \text{s}^{-1}$  (Fig. 8).

## Discussion

In high-resource habitats in the intermountain western United States, the sex ratio of *A. negundo* is skewed such that female trees occur at higher frequencies than co-occurring males (Freeman *et al.*, 1976; Dawson & Ehleringer, 1993; Ward *et al.*, 2002). These sex ratio patterns likely reflect physiological tradeoffs associated with the higher cost of reproduction in females that result in higher resource uptake and growth relative to males. Previous investigations have found that gas exchange parameters, including  $g_s$ ,  $A$ , and  $A : E$  were over 40% higher in mature female trees than co-occurring males along a perennial stream in Red Butte Canyon (Table 5). Likewise, female *A. negundo* trees along stream margins tend to build larger canopies with higher leaf areas (Hultine *et al.*, 2007b) and have faster canopy and radial growth rates than streamside males (Dawson & Ehleringer, 1993; Ward *et al.*, 2002). Differences in resource uptake, canopy structure, and growth gives streamside females a competitive advantage over streamside males, and potentially over other co-occurring tree species as survival in these high-productive habitats depends in part, on canopy dominance and resource acquisition.

Results from this study show that climate change may disrupt the competitive advantage female *A. negundo* trees have over co-occurring males in high-resource habitats. At the lower-elevation artificial stream system, where growing season temperatures were 6–7 °C warmer than where the *A. negundo* trees originated from, the relative physiological advantage of female trees over males was no longer apparent (Table 5). In fact, higher flux rates tended to skew towards males under progressively warmer and drier conditions such that  $E_{\text{tree}}$  and  $A_{\text{tree}}$  were 47 and 32% higher, respectively, in male trees than in females during the latter part of the growing season in August (Fig. 3 and 6). This apparent local adaptation suggests that an increase in growing season temperature may reverse the relative dominance of the two genders

**Table 3** Wind speed ( $\mu$ ), measured 3 m above the ground surface, mean boundary layer conductance ( $g_{bl}$ ), canopy conductance ( $g_c$ ), canopy stomatal conductance ( $g_s$ ) per unit leaf area and mean canopy decoupling coefficient ( $\Omega$ ) for mature female and male *Acer negundo* trees growing at an artificial stream system in Salt Lake City, UT. Data were collected on May 20 (DOY 140), June 13 (DOY 164), June 30 (DOY 181), July 30 (DOY 211), and August 24 (DOY 236) 2007. Numbers in parentheses represent  $\pm 1$  SE of the mean

Date	Daytime $\mu$ ( $m\ s^{-1}$ )	$g_{bl}$ ( $mmol\ m^{-2}\ s^{-1}$ )		$g_c$ ( $mmol\ m^{-2}\ s^{-1}$ )		$g_s$ ( $mmol\ m^{-2}\ s^{-1}$ )		$\Omega$	
		Female	Male	Female	Male	Female	Male	Female	Male
20-May	2.49	2468	2462	69.0 (8.9)	64.6 (6.0)	69.8 (9.1)	65.2 (5.9)	0.07	0.07
13-Jun	1.80	2086	2080	70.2 (8.8)	63.3 (4.5)	71.3 (8.3)	64.1 (4.6)	0.08	0.08
30-Jun	2.46	2443	2437	53.3 (7.4)	58.4 (5.0)	53.7 (7.1)	58.8 (5.1)	0.06	0.07
30-Jul	2.42	2393	2387	48.9 (7.2)	65.9 (6.1)	49.2 (6.9)	66.4 (5.9)	0.06	0.08
24-Aug	1.94	2107	2102	41.0 (4.2)	62.7 (4.9)	41.3 (3.9)	63.3 (5.0)	0.05	0.07

**Table 4**  $F$  values from repeated measures (MANOVA) analysis of canopy stomatal conductance ( $g_s$ ), carbon isotope ratios of leaf soluble sugars ( $\delta^{13}C$ ), carbon assimilation per unit leaf area ( $A_{leaf}$ ), whole-tree carbon assimilation ( $A_{tree}$ ), whole-tree transpiration ( $E_{tree}$ ), and  $A_{tree} : E_{tree}$ . Data were collected on May 20 (DOY 140), June 13 (DOY 164), June 30 (DOY 181), July (DOY 211), and August 24 (DOY 236), 2007

	$g_s$	$\delta^{13}C$	$A_{leaf}$
Time	52.20***	31.16***	48.79***
Gender	0.54	2.77	0.70
Time*Gender	2.81*	1.43	1.98

	$E_{tree}$	$A_{tree}$	$A_{tree} : E_{tree}$
Time	15.54***	39.71***	113.6***
Gender	1.00	0.36	4.91*
Time*Gender	4.15*	0.38	1.04

\* $P < 0.05$ .

