

# Population structure, physiology and ecohydrological impacts of dioecious riparian tree species of western North America

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Received: 15 February 2007 / Accepted: 2 July 2007 / Published online: 31 July 2007  
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**Abstract** The global water cycle is intimately linked to vegetation structure and function. Nowhere is this more apparent than in the arid west where riparian forests serve as ribbons of productivity in otherwise mostly unproductive landscapes. Dioecy is common among tree species that make up western North American riparian forests. There are intrinsic physiological differences between male and female dioecious riparian trees that may influence population structure (i.e., the ratio of male to female trees) and impact ecohydrology at large scales. In this paper, we review the current literature on sex ratio patterns and physiology of dioecious riparian tree species. Then develop a conceptual framework of the mechanisms that underlie population structure of dominant riparian tree species. Finally, we identify linkages between population structure and ecohydrological processes such as evapotranspiration and streamflow. A more thorough understanding of the mechanisms that underlie population structure of dominant riparian tree species will enable us to better predict global change impacts on vegetation and water cycling at multiple scales.

**Keywords** Dioecy · Ecohydrology · Riparian ecology · Plant water relations · Global change

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Communicated by Hannu Ylonen.

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## Introduction

Riparian ecosystems are highly productive corridors in the arid and semi-arid regions of western North America. Riparian areas are valued for their wildlife habitat, biodiversity, water quality, and recreational opportunities, and are characterized by large canopies of dominant vegetation that provide shade and habitat for many species that thrive in these ecosystems. Global change—including both changes in land use and climate—poses a considerable threat to the current composition of riparian forests. Throughout the arid and semi-arid west, climate change coupled with land use change have resulted in, or may result in, dramatic alterations of riparian ecosystems (Stromberg 1993; Patten 1998; Horton et al. 2001). Changes in the timing and amount of precipitation, earlier runoff, and intensified drought from reduced snowpacks are expected to have significant impacts on watershed hydrology and population structure of riparian communities in western North America (Mote et al. 2005; Mote 2006). Likewise, nearly every major watershed in the western United States has been subjected to some form of human induced streamflow modification, and future water demands are anticipated to accelerate stream regulation and groundwater pumping (Graf 1999; Poff et al. 2006).

Dioecy—plants in which male and female flowers are found in separate individuals is common in woody vegetation that typically occurs in riparian ecosystems. In the Intermountain West of the United States and in California, 32% of all individuals that comprise riparian woodland communities are dioecious (Freeman et al. 1980), including some of the most dominant species; cottonwoods (*Populus* spp.), willows (*Salix* spp.), and box elder (*Acer negundo* Sarg.). Dioecious riparian tree species are one example of plants that may be particularly vulnerable to the present

effects of global change. Many dioecious plant species show spatial segregation of the sexes associated with microhabitat differences (Iglesias and Ball 1989; Dawson and Bliss 1989; Dawson and Ehleringer 1993; Eppley et al. 1998). 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 enough proximity for reproduction to be successful) (Freeman et al. 1976; Dawson and Bliss 1989; Dawson and Ehleringer 1993). The spatial segregation of the sexes likely reflects adaptations to different costs associated with reproduction (Freeman et al. 1976; Bierzychudek and Eckhart 1988; Dawson and Geber 1999). Females generally require more resources (e.g., water, nitrogen, etc) for reproduction than males. Because segregation of the sexes may be adaptive, global change, and subsequent changes to resource availability may change the sex ratio and reproductive success of many dioecious species, including important riparian tree species.

In this paper, we set out to review the important mechanisms that underlie the observed sex ratios of dioecious riparian tree species. Then, we discuss how global change impacts on the water cycle may influence future sex ratios of dioecious tree species. And finally, we develop a framework of how sex ratios impact important ecohydrological processes of arid and semi-arid riparian ecosystems, including evapotranspiration (ET) and streamflow.

### The spatial segregation of the sexes

#### The spatial segregation of riparian box elder trees

*A. negundo* is a common dioecious 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 (Freeman et al. 1976; Dawson and Ehleringer 1993; Ward et al. 2002). The ratio of male to female individuals along stream margins in the Intermountain West, where soil water and other resources are abundant, is about 0.67, while the male-to-female ratio on the drier margins of riparian ecosystems (in this case, >1 m from stream channel) is about 1.61 (Ward et al. 2002). How this sex ratio structure develops and how it influences functioning of riparian ecosystems is not well understood. Yet it appears that the sex ratio of drier, non-streamside habitats may evolve from greater incidence of drought induced mortality in female trees than males. For example, the male-to-female ratio in dry sites tends to increase with plant age (Fig. 1), suggesting that spatial segregation can be attributed, at least in part to physiological processes post germination such as sensitivity

