

Sexual differences and sex ratios of dioecious plants under stressful environments

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Abstract

Dioecious plants exhibit sexual dimorphism in both sexual features (reproductive organs) and secondary sex characteristics (vegetative traits). Sexual differences in secondary traits, including morphological, physiological and ecological characters, have been commonly associated with trade-offs between the cost of reproduction and other plant functions. Such trade-offs may be modified by environmental stressors, although there is evidence that sexually dimorphic responses to stress do not always exist in all plant species. When sexual dimorphism exists, sexually different responses appear to depend on the species and stress types. Yet, further studies on dioecious plant species are needed to allow the generalization of stress effects on males and females. Additionally, sexual dimorphism may influence the frequency and distribution of the sexes along environmental gradients, likely causing niche differentiation and spatial segregation of sexes. At the present, the causes and mechanisms governing sex ratio biases are poorly understood. This review aims to discuss sex-specific responses and sex ratio biases occurring under adverse conditions, which will advance our knowledge of sexually dimorphic responses to environmental stressors.

Key words: Dioecy; stress tolerance; sexual dimorphism; sex ratios; competition; spatial segregation

Introduction

The majority of flowering plants show a hermaphroditic sex expression, while dioecy, i.e. the presence of two separate sexes, is relatively rare. It has been reported that dioecious plants represent 5-6% of angiosperm species and they occur in 43% of angiosperm families, with 15600 dioecious angiosperm species in 987 genera and 175 families (Renner 2014). Sex determination systems of flowering plants involving separate sexes have evolved independently many times from hermaphroditism in a lineage-specific manner (Charlesworth 2002; Juvany and Munné-Bosch 2015). Such transitions are often related to the evolution of sexual dimorphism, probably due to maximizing respective female and male fitness (Tonnabel et al. 2017). The incidence of dioecy in flowering plants may represent an evolutionary and ecological advantage.

Dioecious plants exhibit sexual dimorphism, not only in terms of their primary sexual traits but also of their vegetative traits (secondary sexual dimorphism) (Barrett and Hough 2013). Secondary sexual traits involve morphological, physiological and life-history differences between sexes, and they reflect sex-specific adaptations to different resource demands. Sexual dimorphism in secondary sexual traits can be attributable to resource tradeoffs between reproduction and other plant functions (e.g. defense and growth) (Galen et al. 2000; Lei et al. 2017). Such resource tradeoffs between females and males are probably modified by abiotic and biotic environmental factors during their life cycles, for instance, by heavy metal stress, drought, nutrient deficiency, and the presence of pathogens and herbivores (Ribeiro-Mendes et al. 2002; Barrett and Hough 2013; Liu et al. 2020a; Xia et al. 2020).

The theory of resource allocation suggests that reproduction can directly compete with vegetative growth and defense responses when resources are limited (Doust 1989). Therefore, a higher reproductive cost may be detrimental to plant growth and defense in dioecious plants. Generally, females are associated with a greater resource demand to produce flowers and seeds, and they commonly perform worse than males under abiotic stresses (Leigh and Nicotra 2003; Bañuelos et al. 2004), but this pattern is not universal (Juvany and Munné-Bosch 2015). In fact, some studies have shown that the reproductive costs of males may exceed or match those of females due to their high investment in nitrogen-rich pollen in some wind-pollinated plants (Delph 1999; Leigh 2006; Harris and Pannell 2008). Overall, based on previous studies, there is no consistent pattern in the responses of the sexes to environmental stresses, but the responses seem to vary depending on the plant species and the type of stress, but a greater range of studies is needed (Retuerto et al. 2018).

Environmental changes influence secondary sex characteristics of dioecious plants, probably causing biased sex ratios as well (Graff et al. 2013; Petry et al. 2016; Simancas et al. 2018). The sex ratios of dioecious plants are expected to be close to 1:1 when the parental investments producing females and males are equal (Fisher 1930). However, biased sex ratios are commonly found (e.g. Bisang and Hedenäs 2005; Barrett et al. 2010; Sinclair et al. 2012; Pucholt et al. 2017). Male-biased sex ratios are often associated with a long growth period, biotic seed dispersal and fleshy fruits that are prevalent in trees and vines (Wheelwright and Logan 2004; Sinclair et al. 2012; Field et al. 2013). In contrast, female-biased sex ratios are commonly related to clonality and heteromorphic sex chromosomes found in many herbs, annuals and shrubs (Lloyd and Webb 1977; Field et al. 2013).

The evolutionary and ecological mechanisms underlying the biased sex ratios may be attributable to a biased primary sex ratio (Stehlik et al. 2008), mortality differences (Simancas et al. 2018), germination requirements (Stark et al. 2001), sex lability (Mesgaran et al. 2019) and spatial segregation of sexes (Alvarenga et al. 2013). However, no general conclusion is drawn on the relative importance of these mechanisms, depending largely on the plant species and specific environmental factors. Environmental stresses probably impose a threat to plant species and communities, especially in plants with sexually dimorphic breeding systems (Hultine et al. 2016; Varga and Soulsbury 2020). Importantly, highly skewed sex ratios may cause population declines and even mass extinctions, with potential effects on the structure and stability of populations (Petty et al. 2016). Therefore, it is urgent to reveal the effects of environmental changes on dimorphic species.