\*\* $P < 0.001$ .

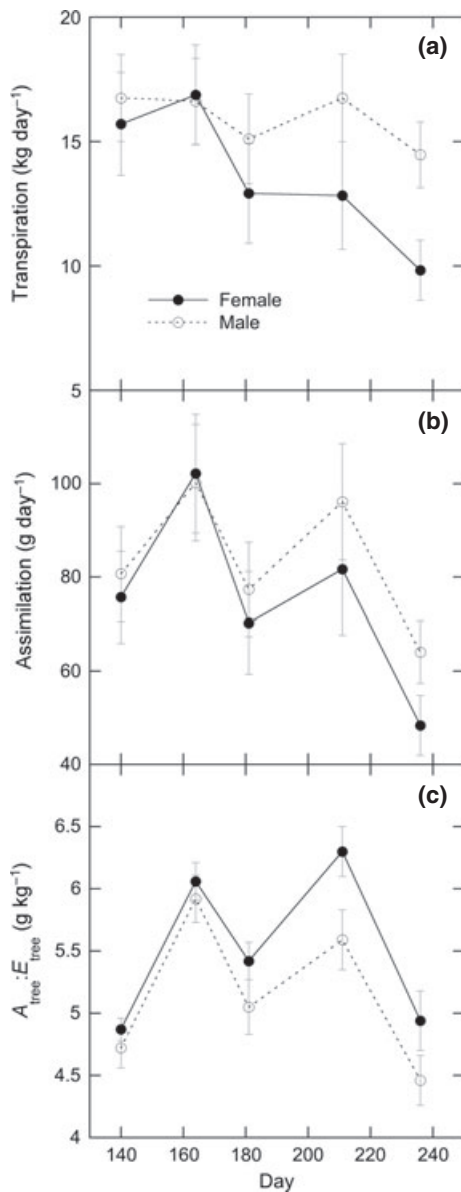
\*\*\* $P < 0.0001$ .

along stream margins in arid and semi-arid regions of the West. If climate change results in the predicted warmer growing season temperatures, then it is likely that the population structure of *A. negundo* may be significantly altered in ways that will not favour successful recruitment and establishment of this species along lower-elevation riparian corridors in the arid western US.

Seasonal patterns of resource uptake may be linked to the timing of flowering that differs between genders. Male *A. negundo* trees at the artificial stream system flower in April just before leaf flush, whereas female trees flower from mid May to mid June, well after the onset of leaf emergence. Males therefore draw on stored carbohydrates from the previous year's photosynthate. Females on the other hand 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 (Hultine *et al.*, 2008a). Unlike under native climate conditions, resource uptake was no higher in female trees than in male trees during the period of female flowering (Fig. 3 and 6). If warmer growing season temperatures inhibits resource uptake during the critical period of flowering, then it is plausible that flower production in female *A. negundo* will ultimately decrease with climate change.

The contrasting physiological response between genders to warmer temperatures and drier atmospheric conditions suggests that female and male trees have evolved different traits related to water transport and whole-plant water balance. One explanation is that female trees tend to have xylem with larger diameter conduits and pit pores with higher porosities than co-occurring males. In this case, females would have a higher xylem conducting efficiency to support larger canopies and higher canopy gas exchange rates under well-watered conditions with the possible tradeoff of being less tolerant to drought than males (Zimmermann, 1983; Tyree *et al.*, 1994; Hacke *et al.*, 2001; Wheeler *et al.*, 2005). However, despite having higher transpiration rates and higher maximum stomatal conductance, streamside female trees in RBC had stem xylem that was no more efficient, or no less susceptible to cavitation than co-occurring males (Hultine *et al.*, 2008a). Nevertheless, as with this study, female trees in RBC expressed a larger May to August decline in canopy  $g_s$  than males. Perhaps the larger decline in  $g_s$  is simply an artifact of the disproportionately higher maximum canopy  $g_s$  in female trees compared with males (Dawson & Ehleringer, 1993; Hultine *et al.*, 2008a). Alternatively, the root systems of female trees may have been more vulnerable to cavitation than co-occurring males, although at present there are no data that