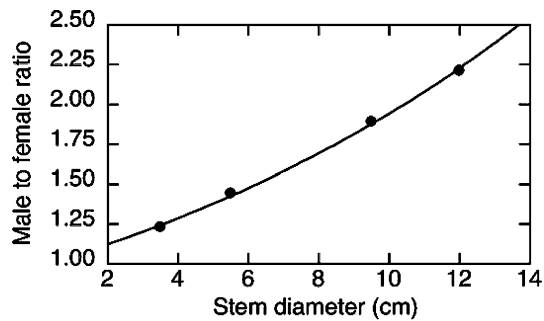
to decreased soil moisture (Dawson and Ehleringer 1993). Males consistently use less water and are better able to avoid drought stress compared to females (discussed below). Greater drought tolerance in males, however, comes with the apparent tradeoff of being less competitive when and where water supplies are more stable, such as along stream margins or during very wet years. Under conditions of high water availability, females develop larger canopies (Dawson and Ehleringer 1993) and have faster growth rates than males (Ward et al 2002). Consequently, females along stream habitats may out-compete males through greater resource uptake capacity and use.

#### The spatial segregation of riparian cottonwood and willow species

*Populus* and *Salix* are dioecious tree species that dominate riparian forests throughout western North America. As with *A. negundo*, skewed sex ratios have been observed in many populations of *Populus* (Grant and Mitton 1979; Comtois et al. 1986; Braatne et al. 1996; Gom and Rood 1999; Braatne et al. 2007), but not all (Kaul and Kaul 1984; Stanton and Villar 1996; Rowland and Jackson 2001). In cases where sex ratios occur, males are relegated to more extreme environments (Braatne et al. 1996; Rowland and Jackson 2001). For example, male *Populus deltoides* trees were favored in drier habitats along the Rio Grande River in New Mexico (Rowland and Johnson 2001), suggesting that riparian *Populus* spp. follow similar sex ratio patterns to *A. negundo*.

Alternatively, resource gradients often impact the population structure of riparian cottonwoods in ways other than sex ratio. Male and female *P. deltoides* along the Rio Grande River switch from being reproductive to non-reproductive in response to environmental stress (Rowland and Jackson 2001). Moreover, reproductive status and mortality are strongly correlated in *P. deltoides* (Rowland and Jackson et al. 2001). Perhaps reproductive status of some dioecious tree species is a stronger indicator of environmental stress than the spatial segregation of the sexes. Many non-reproductive individuals regain reproductive status in response to inter-annual increases in resource availability. However, does switching between reproductive and non-reproductive states influence resource acquisition potential? Further research is needed to address this important question.

Information on the spatial segregation of the sexes in riparian *Salix* species is somewhat ambiguous compared to *A. negundo* and *Populus*. Although *Salix arctica* (Arctic willow) and *Salix glauca* express strong spatial segregation across resource gradients (Dawson and Bliss 1989; Dudley 2006), riparian willows generally do not express sex ratio biases (Koal and Koal 1984; Alliende and Harper 1989)



**Fig. 1** Changes in sex ratio in *Acer negundo* (box elder) as a function of plant size in non-streamside habitats in northern Utah, based on data presented by Dawson and Ehleringer (1993). While the region-wide average male-to-female sex ratio is 1.61, this ratio becomes progressively higher as trees get larger, implying greater female mortality through time

unless reproduction occurs via vegetative propagation (Shafroth et al. 1994). Where seedling propagation occurs, opportunities for spatial sex ratio biases in willow may be limited because they are typically obligate phreatophytes (Snyder and Williams 2000), meaning they are usually confined to high-resource microsites and along stream margins. Therefore, riparian willows only occur within very limited resource gradients, reducing opportunities for spatial segregation of the sexes to develop.

On the other hand, vegetative reproduction, common in both riparian *Populus* and *Salix* spp., often results in very high sex ratio biases within populations (Shafroth et al. 1994; Gom and Rood 1999). For example, populations of an exotic riparian willow species: *Salix × rubens* Schronk and *Salix alba* Arcang. along several streams in Colorado showed extreme female sex ratio biases. In fact, *S. × rubens* were 99% female (Shafroth et al. 1994). Although *S. × rubens* and *S. alba* produce viable seed, the unusual sex ratios were apparently the result of exclusive vegetative reproduction. Clonal reproduction was also attributed to a near 2:1 female-biased sex ratio of individual stems within several riparian *Populus* spp. in Alberta Canada, although a 1:1 sex ratio was observed among individual trees (Gom and Rood 1999).

### Resource acquisition capacity and resource use efficiency

Previous work has led to the hypothesis that spatial segregation of the sexes in dioecious riparian tree species emerges in part from physiological adaptation that allows each sex to specialize in separate habitats (Dawson and Geber 1999). In general, female plants maximize resource acquisition capacity, thereby allowing individuals to specialize (and out-compete) in high-resource environments.

