POPULATION ECOLOGY

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

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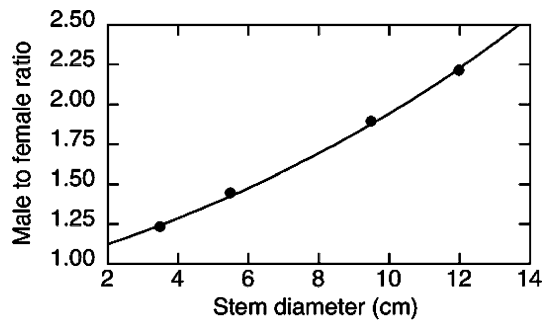
Fig. 1 Changes in sex ratio in *Acer negundo* (box elder) as a function of plant size in non-streamside habitats in northern Utah, based on data presented by Dawson and Ehleringer (1993). While the region-wide average male-to-female sex ratio is 1.61, this ratio becomes progressively higher as trees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

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, Δ carbon isotope discrimination

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

[a] Numbers *in parentheses* are SDs, based on data from Dawson et al. (2004)

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.

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 (Δ), 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
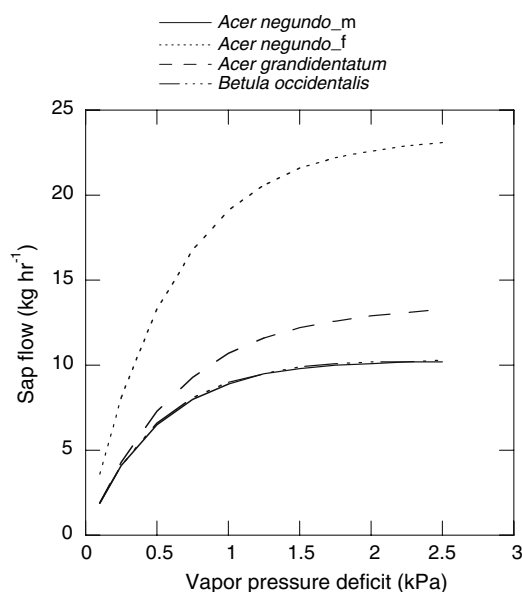
(VPD) in hypothetical 20-cm-diameter trees (a common size for riparian tree populations in the western US), modeled from previously published data (Hultine et al 2007). Populations include streamside male and female *A. negundo*, and two monoecious riparian tree species that are also common in mid-elevation 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^{-1}. Transpiration rates in a 20 cm diameter *A. grandidentatum* would be slightly higher, exceeding 13 kg h^{-1}. 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
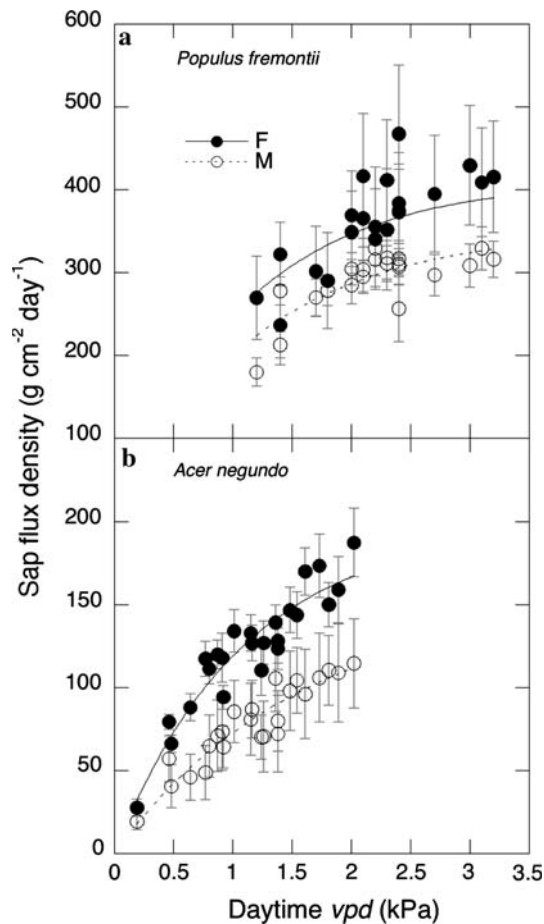

Fig. 2 Modeled transpiration rate (T; kg h^{-1}) in 20-cm-diameter male (m) and female (f) *A. negundo*, *Acer grandidentatum* (big tooth maple), and *Betula occidentalis* (water birch) trees occurring near Salt Lake City, Utah. Data are modeled from gender/species-specific sap flux coefficients, and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

Fig. 3a, b Sap flux density (J_s; g cm^{-2} 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 ± 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

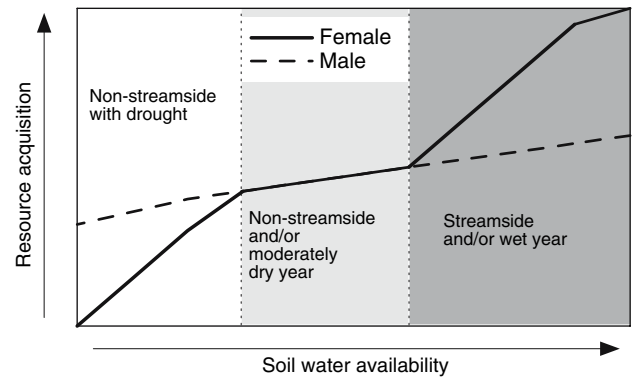|	VPD (kPa)	Q (mol m^{-2} s^{-1})	VPD × Q	Gender
P. fremontii	0.0021	0.29	0.45	<0.0001
A. negundo	<0.0001	0.0012	0.26	<0.0001

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 disproportionally 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:

$$P = \mathrm{ET} + R + S \tag{1}$$

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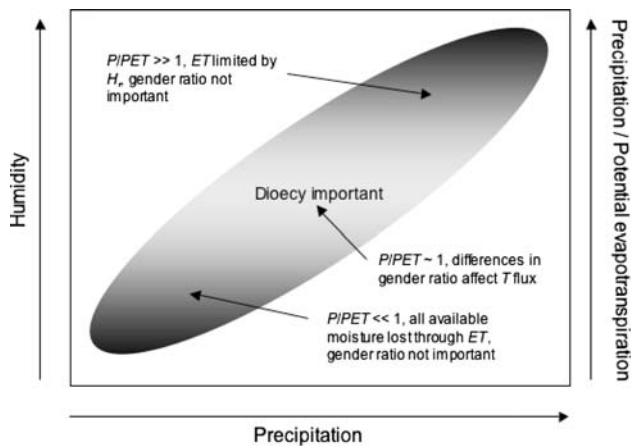
Fig. 5 A conceptual model of the climate conditions in which we expect the spatial segregation of the sexes of dominant riparian vegetation to impact evapotranspiration (*ET*) and subsequent streamflow. *P/PET* Ratio of precipitation to potential ET

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.

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