**Fig. 6** Whole-plant water use and carbon uptake of female and male *Acer negundo* trees at an artificial stream and riparian system in Salt Lake City, UT on May 20 (day 140), June 13 (day 164), June 30 (day 181), July 30 (day 211), and August 24 (day 236), 2007. Data were calculated from measurements of sap flux,  $\delta^{13}\text{C}$  of soluble leaf sugars, and allometric measurements of total leaf area per tree. (a) Whole-plant transpiration per day ( $E_{\text{tree}}$ ), (b) whole-plant carbon assimilation per day ( $A_{\text{tree}}$ ) and (c) whole-plant water use efficiency ( $A_{\text{tree}} : E_{\text{tree}}$ ). Error bars represent  $\pm 1$  SE of the mean.

compare belowground xylem functional traits between female and male *A. negundo*.

A second possible explanation is that female trees maintained a much larger leaf area to absorbing root area ratio compared with males. If all else were equal

(including  $g_s$  per unit leaf area), increases in leaf area to root area would increase the water potential gradient from canopy to rhizosphere, resulting in either higher xylem cavitation and/or greater losses in rhizosphere conductivity (Sperry *et al.*, 1998), either of which would decrease water transport to the canopy regardless of cavitation vulnerability. Although we do not have data for leaf area root area ratios, female trees at the experimental stream system did maintain more leaf area relative to males, despite having a lower  $J_s$  throughout the latter half of the growing season.

A third potential hypothesis is that the stomatal sensitivity of female trees to internal water potential gradients and/or leaf to air  $vpd$  is lower than co-occurring males. In other words, female trees may operate with a significantly narrower safety margin between the actual rate of transpiration and the critical rate of transpiration ( $E_{\text{crit}}$ ) that will cause runaway cavitation (Sperry *et al.*, 1998, 2002). However, sap flux data from RBC and the artificial stream system do not support the hypothesis of female *A. negundo* having a more 'anisohydric' stomatal regulation than males. As mentioned above, female *A. negundo* in RBC display a much larger seasonal decline in  $g_s$  compared with co-occurring males (Hultine *et al.*, 2008a), and in this study, mean  $g_s : g_{s\text{ref}}$  was somewhat higher in male trees compared with females (0.55 compared to 0.51). Although  $g_s : g_{s\text{ref}}$  of both genders fell below the theoretical value of 0.6 (Oren *et al.*, 1999; Ewers *et al.*, 2005), indicating some anisohydric behaviour, the higher  $g_s : g_{s\text{ref}}$  (i.e. lower  $-m$ ) in male trees suggests they operated with a somewhat lower stomatal sensitivity to increases in  $vpd$ . The lower  $-m$  in male trees may also be a function of having a lower maximum  $g_s$  than females, resulting in a smaller overall reduction in  $g_s$  compared with females. In RBC, for example, maximum  $g_s$  was about twofold higher in female *A. negundo* than in males, before converging on similar mean daily  $g_s$  values during latter periods of the growing season. In this study, maximum mean daily  $g_s$  during the coolest period of the growing season was 15–20% higher in female trees (Fig. 4a). As in RBC, female trees again displayed a substantially larger seasonal reduction in mean daily  $g_s$  than males (compare 4a–4b). Therefore, if we assume that the genders share similar hydraulic architectures, the higher maximum  $g_s$  suggest that warmer air temperatures and subsequently higher  $vpd$  could edge female trees precariously close to the  $E_{\text{crit}}$  if they are adapted to a narrow range of temperature regimes (O'Neill *et al.*, 2008; Grady *et al.*, 2011, 2013).