**Table 1** Comparisons of ecophysiological traits in mature streamside female and male *Acer negundo* (box elder) trees. A Net carbon assimilation,  $g_s$  stomatal conductance,  $\Delta$  carbon isotope discrimination

Measurement	Female	Male	% Difference
A ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	15.6 (2.33) <sup>a</sup>	9.5 (1.32)	64
$g$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	0.46 (0.10)	0.23 (0.03)	100
A/g ( $\mu\text{mol mol}^{-1}$ )	34.2 (12)	41.7 (13)	22
$\Delta$	23.7 (0.40)	19.3 (0.31)	23
Leaf nitrogen ( $\text{mmol m}^{-2}$ )	175 (26.6)	129 (18.1)	36
Stomatal density (no. $\text{mm}^{-2}$ )	251 (33.8)	194 (27.7)	33

<sup>a</sup> Numbers in parentheses are SDs, based on data from Dawson et al. (2004)

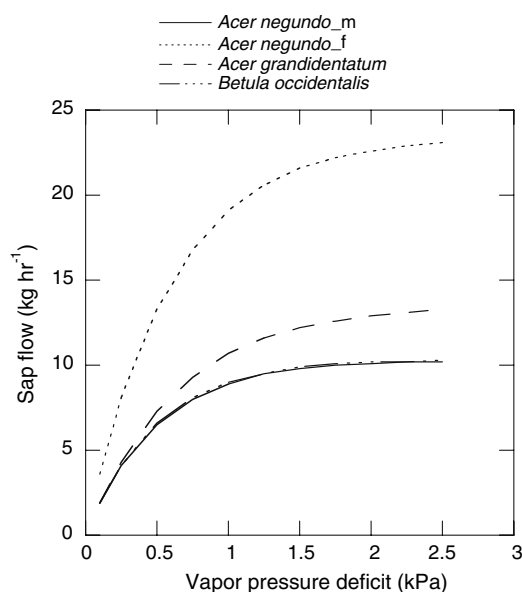
On the other hand, males maximize resource use efficiency, allowing them to persist in less favorable habitats, or during periods when resources are limited. In other words, sex ratio biases across resource gradients may reflect tradeoffs between resource uptake and resource use efficiency, whereby females are selected for greater resource uptake in order to meet the high costs of reproduction, and males are selected for greater resource use efficiency to maximize mating opportunities in low-resource habitats (Bateman 1948; Dawson and Ehleringer 1993).

The most notable example of this pattern might be *A. negundo*, where functional differences between genders in both resource acquisition capacity and resource use efficiency parallel observed patterns of spatial segregation of the sexes. At the leaf level, female *A. negundo* have a higher resource uptake capacity than males. Females have higher stomatal conductance ( $g_s$ ), net carbon assimilation (A), and carbon isotope discrimination ( $\Delta$ ), and lower water use efficiency ( $A/g_s$ ) than males, regardless of habitat (Dawson and Ehleringer 1993; Dawson et al. 2004; Table 1), although the largest differences in A and  $g$  are in high-resource streamside locations. Streamside female *A. negundo* have 60% higher A and up to 100% higher  $g_s$  than co-occurring streamside male *A. negundo* (Table 1). Moreover, leaf physiological differences between genders are also accompanied by differences in leaf structure; females have roughly 33% higher stomatal densities on abaxial (lower) leaf surfaces, and 30% more leaf nitrogen per unit area than males (Dawson et al. 2004; Table 1).

Gender-specific patterns in resource acquisition and resource use scale from the leaf to the whole plant. Stem sap flux density ( $J_s$ ), measured with Granier-style sap flux sensors (Granier 1985, 1987), was on average 76% higher throughout one whole growing season (2004) in streamside female *A. negundo* compared to streamside males (Hultine et al. 2007). Differences in  $J_s$  were accompanied by significant differences in both conducting sapwood

area-to-basal area and leaf area-to-basal area ratios, whereby females had more sapwood area and leaf area per unit basal area (Hultine et al. 2007). Differences between genders in both  $J_s$  and above-ground allocation resulted in large differences in whole-plant transpiration, and canopy stomatal conductance. In fact, in spring and early summer, canopy  $g_s$  of mature streamside female *A. negundo* trees was twice as high as in streamside males (Hultine et al. 2007). Given that growth and productivity is proportional to water transport through plants (Enquist 2002), one would expect streamside females to have a competitive advantage over streamside males given their higher resource uptake versus males. Streamside female trees have faster canopy and radial growth rates than streamside males (Dawson and Ehleringer 1993; Ward et al. 2002). Differences in growth rate may play a key role in the population structure of streamside microsites where survival in these high-productive habitats depends in part, on canopy dominance and sunlight acquisition.

If we assume that growth is in fact proportional to water transport, then it is not surprising that female *A. negundo* not only occurs at higher frequency in high-resource sites than male *A. negundo* but also dominates mid-elevation riparian zones throughout much of western North America (Sargent 1965). This is because whole-tree transpiration is higher in streamside female *A. negundo* than other dominant riparian tree species. Figure 2 shows the relationship between transpiration rates ( $T$ ) and atmospheric vapor pressure deficit

