Commentary

Adaptation to climate change of dioecious plants: does gender balance matter?

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Since the 1877 publication of Charles Darwin’s *The Different Forms of Flowers on Plants of the Same Species*, interest in understanding the fundamental biological processes of sexual and gender dimorphism in dioecious plant species has continued. Dioecy is found in 157 flowering plant families and 7.5% of flowering plant genera, about 6% of the 240,000 angiosperm species (Renner and Ricklefs 1995). Dioecious plants provide an excellent opportunity for examining the trade-offs in resource allocation related to plant reproduction (Cepeda-Cornejo and Dirzo 2010). Natural selection (acting within phylogenetic, physiological and ecological constraints) shapes patterns of resource allocation, balancing the costs and benefits associated with these trade-offs, resulting in the evolution of life-history strategies maximizing fitness. Male and female individuals play different roles in the reproductive biology of a dioecious species and hence have very different resource demands imposed upon them (Thomas and LaFrankie 1993). The selection pressures presented by different resource demands could in turn lead to the evolution of sexual dimorphism (Meagher 1984), the separation of male (androecium) and female (gynoecium) plant characters that are not directly related to gamete production. Plants are predicted to allocate more resources to the sexual function that has the greater marginal rate of return (Charnov 1982). Resources that could be used for the production of new leaves, stems and roots are shifted to the production of flowers, fruits and seeds. Males and females of many dioecious species differ from one another in terms of their life histories, involving differences in photosynthetic performance (Dawson and Geber 1999) water use (Rowland and Johnson 2001), plant phenology (Delph 1999) and herbivory tolerance (Cornelissen and Stiling 2005).

The theory of ecological causation explains differentiation in secondary characteristics between sexes by postulating that males and females have adapted to different ecological niches (Shine 1989). Spatial segregation of the sexes associated with microhabitat differences is common in dioecious tree species (Grant and Mitton 1979, Dawson and Ehleringer 1993, Dudley 2006, Li et al. 2007, Zhang et al. 2010), for which sexes are generally distributed such that females are more common in high-resource microsites and males are more common in low-resource microsites (Dawson and Bliss 1989). Because segregation of the sexes may be adaptive, global change and subsequent changes to resource availability and allocation pattern may change the sex ratio and reproductive success of many dioecious species (Hultine et al. 2008). Land clearing and environmental pollution may lead to the subdivision of continuous habitats into fragmented patches, eventually leading to loss of biodiversity. Dioecious plants are expected to be particularly vulnerable to change in population size and structure, and thus also sensitive to habitat fragmentation (Yu and Lu 2011).

Gender-specific physiological responses to rising air temperature and CO₂ concentration raise the question of whether global change could lead to drastic changes in sex ratio and in the range of species’ distribution. Male plants of *Salix arctica* Pall. had a significantly higher photosynthetic rate than females at elevated CO₂, but only at a higher temperature (Jones et al. 1999). Male saplings of *Populus tremuloides* Michx. had higher photosynthesis than females throughout the growing season, regardless of CO₂ concentrations, but sexual difference in photosynthesis was greater at elevated than at ambient CO₂ (Wang and Curtis 2001). If carbon assimilation of male and female individuals of dioecious species is differentially affected by
elevated atmospheric CO₂ concentration, their productivity, distribution and population structure might also be altered as CO₂ emissions continue to rise. In this issue, Zhao et al. (2012) extend sex-related research on dioecious species, studying the response of *Populus cathayana* Rehder to elevated CO₂ concentration and increased air temperature, and conclude that males benefited more from elevated CO₂ by increasing the leaf expansion rate and final plant sink size through maintaining a higher biomass accumulation than do females. These findings are consistent with previous studies showing that sex-related differences in the responses of dioecious plants to elevated CO₂ are probably due to males being able to sustain a higher rate of carbon assimilation with higher sink activities throughout the growing season (Wang and Curtis 2001, Xu et al. 2008). Gender-specific variation in carbon assimilation and allocation in dioecious tree species indicates the importance of defining both sex and habitat conditions when making observations on dioecious species. These findings may also have significance in predicting the potential response of dioecious species to global environmental changes and to fully exploit the sink strength of multipurpose tree plantations.

According to the resource allocation principle, if resources are limited, reproduction, growth and maintenance (i.e., metabolism or defense) functions compete directly with one another and an increase in resources allocated to one function will result in a decrease in resources allocated to the other(s) (Bazzaz 1997). Resource allocation patterns are the expression of source–sink interactions within the plant and their controls on assimilate partitioning. Young leaves depend, in part, on carbohydrates imported from other regions of the plant, while mature leaves produce an excess of photo assimilates and act as the major source of transport sugars. The timing of the transition from the import (sink) to the export (source) phase coincides with a net positive accumulation of carbon in the leaf (e.g., Marchi et al. 2005a, 2005b). The relative importance that structural and functional leaf traits have on photosynthetic capacity would depend on a complex interaction of internal architecture and physiological differences (Marchi et al. 2007, 2008). The study by Zhao et al. (2012) reports that, during the carbohydrate import phase, female newly developing leaves can sustain further growth to accommodate expansion. However, when leaves were older and fully expanded, male fully expanded leaves showed greater increases in gas exchange, chlorophyll *a/b* ratio and leaf nitrogen content per leaf area, and soluble protein under elevated CO₂. This implies that CO₂ enrichment might make sink capacity more responsive in males than in females because of their greater adaptability and better carbohydrate use efficiency. On the other hand, translocation of resources from non-reproductive to reproductive shoots within a plant may partly offset reproductive costs. If resource translocation occurs among shoots to support fruit set, then physiological or growth costs of reproduction may be more evident in young plantlets than in mature trees. In this sense, comparisons of short-term studies alone can be misleading because correlations of fitness and growth to physiological traits varies widely among plant species, environmental conditions and life stages (Dudley 2006). Comparisons of the performance between sexes of dioecious plants on long-term growth rather than on short-term physiological measurements only are warranted.