Unlike the gas exchange parameters, differences in leaf nitrogen between genders at the artificial stream system mirrored those previously reported in RBC (Table 5). Over the course of the growing season, LMA,

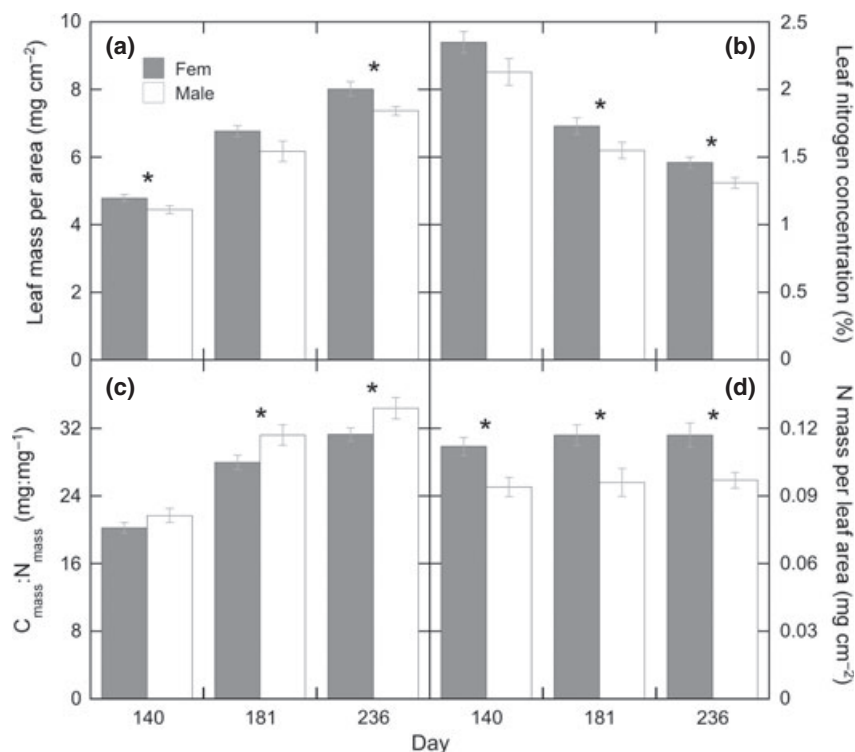


**Table 5** Physiological traits of female and male *Acer negundo* trees occurring in Red Butte Canyon, near Salt Lake City, UT and at an artificial stream system in Salt Lake City, UT. Traits include carbon isotope discrimination ( $\Delta$ ), percent leaf N per mass ( $N_{\text{mass}}$ ), stomatal conductance ( $g_s$ ), carbon assimilation rate ( $A$ ), and water use efficiency ( $A : E$ ), where  $E$  is transpiration rate. Stomatal conductance,  $A$  and  $A : E$  data reported by Dawson and Ehleringer are from instantaneous leaf gas exchange measurements

	$\Delta$ (%)	$N_{\text{mass}}$ (%)	$g_s$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	$A$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$A : E$ ( $\text{mmol mol}^{-1}$ )
Red Butte Canyon					
Female	21.51*	3.22*	460*	144.8**	14.89*
Male	20.03*	2.68*	270*	74.1**	8.92*
% difference	6.9	16.8	41.3	48.8	40.1
Artificial stream system (Salt Lake City)					
Female	20.03	1.84	57.1	4.33	8.28
Male	20.40	1.66	63.6	4.59	7.84
% difference	-1.8	9.8	-11.4	-6.0	5.3

\*Data are from Dawson & Ehleringer (1993).

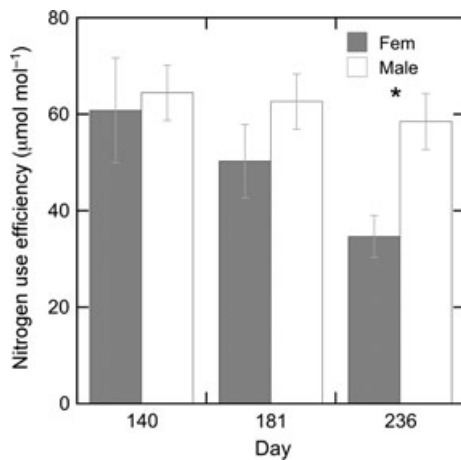
\*\*Data are from Hultine *et al.* (2008a).



**Fig. 7** Bulk leaf traits of leaves collected from female and male *Acer negundo* trees at an artificial stream and riparian system in Salt Lake City, UT on May 20 (day 140), June 30 (day 181), and August 24 (day 236), 2007. (a) Leaf mass per area (LMA), (b) Percent leaf nitrogen concentration per unit mass  $N_{\text{mass}}$ , (c) leaf carbon to nitrogen concentrations per unit mass ( $C_{\text{mass}} : N_{\text{mass}}$ ) and (d) leaf nitrogen content per unit leaf area ( $N_{\text{area}}$ ). Error bars represent  $\pm 1$  SE of the mean. Asterisks show significant differences between genders ( $P < 0.05$ ).