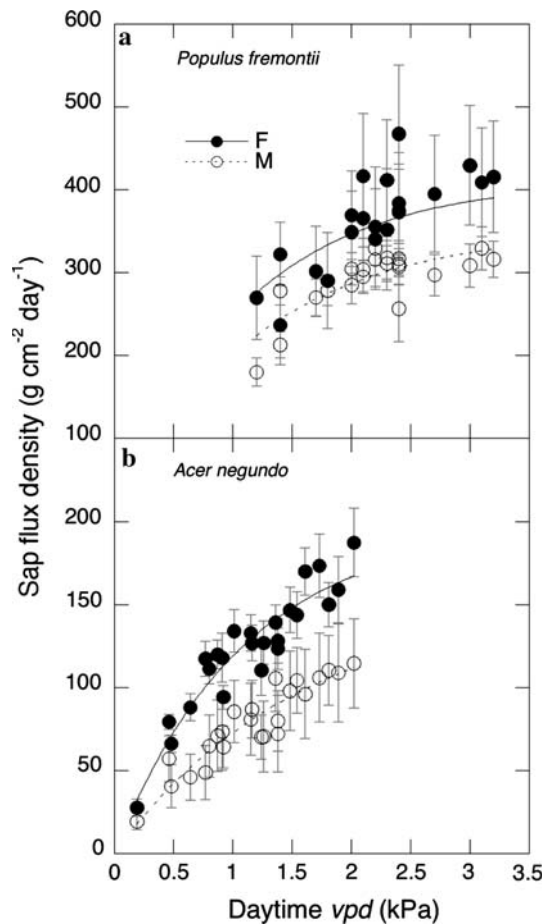


**Fig. 2** Modeled transpiration rate ( $T$ ; kg h<sup>-1</sup>) in 20-cm-diameter male ( $m$ ) and female ( $f$ ) *A. negundo*, *Acer grandidentatum* (big tooth maple), and *Betula occidentalis* (water birch) trees occurring near Salt Lake City, Utah. Data are modeled from gender/species-specific sap flux coefficients, and sapwood area-to-stem diameter relationships (Hultine et al. 2007)

(VPD) in hypothetical 20-cm-diameter trees (a common size for riparian tree populations in the western US), modeled from previously published data (Hultine et al. 2007). Populations include streamside male and female *A. negundo*, and two monoecious riparian tree species that are also common in mid-elevation riparian zones in the western United States: *Acer grandidentatum* Nutt. (bigtooth maple) and *Betula occidentalis* Hook. (water birch). Twenty-centimeter-diameter, streamside male *A. negundo* and *B. occidentalis* would have similar transpiration rates with both populations saturating at about 10 kg h<sup>-1</sup>. Transpiration rates in a 20 cm diameter *A. grandidentatum* would be slightly higher, exceeding 13 kg h<sup>-1</sup>. However, modeled  $T$  in a 20 cm diameter, streamside female *A. negundo* tree would be visibly higher than all other populations, more than doubling that of both male *A. negundo* and *B. occidentalis* over a range of VPD from 0.1 to 2.5 MPa (Fig. 3). The higher transpiration rates in female *A. negundo* not only suggest that they are more productive than other mid-elevation riparian trees, but that the population structure of riparian tree communities could have significant impacts on large-scale ecohydrological processes including stream discharge and groundwater recharge (discussed later).

Low-elevation riparian zones of the western United States are typically dominated by cottonwood/willow species (Stromberg 1993). In the desert southwest of the United States, *Populus fremontii* Wats. (Fremont cottonwood) is the most common riparian tree species, along with non-native *Tamarisk* spp. As with *A. negundo*, streamside female *P. fremontii* trees have higher stem sap flux rates than co-occurring males (Fig. 3). Sap flux measured on eight male and female trees in spring and summer of 2005 near Salt Lake City, Utah was 25% higher in female versus male trees (Fig. 3a; previously unpublished data). Differences between genders were similar to those reported by Hultine et al. (2007) in *A. negundo* during the same period in 2004 (Fig. 3b). As with *A. negundo*, differences between genders in the response to environmental drivers VPD and photosynthetic active radiation ( $Q$ ) were highly significant (Table 2). Taken together, these data suggest that there are general patterns among dioecious riparian tree species, whereby each gender has different resource requirements.

Based on previous observations from *A. negundo* and *P. fremontii*, we have constructed a conceptual model of growth and mortality of male and female dioecious riparian tree species along a resource gradient away from a typical stream system (Fig. 4). According to the model, growth and reproductive output of female trees is significantly enhanced relative to males along streamside habitats or during wet years due to a greater resource acquisition capacity in females relative to males. Table 1, for example, shows maximum photosynthesis and leaf conductance is higher in streamside female *A. negundo* trees compared to streamside