Zhao et al. (2012) also found that *P. cathayana* males were more responsive to the combined elevated CO₂ and elevated temperature treatment in vegetative mass production than females. The higher relative biomass allocation to roots in males helped meet their higher nitrogen demand for continuously accelerated photosynthetic capacities under the combined treatment, in accordance with the hypothesis that sex-related differences in nutrient uptake could be facilitated by elevated temperature, with males showing better adaptability under a warmer climate. In the same species, sex-related differences in nitrogen-use efficiency and leaf senescence rates, mainly due to females having lower source activities than males under suboptimal environments, were also found by Zhao et al. (2009) and Chen et al. (2010). Again, Zhang et al. (2011) found evidence that sexually different responses to chilling in *P. cathayana* are significant and males possess a better self-protection mechanism than do females. Xu et al. (2008) found that female individuals of *P. cathayana* were also morphologically, physiologically and biochemically more responsive, and experienced greater negative effects than did males when grown under environments with increased drought stress and elevated temperature. *Populus cathayana* males suffered less from adverse effects of drought than did females at the proteome level. Transcriptional profiling analysis may further reveal down- and up-regulated genes in response to stress, identifying genes with different expression patterns between males and females as excellent targets to uncover regulatory mechanisms of sexual differences in plant tolerance to stress (Di Baccio et al. 2011, Jiang et al. 2012).

Plant species in which male and female flowers are found in separate individuals are common in woody vegetation that typically occurs in riparian ecosystems, such as *Populus* and *Salix*. Riparian tree species are one example of plants that may be particularly vulnerable to the present effects of global change, including both changes in land use and climate (Hultine et al. 2007). Skewed sex ratios have been observed in many populations of *Populus* (Grant and Mitton 1979, Comtois et al. 1986, Braatne and Rood 1996, Gom and Rood 1999, Braatne et al. 2007, Chen et al. 2010, 2011; but see Kaul and Kaul 1984, Stanton and Villar 1996, Rowland and Jackson 2001). As hypothesized by Zhao et al. (2012), the indication that photosynthetic responses to elevated CO₂ and elevated temperature were sex specific can result in contrasting survival rates and distinct growth patterns. Indeed, male *P. cathayana* trees
grown under elevated CO\textsubscript{2} exhibited greater soluble protein content and photosynthetic nitrogen-use efficiency than do females. Salicaceae are being used in a variety of ecosystem management projects, such as biomass crops and in environmental restoration. Management practices informed by morph differences in niche dimensions could be beneficial. In plantation forestry, females might be preferentially established in wet areas and males in dry microsites, providing better yield or coverage than a random distribution of the sexes. This approach could be important in water-limited environments, for maximizing carbon gain and minimizing water stress. Plants could benefit from slightly warmer temperatures and higher CO\textsubscript{2} concentration, but not all plants will benefit equally from these conditions, and some may even be harmed in more extreme conditions. Because offspring have one mother and one father, any deviation from a 1:1 population sex ratio will cause frequency-dependent natural selection. In their study, Zhao et al. (2012) provide helpful insights into sex-specific phenomena of plant adaptability to warming climate and sex-related source-to-sink transitions in dioecious tree species.

If sexes differ in performance across gradients of environmental stress or resource availability, sex-specific fitness payoff may occur in extreme years (Figure 1). There will be winners and losers in the warmer world of the near future, and males may be more resilient than females under recurrent stressful conditions. If differential natural selection on sex phenotypes caused by abiotic resource availability or natural biotic enemies is contributing to variation in sex ratio, altering plant fitness and sex ratio, the losers may greatly outnumber the winners in progeny of dioecious trees. Indeed, a strong impact on ecological processes of ecosystems in which \textit{Populus} (and \textit{Salix}) dominate may be expected. Along water course margins and riparian floodplains, in otherwise arid environments, the root system of these dioecious tree species may extract large amounts of water from shallow stream aquifers (Freeman et al. 1980); carbon metabolism and hydraulic architecture are coupled via multiple interactions (McDowell 2011). Under increasing air temperature, enhanced risk of female mortality in species that maintain narrow margins of hydraulic safety, such as \textit{Populus}, may derive from carbon starvation (when resource acquisition and storage mobilization fail to meet consumption for metabolic maintenance, transport processes and defense mechanism) rather than hydraulic failure (if reduced soil water supply coupled with critically high evaporative demand causes xylem conduits to cavitate). Higher reproductive costs of female function might be expected to make pistillate trees more responsive to elevated CO\textsubscript{2} following reproductive onset, by increasing sink strength. Zhao et al. (2012) examined non-reproductive cuttings, but growing trees to reproductive maturity will be critical to interpret the response to global change in dioecious woody plants.

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**References**


![Figure 1](image-url)  

Figure 1. Theoretical relationship based on the progeny sex ratio framework, between air temperature, total precipitation, resource acquisition and environmental disturbance. Male-biased sex ratio is hypothesized to occur when extreme years limit the availability of resources. Female progeny can suffer higher mortality rates in stressful habitats or in climatically stressed environments.