$N_{\text{mass}}$  and  $N_{\text{area}}$  were all higher in the leaves of female trees, while  $C_{\text{mass}} : N_{\text{mass}}$  remained lower in female trees compared with males. Because the large majority of leaf N is present in either the chloroplasts or photosynthetic enzymes (primarily RUBISCO in C3 plants) (Evans & Seemann, 1989), there is a strong positive

relationship between the photosynthetic capacity of a leaf and its N concentration (Field & Mooney, 1986; Evans, 1989). Given that maximum photosynthetic capacity and plant hydraulic function do not operate independently (Brodribb & Feild, 2000; Katul *et al.*, 2003), female *A. negundo* trees should maintain higher



**Fig. 8** Nitrogen use efficiency of female and male *Acer negundo* trees at an artificial stream and riparian system in Salt Lake City, UT on May 20 (day 140), June 30 (day 181), and August 24 (day 236), 2007. Data were calculated from estimates of carbon assimilation, evaluated from measurements of sap flux,  $\delta^{13}\text{C}$  of soluble leaf sugars, and allometric measurements of total leaf area per tree, and measurements of  $N_{\text{area}}$ . Error bars represent  $\pm 1$  SE of the mean.

leaf N concentrations to match their higher maximum leaf  $g_s$  than males under native climate conditions. In other words, under native conditions, photosynthetic NUE should more or less be equal between female and male trees. In this study, mean NUE in female and male trees were similar in late May and late June. However, NUE in female trees fell sharply to only 59% of that in male trees in late August (Fig. 8), largely due to a drop in  $g_s$  and subsequently  $A$  by the end of the growing season. These results suggest that females may be poorly adapted to changes in climate (especially when compared to conspecific males) that are predicted for the region over the next century.

Our approach to estimate photosynthesis was based on the theory following the approach of Hu *et al.* (2010) and combined sap-flux-scaled measurements of  $E$  with measurements of carbon isotope ratios in leaf soluble sugars to estimate WUE (i.e.  $A : E$ ). To use this approach to successfully calculate  $A$ , two assumptions must first be met: (i) leaf temperature is equal to bulk air temperature; and (ii) internal conductance ( $A/c_i - c_c$ , where  $c_c$  is the  $\text{CO}_2$  concentration at the site of carboxylation) is equal between genders.

For the first assumption, leaf temperature of broad leaved plants, such as *A. negundo* can shift plus or minus air temperature by several degrees C depending on the balance between radiative heat load and transpirational cooling (Gutschick, 1999). A sensitivity analysis showed that offsets between mean daytime air temperature and

mean daytime leaf temperature of  $\pm 2.5$  °C would result in an under or over estimation of  $A$  by 20% and 8% respectively. Nevertheless, the similarities in leaf characteristic dimension, canopy structure, and canopy decoupling should also yield similar diurnal patterns in leaf temperature between the two genders. Therefore, differences in  $A$  between female and male trees should remain fairly constant across a reasonable range of temperature offsets between air and leaf temperature if any were present throughout the study period.

Our use of carbon isotope discrimination to investigate WUE and subsequent variation in  $A$  is based on the assumption that the internal resistance from the substomatal cavity to the sites of carboxylation is equal between genders. Recent evidence shows that internal conductance can vary substantially across a broad range of species and result in up to a 3% difference in  $\Delta$  among species (Warren & Adams, 2006). Shifts in  $\Delta$  caused by variation in internal conductance present potential challenges for investigating WUE among species and ecosystems (Hanba *et al.*, 2003; Ripullone *et al.*, 2004; Warren & Adams, 2006). However, internal conductance varies considerably less within species or among species with similar leaf anatomy and physiology (Warren & Adams, 2006), and there is no evidence that internal conductance varies significantly among genders of dioecious plants. Therefore, we suspect that internal conductance scaled equally between female and male *A. negundo* plants during this study.