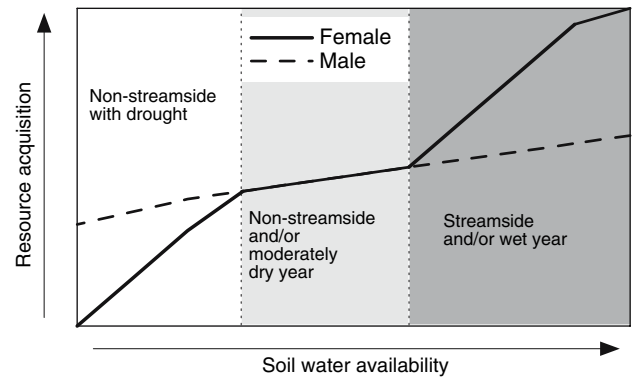


**Fig. 3a, b** Sap flux density ( $J_s$ ;  $\text{g cm}^{-2} \text{ day}^{-1}$ ) of mature dioecious riparian tree species measured during spring and early summer of 2005. **a**  $J_s$  in male (M) and female (F) *Populus fremontii* (Fremont cottonwood) trees occurring within 1 m of a perennial stream channel in Salt Lake City, Utah (previously unpublished data). **b**  $J_s$  in male and female *A. negundo* trees occurring within 1 m of a perennial stream channel near Salt Lake City, Utah. Figure 4 is based on data presented by Hultine et al. (2007). Error bars represent  $\pm 1$  SE of the mean. *vpd* Vapor pressure deficit

males (Dawson et al. 2004). The greater resource acquisition in high-resource locations apparently translates into higher growth rates in females compared to males. In a common garden study, female *A. negundo* had 35% higher radial growth rates than males during years with above average

**Table 2** Probability values from analysis of covariance of sap flux density ( $J_s$ ) against mean daytime vapor pressure deficit (VPD), and total daily photosynthetic active radiation ( $Q$ ), and gender in mature male and female *Populus fremontii* (Fremont cottonwood) and *A. negundo* trees in Salt Lake City, Utah

	VPD (kPa)	$Q$ ( $\text{mol m}^{-2} \text{ s}^{-1}$ )	VPD $\times$ $Q$	Gender
<i>P. fremontii</i>	0.0021	0.29	0.45	<0.0001
<i>A. negundo</i>	<0.0001	0.0012	0.26	<0.0001



**Fig. 4** A conceptual model of how resource acquisition, and subsequent growth and mortality of female and male dioecious riparian trees, vary along a resource gradient away from a typical stream system. The quality of a year (wet versus dry) will amplify the effects of the streamside-to-non streamside gradient

rainfall (Ward et al. 2002). As stated earlier, high growth rates in resource rich habitats are critical in order to out-compete neighbors for sunlight. Conversely, there are smaller differences in photosynthesis and conductance in non-streamside habitats. Data in Table 1 for non-streamside habitats are analogous to the “mid-range conditions” shown in Fig. 4, where neither gender has an advantage or disadvantage over the other. During dry years, radial growth rates of male and female trees were similar (Ward et al. 2002), again suggesting under many conditions neither gender has a competitive advantage or disadvantage.

In non-streamside locations and during extreme drought, resource acquisition and growth should be reduced in female trees relative to males, to the extent that rates of mortality are higher in females than in males (see Fig. 1). One possible explanation for this hypothesis is that the hydraulic conducting system of female trees becomes dysfunctional during drought and water transport to leaves, and subsequent carbon acquisition, is inhibited. In many species there is a tradeoff between hydraulic efficiency (the maximum rate at which water may be transported from the soil to the leaves) and xylem cavitation resistance (Tyree et al. 1994; Pockman and Sperry 2000; Hacke et al. 2006). If so, the propensity for female riparian trees to out perform males for resources in wet habitats may be countered by lower drought tolerance in dry habitats. Whether male and female plants have evolved disparate structural and functional xylem traits that correspond with habitat preference remains an open question that deserves considerable evaluation.

**The spatial segregation of the sexes in response to climate and land use change**

Alterations in the water cycle, due to changes in climate, could have considerable consequences on the population



structure of dioecious riparian tree species in the arid west. At present, global climate models are not consistent in their predictions as to whether precipitation in western North America will increase, decrease, or remain the same (Houghton et al. 2001). Regardless of how precipitation might change, the inter- and intra-annual variation in precipitation patterns in the west will likely increase over the next several decades (Parker et al. 1994; Smith et al. 1998; Weltzin et al. 2003), likely intensifying drought/inter-drought cycles. Enhanced inter- and intra-annual variability coupled with warmer temperatures (Houghton et al. 2001) is expected to reduce future snowpacks, and subsequent streamflow in the western United States (Mote et al. 2005). Streamflow reductions will decrease recharge into adjacent soils and shallow aquifers, and thus reduce the amount of water available for plant uptake of some riparian systems and microhabitats (Stromberg 1993; Patten 1998; Weltzin et al. 2003). Such changes may have non-linear consequences on the success of individual male and female riparian trees given that males are apparently less sensitive to water limitations.

Likewise, the implementation of water-control practices such as dam construction and groundwater pumping could impose significant alterations in the population structure of western North American riparian forests (Mahoney and Rood 1992; Busch and Smith 1995; Horton et al. 2001). Groundwater pumping could disproportionately impact female individuals due to their greater susceptibility to drought-induced mortality relative to males (Dawson and Ehleringer 1993). Stream diversions would likewise have a strong negative impact on females by inhibiting episodic flooding that serves to recharge flood basins (Smith et al. 1991; Stromberg 1993). Male-dominated sex ratios in young *Populus trichocarpa* Torr. (black cottonwood) populations along the Yakima River in eastern Washington have been correlated with more than 30 years of regulated flow regimes (Braatne et al. 2007). The skewed sex ratios were attributed to poor recruitment of female individuals relative to males because of reduced habitat quality caused by altered flow regimes (Braatne et al. 2007).