Results from this study suggest that the spatial segregation of the sexes may shift under global warming scenarios such that female plants lose their dominance along streamside locations, and males increase their dominance in non-streamside locations. If so, warmer growing season temperatures that are predicted for the southwestern United States may present considerable challenges for riparian restoration programs, including those that focus on *Populus fremontii* and *Salix goodingii* gallery forests that are among the most threatened forest types in the United States (Stromberg, 1993; Webb *et al.*, 2007). As with *A. negundo*, *P. fremontii*, and *S. goodingii* are dioecious tree species that often display a spatial segregation of the sexes in riparian ecosystems (Grant & Mitton, 1979; Comtois *et al.*, 1986; Braatne & Rood, 1996; Gom & Rood, 1999; Braatne *et al.*, 2007). Moreover, *P. fremontii* and *S. goodingii* populations appear to be adapted to a narrow climate regime and may become maladapted under progressively warmer temperatures (Grady *et al.*, 2011, 2013). Therefore, riparian restoration programs that include dioecious tree species should consider both genotype, and gender selection to maximize opportunities for success in the face of global climate change.

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## References

- Bierzuchudek P, Eckhart V (1988) Spatial segregation of the sexes of dioecious plants. *American Naturalist*, **132**, 34–43.
- Braatne JH, Rood SB (1996) Life history, ecology and conservation of riparian cottonwoods in North America. In: *Biology of Populus and its Implications for Management and Conservation* (eds Stettler RF, Bradshaw HD, Heilman PE, Hinckley TM), pp. 57–85. NRC Research, Ottawa.
- Braatne JH, Jamieson R, Gill KM, Rood SB (2007) Instream flows and the decline of riparian cottonwoods along the Yakime River, Washington, USA. *River Research and Applications*, **23**, 247–267.
- Brodribb TJ, Feild TS (2000) Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. *Plant, Cell and Environment*, **23**, 1381–1388.
- Brugnoli E, Farquhar GD (1998) Photosynthetic fractionation of carbon isotopes. In: *Photosynthesis: Physiology and Metabolism, Advances in Photosynthesis* (eds Leegood RC, Sharkey TD, von Caemmerer S), pp. 399–434. Kluwer Academic Publishers, Dordrecht.
- Brugnoli E, Hubick KT, von Caemmerer S, Wong SC, Farquhar GD (1988) Correlation between carbon isotope discrimination in leaf starch and carbohydrates of C<sub>3</sub> plants and the ratio of intercellular and atmospheric partial pressures of carbon dioxide. *Plant Physiology*, **88**, 1418–1424.
- Bunce JA (1996) Does transpiration control stomatal response to water vapour pressure deficit? *Plant, Cell and Environment*, **19**, 131–135.
- Campbell GS, Norman JN (1998) *An Introduction to Environmental Biophysics*. Springer-Verlag, Berlin.
- Clearwater MJ, Meinzer FC, Andrade JL, Goldstein G, Holbrook NM (1999) Potential errors in measurement of nonuniform sap flow using heat dissipation probes. *Tree Physiology*, **19**, 681–687.
- Comtois P, Simon JP, Payett S (1986) Clonal constitution and sex ratio in northern populations of balsam poplar, *Populus balsamifera*. *Holarctic Ecology*, **9**, 251–260.
- Dawson TE, Bliss LC (1989) Patterns of water use and the tissue water relations in the dioecious shrub, *Salix arctica*: the physiological basis for habitat partitioning between the sexes. *Oecologia*, **79**, 332–343.
- Dawson TE, Ehleringer JR (1993) Gender-specific physiology, carbon isotope discrimination, and habitat distribution in box elder, *Acer negundo*. *Ecology*, **74**, 798–815.
- Dawson TE, Geber MA (1999) Sexual dimorphism in physiology and morphology. In: *Gender and Dimorphism of Flowering Plants* (eds Geber MA, Dawson TE, Delph LF), pp. 175–215. Springer, Berlin.
- Dawson TE, Ward JK, Ehleringer JR (2004) Temporal scaling of physiological responses from gas exchange to tree rings: a gender-specific study of *Acer negundo* (Boxelder) growing under different conditions. *Functional Ecology*, **18**, 212–222.
- Ehleringer JR, Arnow LA, Arnow T, McNulty IB, Negus NC (1992) Red Butte Canyon Research Natural Area: history, flora, geology, climate and ecology. *Great Basin Naturalist*, **52**, 95–121.
- Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C<sub>3</sub> plants. *Oecologia*, **78**, 9–19.
- Evans JR, Seemann JR (1989) The allocation of protein N in the photosynthetic apparatus costs, consequences, and control. In: *Photosynthesis* (ed. Briggs WR), pp. 183–205. Alan R Liss, New York.
- Ewers BE, Gower ST, Bond-Lamberty B, Wang CK (2005) Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forests. *Plant, Cell and Environment*, **28**, 660–678.
- Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology*, **9**, 121–137.
- Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: *On the Economy of Form and Function* (ed. Givnish TJ), pp. 25–55. Cambridge University Press, Cambridge, UK.
- Freeman DC, Klikoff LJ, Harper KT (1976) Differential resource utilization by the sexes dioecious plants. *Science*, **193**, 597–599.
- Gom LA, Rood SB (1999) Patterns of clonal occurrence in a mature cottonwood grove along the Oldman River, Alberta. *Canadian Journal of Botany*, **77**, 1095–1105.
- Grady KC, Ferrier SM, Kolb TE, Hart SC, Allan GJ, Whitham TG (2011) Genetic variation in productivity of foundation riparian species at the edge of their distribution: implications for restoration and assisted migration in a warming climate. *Global Change Biology*, **17**, 3724–3735.
- Grady KC, Laughlin DC, Ferrier SM, Kolb TE, Hart SC, Allan GJ, Whitham TG (2013) Conservative leaf traits correlate with fast growth of genotypes of a foundation riparian species near the thermal maximum extent of its geographic range. *Functional Ecology*, **27**, 428–438.
- Granier A (1987) Evaluation of transpiration in a Douglas fir stand by means of sap flow measurements. *Tree Physiology*, **3**, 309–320.
- Granier A (1996) *Sap Flow Measurements Using the Radial Flowmeter Technique*, pp. 1–9. INRA-Unité d'Ecophysiologie Forestière, Champenoux.
- Grant MC, Mitton JB (1979) Elevational gradient in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. *Evolution*, **33**, 914–918.
- Gutschick VP (1999) Biotic and abiotic consequences of differences in leaf structure. *New Phytologist*, **143**, 3–18.
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, **126**, 457–461.
- Hanba YT, Kogami H, Terashima I (2003) The effect of internal CO<sub>2</sub> conductance and leaf carbon isotope ratio. *Isotopes in Environmental and Health Studies*, **39**, 5–13.
- Hu J, Moore DJP, Riveros-Iregui DA, Burns SP, Monson RK (2010) Modeling whole-tree carbon assimilation rate using observed transpiration rates and needle sugar carbon isotope ratios. *New Phytologist*, **16**, 771–783.
- Hultine KR, Bush SE, West AG, Ehleringer JR (2007a) Population structure, physiology and ecophysiological impacts of dioecious riparian tree species in western North America. *Oecologia*, **154**, 85–93.
- Hultine KR, Bush SE, West AG, Ehleringer JR (2007b) The effects of gender on sap-flux-scaled transpiration in a dominant riparian tree species: box elder (*Acer negundo*). *Journal of Geophysical Research Biogeosciences*, **112**, G03S06, doi: 10.1029/2006JG000232.
- Hultine KR, Bush SE, West AG, Burtch KG, Pataki DE, Ehleringer JR (2008a) Gender specific patterns of above ground allocation, and water use in a dominant riparian tree species: box elder (*Acer negundo*). *Tree Physiology*, **28**, 1383–1394.
- Hultine KR, Jackson TL, Burtch KG, Schaeffer SM, Ehleringer JR (2008b) Elevated stream inorganic nitrogen impacts on a dominant riparian tree species: results from an experimental riparian stream system. *Journal of Geophysical Research Biogeosciences*, **113**, G04025, doi: 10.1029/2008JG000809.
- Iglesias MC, Bell G (1989) The small-scale spatial distribution of male and female plants. *Oecologia*, **80**, 229–235.
- Jarvis PG, McNaughton KG (1986) Stomatal control of transpiration: scaling up from leaf to region. *Advances in Ecological Research*, **15**, 1–49.
- Jones HG (1992) *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology*. Cambridge University Press, Cambridge.
- Karl TR, Melillo JR, Peterson TC (eds) (2009) *Global Climate Change Impacts in the United States*. Cambridge University Press, New York.
- Katul G, Leuning R, Oren R (2003) Relationship between plant hydraulic and biochemical properties derived from a steady-state coupled water and carbon transport model. *Plant, Cell and Environment*, **26**, 339–350.
- Martin P (1989) The significance of radiative coupling between vegetation and the atmosphere. *Agricultural and Forest Meteorology*, **49**, 45–53.
- Meinzer FC, Andrade JL, Goldstein G, Holbrook NM, Caveller J, Jackson P (1997) Control of transpiration from the upper canopy of a tropical forest: the role of stomatal, boundary layer and hydraulic architecture components. *Plant, Cell and Environment*, **20**, 1242–1252.
- Monteith JL (1995) A reinterpretation of stomatal response to humidity. *Plant, Cell and Environment*, **18**, 357–364.
- Monteith JL, Unsworth MH (1990) *Principles of Environmental Physics*. Arnold, London.
- O'Neill GA, Hamann A, Wang T (2008) Accounting for population variation improves estimate of the impact of climate change on species' growth and distribution. *Journal of Applied Ecology*, **45**, 1040–1049.
- Oren R, Sperry JS, Katul G, Pataki DE, Ewers BE, Phillips N, Schäfer KVR (1999) Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell and Environment*, **22**, 1515–1526.
- Parnesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics*, **37**, 637–669.