### Dioecy impacts on ecohydrology

#### Dioecy impacts on streamflow

Water cycling of riparian ecosystems is tightly linked to vegetation (Sala et al. 1996; Schaefer et al. 2000; Jackson et al. 2001), thus, changes in the sex ratio of dioecious riparian tree species may have profound impacts on ecohydrology (Dawson and Ehleringer 1993; Hultine et al. 2007). Streamflow is tightly linked to the surrounding stream aquifer. Therefore, removal of water by phreatophytic plants

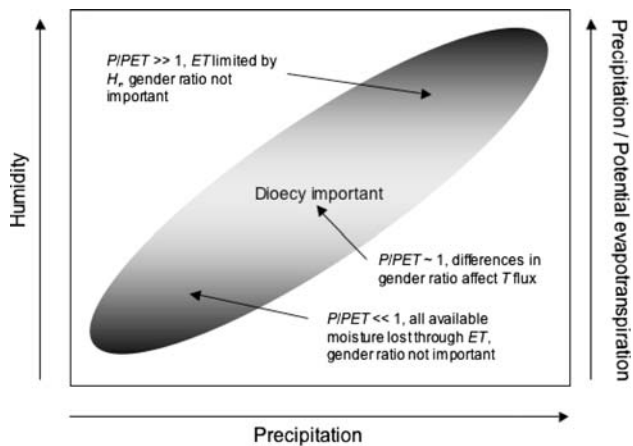
from the aquifer will result in reduced streamflow. Phreatophytic plants such as *Populus* spp., *Salix* spp. and *A. negundo* thrive along stream margins and riparian floodplains in otherwise arid environments because their root systems extract large amounts of water from shallow stream aquifers. Individual *P. fremontii* trees, for example, remove up to 500 l of water per day when air temperature is high and humidity is low (Schaefer et al. 2000). Dense riparian forests therefore have substantial impacts on many key hydrological processes including streamflow, groundwater recharge, and biogeochemical cycling. However, the amount of water recycled to the atmosphere by mature *Populus* or *A. negundo* stands appear to be highly sensitive to the ratio of male to female individuals (see Fig. 4).

Given the stark differences in transpiration between genders, we can construct a conceptual framework on how the spatial segregation of the sexes might influence ecosystem water cycling at the watershed scale. We start with a simple water budget to frame the major hydrologic fluxes:

$$P = ET + R + S \quad (1)$$

where  $P$  is precipitation,  $R$  is surface runoff measured as streamflow, and  $S$  is deep soil recharge (recharge beyond the rooting zone).  $ET$  can be subdivided further into the summation of three components: interception of rain water by plant canopies and assumed to evaporate ( $I$ ), evaporation from soil ( $E$ ), and water transpired by plants following soil water uptake ( $T$ ). The relative importance of  $ET$  on ecosystem water budgets is primarily a function of climate, vegetation cover, and vegetation type. Ecosystems dominated by woody plants produce more  $ET$  because of more expansive root systems and larger canopies (Huxman et al. 2005). Trees that occur along stream margins remove water stored in and around stream banks. Therefore, there is often an inverse relationship between forest cover and streamflow (Bosch and Hewlett 1982; Trimble et al. 1987).

We can use the above framework to predict where spatial segregation of the sexes will influence  $ET$  and subsequent streamflow. In extremely arid environments, such as at low elevations in the desert southwest, mean annual precipitation, humidity ( $H_r$ ), and the ratio of precipitation to potential  $ET$  ( $PET$ ) are extremely low (Fig. 5). In these habitats, dioecy has little impact on streamflow because nearly all precipitation is lost to  $ET$  regardless of vegetation cover (Reynolds et al. 2000; Wilcox et al. 2003). Streamflow may occur intermittently or episodically, but  $R$  is more or less negligible in the water budget. Habitats that are intermediate between extremely arid and extremely moist are defined as having a mean annual precipitation that is at or near equal to  $PET$ , and having perennial streamflow that may originate upstream in a more



**Fig. 5** A conceptual model of the climate conditions in which we expect the spatial segregation of the sexes of dominant riparian vegetation to impact evapotranspiration (ET) and subsequent streamflow. *PIPET* Ratio of precipitation to potential ET

humid mountainous region (Fig. 5). These habitats are characterized as mostly arid but with a well-defined snowmelt and/or rainy seasons, and high evaporative demand throughout most of the growing season. It is in these habitats that we predict that the spatial segregation of the sexes results in large impacts on streamflow (Fig. 5), because streamside female-dominated systems recycle a larger proportion of precipitation to the atmosphere compared to males (Hultine et al. 2007). In extremely moist habitats, where precipitation occurs frequently and potential evaporation is markedly less than precipitation during most of the growing season, dioecy has little or no impact on ET fluxes or streamflow. This is because higher water use by females is constrained by low evaporative demand in humid environments, and therefore differences between genders become nearly indistinguishable (Fig. 5). These habitats are rare, however in the western United States and are generally constrained to the Pacific Northwest and high elevations.