- Pataki DE, Bowling DR, Ehleringer JR, Zobitz JM (2006) High resolution atmospheric monitoring of urban carbon dioxide sources. *Geophysical Research Letters*, **33**, L03813, doi: 10.1029/2005GL024822
- Potvin C, Lechowicz MJ, Tardiff S (1990) The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology*, **71**, 1389–1400.
- Ripullone F, Lauteri M, Grassi G, Amatao M, Borghetti M (2004) Variation in nitrogen supply changes water-use efficiency of *Pseudotsuga menziesii* and *Populus x euroamaricana*; a comparison of three approaches to determine water use efficiency. *Tree Physiology*, **24**, 671–679.
- Sperry JS, Adler FR, Campbell GS, Comstock JP (1998) Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant Cell and Environment*, **21**, 347–359.
- Sperry JS, Hacke UG, Oren R, Comstock JP (2002) Water deficits and hydraulic limits to leaf water supply. *Plant Cell and Environment*, **25**, 251–263.
- Stromberg JC (1993) Fremont cottonwood–Gooding willow riparian forests: a review of their ecology, threats, and recovery potential. *Journal of the Arizona-Nevada Academy of Science*, **26**, 97–111.
- Tardieu F, Simonneau T (1998) Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modeling isohydric and anisohydric behaviours. *Journal of Experimental Botany*, **49**, 419–432.
- Tognetti R (2012) Adaptation to climate change of dioecious plants: does gender matter? *Tree Physiology*, **32**, 1321–1324.
- Tyree MT, Davis SD, Cochard H (1994) Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction. *International Association of Wood Anatomists Journal*, **14**, 335–360.
- Ward JK, Dawson TE, Ehleringer JR (2002) Response of *Acer negundo* genders to inter-annual differences in water availability determined from carbon isotope ratios of tree ring cellulose. *Tree Physiology*, **22**, 339–346.
- Warren CR, Adams MA (2006) Internal conductance does not scale with photosynthetic capacity: implications for carbon isotope discrimination and the economics of water and nitrogen use in photosynthesis. *Plant, Cell and Environment*, **29**, 192–201.
- Webb RH, Leake SA, Turner RM (2007) *The Ribbon of Green: Change in Riparian Vegetation in the Southwestern United States*. University of Arizona Press, Tucson, Arizona, USA.
- West AG, Hultine KR, Burtch KG, Ehleringer JR (2007) Seasonal variations in moisture use in a piñon-juniper woodland. *Oecologia*, **153**, 787–798.
- Wheeler JK, Sperry JS, Hacke UG, Hoang N (2005) Inter-vessel pitting and cavitation in woody Rosaceae and other vesselless plants: a basis for a safety versus efficiency trade-off in xylem transport. *Plant, Cell and Environment*, **28**, 800–812.
- Wullschlegel SD, Gunderson CA, Hanson PJ, Wilson KB, Norby RJ (2002) Sensitivity of stomatal and canopy conductance to elevated CO<sub>2</sub> concentration—interacting variables and perspectives of scale. *New Phytologist*, **153**, 485–496.
- Zimmermann MH (1983) *Xylem Structure and the Ascent of sap*. Springer, New York.