## Conclusions

Dioecy is a major component of population structure of western North American riparian forests. Nevertheless, scientists have mostly underappreciated dioecy impacts on important ecosystem processes such as water and carbon cycling, streamflow, and habitat quality. Intrinsic physiological differences between male and female trees may lead to large-scale differences in resource demands that influence population structure, and ecohydrological processes. Females, due to their higher resource demands to offset the high costs for female reproduction, tend to dominate

high-resource habitats. Along stream margins, for example, females recycle a larger amount of water to the atmosphere than males, possibly resulting in larger reductions in streamflow and higher net ecosystem productivity. On the other hand, males often dominate lower-resource habitats due to a higher incidence of mortality in female trees. The ratio of male to female individuals is not static, however, and may change dramatically in response to climate and human land use changes. Exactly how future global change scenarios will affect the population structure of dioecious riparian trees is not well understood (Geber and Dawson 1993). Yet, if we are to balance the increasing demand for water by human enterprise with preserving native riparian forests, we will need to improve our understanding of how land use change alters the functioning of riparian ecosystems that are critical elements of arid western landscapes. We suggest that future research focuses on: (1) identifying dioecious species' sex ratio distributions at large scales; (2) determining the impact changes in sex ratio structure has on ET relative to other changes in population and community structure, such as stand density, age structure and species composition; and (3) assessing how hydrologic and biochemical cycling impacts sex ratio distributions and vice versa.

**Acknowledgements** The authors would like to thank the Mellon Foundation for financial support for this project. Additional support was provided by a National Science Foundation, Water, the Environment, Science and Teaching (WEST) fellowship awarded to S. E. Bush.

## References

- Alliende MC, Harper JL (1989) Demographic studies of a dioecious tree. I. Colonization, sex, and age structure of a population of *Salix cinerea*. *J Ecol* 77:1029–1047
- Bateman AJ (1948) Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368
- Bierzchudek P, Eckhart V (1988) Spatial segregation of the sexes of dioecious plants. *Am Nat* 132:34–43
- Bosch JH, Hewlett JD (1982) A review of catchment experiments to determine the effect of vegetation changes and water yield and evapotranspiration. *J Hydrol* 55:3–23
- Braatne JH, Rood SB (1996) Life history, ecology, and conservation of riparian cottonwoods in North America. In: Stettler RF, Bradshaw HD, Heilman PE, Hinckley (eds) *Biology of Populus and its implications for management and conservation*. NRC Research, Ottawa
- Braatne JH, Jamieson R, Gill KM, Rood SB (2007) Instream flows and the decline of riparian cottonwoods along the Yakima River, Washington, USA. *River Res Appl* 23:247–267
- Busch DE, Smith SD (1995) Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. *Ecol Mongr* 65:347–370
- Comtois P, Simon JP, Payett S (1986) Clonal constitution and sex ratio in northern populations of balsam poplar, *Populus balsamifera*. *Holarctic Ecol* 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: Geber MA, Dawson TE, Delph LF (eds) *Gender and dimorphism of flowering plants*. 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. *Funct Ecol* 18:212–222
- Dudey LS (2006) Ecological correlates of secondary dimorphism in *Salix glauca* (Salicaceae). *Am J Bot* 93:1775–1783
- Enquist BJ (2002) Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. *Tree Physiol* 22:1045–1064
- Eppley SM, Stanton ML, Grosberg RK (1998) Intrapopulation sex ratio variation in the salt grass *Distichlis spicata*. *Am Nat* 152:659–670
- Freeman DC, Klikoff LG, Harper KT (1976) Differential resource utilization by the sexes dioecious plants. *Science* 193:597–599
- Freeman DC, Harper KT, Ostler WK (1980) Ecology of plant dioecy in the intermountain region of western North America and California. *Oecologia* 44:410–417
- Geber MA, Dawson TE (1993) Evolutionary responses of plants to global change. In: Kareiva PM, Kingsolver JG, Huey RB (eds) *Biotic interactions and global change*. Sinauer, Sunderland, Mass.
- Gom LA, Rood SB (1999) Patterns of clonal occurrence in a mature cottonwood grove along the Oldman River, Alberta. *Can J Bot* 77:1095–1105
- Graf WL (1999) Dam nation, a geographic census of American dams and their large-scale hydrologic impacts. *Water Resour Res* 35:1305–1311
- Granier A (1985) Une nouvelle methode pour la mesure de flux de seve brute dans le tronc des arbres. *Ann For Sci* 42:193–200
- Granier A (1987) Evaluation of transpiration in a Douglas fir stand by means of sap flow measurements. *Tree Physiol* 3:309–320
- 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
- Hacke UG, Sperry JS, Wheeler JK, Castro L (2006) Scaling angiosperm xylem structure with safety and efficiency. *Tree Physiol* 26:689–702
- Horton JL, Kolb TE, Hart SC (2001) Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. *Plant Cell Environ* 24:293–304
- Houghton JT, Ding Y, Griggs DJ, Noguer M, vander Linden PJ, Dai X, Maskell K, Johnson CA (2001) *Climate change 2001: the scientific basis*. Cambridge University Press, Cambridge
- Hultine KR, Bush SE, West AG, Ehleringer JR (2007) The effect of gender on sap flux-scaled transpiration in a dominant riparian tree species: box elder (*Acer negundo*). *JGR Biogeosci* (in press)
- Huxman TE, Wilcox BP, Breashears DD, Scott RL, Snyder KA, Small EE, Hultine K, Pockman WT, Jackson RB (2005) Ecohydrological implications of woody plant encroachment. *Ecology* 86:308–319
- Iglesias MC, Bell G (1989) The small-scale spatial distribution of male and female plants. *Oecologia* 80:229–235
- Jackson RB, Carpenter SR, Dahm CN, McKnight DM, Naiman RJ, Postal SL, Running SW (2001) Water in a changing world. *Ecol Appl* 11:1027–1045
- Kaul RB, Kaul MN (1984) Sex ratios of *Populus deltoids* and *Salix amygdaloides* (Salicaceae) in Nebraska. *Southwest Nat* 29:265–269
- Mahoney JM, Rood SB (1992) Response of hybrid poplar to water table decline in different substrates. *For Ecol Manage* 54:141–156
- Mote PW (2006) Climate-driven variability and trends in mountain snowpack in western North America. *J Clim* 19:6209–6220
- Mote PW, Hamlet AF, Clark MP, Lettenmaier DP (2005) Declining mountain snowpack in western North America. *Bull Am Meteorol Soc* 86:39–49
- Parker DE, Legg TP, Folland CK (1994) Interdecadal changes of surface temperatures since the late 19th century. *Clim Change* 31:14373–14399
- Patten DT (1998) Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands* 18:498–512
- Pockman WT, Sperry JS (2000) Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *Am J Bot* 87:1287–1299
- Poff NL, Bledsoe BP, Cuhacyan CO (2006) Hydrologic variation with land use across the contiguous United States: geomorphic and ecological consequences for stream ecosystems. *Geomorphology* 79:264–285
- Reynolds JF, Kemp PR, Tenhunen JD (2000) Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan Desert: a modeling analysis. *Plant Ecol* 150:145–159
- Rowland DL, Johnson NC (2001) Sexual demographics of riparian populations of *Populus deltoids*: can mortality be predicted from change in reproductive status? *Can J Bot* 79:702–710
- Sala A, Smith SD, Devitt DA (1996) Water use by *Tamarix ramississima* and associated phreatophytes in a Mojave Desert floodplain. *Ecol Appl* 6:888–898
- Sargent CS (1965) *Manual of trees in North America*, vol II. Dover, New York
- Schaefer SM, Williams DG, Goodrich DC (2000) Transpiration of cottonwood/willow forest estimated from sap flux. *Agric For Meteorol* 105:257–270
- Shafroth PB, Scott ML, Friedman JM, Laven RD (1994) Establishment, sex structure and breeding system of an exotic riparian willow, *Salix × rubins*. *Am Midl Nat* 132:159–172
- Smith SD, Wellington AB, Nachlinger JL, Fox CA (1991) Functional response of riparian vegetation to streamflow diversion in the eastern Sierra Nevada. *Ecol Appl* 1:89–97
- Smith SD, Devitt DA, Sala A, Cleverly JR, Busch DE (1998) Water relations of riparian plants from warm desert regions. *Wetlands* 18:687–696
- Snyder KA, Williams DG (2000) Water sources used by riparian trees varies among stream types on the San Pedro River, Arizona. *Agric For Meteorol* 105:227–240
- Stanton BJ, Villar M (1996) Controlled reproduction in *Populus*. In: Stettler RF, Bradshaw HD, Heilman PE, Hinckley (eds) *Biology of Populus and its implications for management and conservation*. NRC Research, Ottawa
- Stromberg JC (1993) Fremont cottonwood-Gooding willow riparian forests: a review of their ecology, threats, and recovery potential. *J Ariz Nev Acad Sci* 26:97–111
- Trimble SW, Weirich FH, Hoag BL (1987) Reforestation and the reduction of water yield on the Southern Piedmont since circa 1940. *Water Resour Res* 23:425–437
- Tyree MT, Davis SD, Cochard H (1994) Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction. *Int Assoc Wood Anat J* 14:335–360
- Ward JK, Dawson TE, Ehleringer JR (2002) Response of *Acer negundo* genders to interannual differences in water availability



- determined from carbon isotope ratios of tree ring cellulose. *Tree Physiol* 22:339–346
- Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Harte J, Huxman TE, Knapp AK, Lin G, Pockman WT, Shaw MR, Small EE, Smith MD, Smith SD, Tissue DT, Zak JC (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience* 53:941–952
- Wilcox BP (2003) Runoff from rangelands: the role of shrubs. In: McGinty A, Hanselka CW, Ueckert DN, Hamilton W, Lee M (eds) *Shrub management*. A&M University Press, College Station, Texas