In this review, we comprehensively analyze how males and females respond to abiotic and biotic stressors, and provide possible causes for sex-related differences in stress responses and tolerance. Firstly, we develop a comprehensive synthesis of sexual differences and adaptive responses under environmental stress conditions (abiotic and biotic stresses). Secondly, we evaluate and discuss the potential causes, processes and consequences of biased sex ratios under changing environmental conditions. Finally, we introduce the role of sexual interactions in responses to environmental factors. Thus, this review will expand our knowledge of the biology of dioecious plant species.

Sexual differences in responses to environmental stressors

Abiotic stresses

In dioecious plants, differences in reproductive costs and demands for resources between sexes may lead to sex-specific adaptations and responses to environmental constraints or stressors (Figure 1). Dimorphic investments in reproduction may be reflected in different physiological responses to abiotic stresses in males and females (Figure 2). Generally, females have higher reproductive costs for the production of flowers, fruits and seeds, i.e. a higher reproductive investment when compared to males. As discussed in the study of Juvany and Munné-Bosch (2015), higher reproductive investment in females may cause a decrease in the energy invested into growth and defense, thus reducing stress tolerance. Indeed, female plants have been reported to perform worse than males under environmental stresses (Pickering et al. 2003; Bañuelos et al. 2004; Liu et al. 2021a; Yu et al. 2020).

The differential plasticity hypothesis suggests that females and males exhibit sex-specific plasticity in responses to environmental factors, probably associated with the different demands of resource ‘currencies’ (such as carbon and nitrogen) for their reproduction (Obeso 2002; Delph and Bell 2008). Owing to the demands for carbon and water during fruiting and seed setting, females tend to increase water acquisition and photosynthetic carbon gain, which is probably achieved by the high stomatal conductance and hydraulic conductivity (Olano et al. 2017). Such resource acquisition in females easily suffers from hydraulic failure and carbon starvation, potentially as a consequence of higher stomatal sensitivity and more

vulnerable xylem cavitation, especially under xeric conditions (Chen et al. 2010; Han et al. 2013; Olan et al. 2017). In contrast, the superior performance of males observed in some studies is associated with the more conservative strategy to maximize abiotic stress tolerance, especially in drier sites. Interestingly, under well-watered conditions, secondary sexual dimorphisms in physiological characters may disappear (Chen et al. 2014).

The “functional equilibrium” of biomass allocation assumes that biomass allocation is associated with the growth-limiting factors. That is, plants would allocate relatively more biomass to roots, if the growth-limiting factors are below ground. However, relatively more biomass would be allocated to shoots, if the growth-limiting factors are above ground (Brouwer 1963; Thornley 1972; Poorter et al. 2012). The great demand for carbon in females may be met by higher photosynthetic rates. Generally, females of dioecious poplars tend to have a higher resource uptake and carbon costs for the root system and shoot growth under sufficient phosphorus and nitrogen supplies (Song et al. 2018; Xia et al. 2020). Conversely, males usually have a higher resource use efficiency and more conservative nutrient demand to maximize stress tolerance and gain opportunities to survive in low-resource habitats (Zhang et al. 2019; Xia et al. 2020).

In *P. cathayana*, females have a higher specific root length and root length density to maximize resource uptake, while males have a lower root biomass allocation, as well as a higher antioxidation, acid phosphatase exudation, and colonization and hyphal biomass of arbuscular mycorrhizal fungi in response to a heterogeneous phosphorus distribution (Zhang et al. 2019; Xia et al. 2020). Interestingly, the resource consumption traits of females in some species appear not to distinguish ions, which are toxic or necessary for plants. For example,

when compared to male poplars, females have a better capacity to acquire nitrogen (Zhang et al. 2014), phosphorus (Xia et al. 2020) and potassium (Yang et al. 2015) under a sufficient nutrient supply, but they also accumulate more sodium, chloride, cadmium and zinc under salinity and heavy metal stress in the shoots (Li et al. 2016; Song et al. 2018; Liu et al. 2020b, 2021b). The excessive accumulation of salt and heavy metal ions and the inability of detoxification certainly cause more adverse effects in females (Li et al. 2016; Liu et al. 2020b).

However, it has been suggested that males have higher reproductive costs than females, particularly in some wind-pollinated herbaceous species (Delph 1999; Harris and Pannell 2008). Herbs tend to have a greater demand for nitrogen than woody plants, as pollen is richer in nitrogen than fruit and seed (Ishida et al. 2005; Kerkhoff and Enquist 2006). Thus, when nitrogen is limited, the allocation of nitrogen to pollen production in males could compromise the growth of males more than that of females with more carbon allocation to fruits and seeds. It is worth noting that reproductive costs are probably linked to the timing of the resource allocation (Sánchez-Vilas and Pannell 2010; Barrett and Hough 2013). For example, males have higher reproductive costs during flowering and those are associated with flowering times, pollen production and amounts of nectar per flower. Actually, final reproductive costs are higher in females producing fruits and seeds, at least if we consider the whole reproduction season (Cepeda-Cornejo and Dirzo 2010; Núñez-Farfán and Valverde 2020). However, the costs of reproduction and perennial organs in the males of wind-pollinated species cause reduced defense responses (Harris and Pannell 2008; Oñate et al. 2012; Morales et al. 2013).

Under drought conditions, *Humulus scandens* and *Silene otitis* males maintain lower photosynthesis and show greater photosynthetic damage, thus rendering them higher drought sensitivity and mortality than females during the vegetative growth stage (Soldaat et al. 2000; Liu and Duan 2013). Comparably in *Phillyrea angustifolia*, females exhibit higher photosynthesis and intrinsic water use efficiency, and better growth performance than males under salt stress and desiccation (Medina-Gavilán et al. 2008). On the other hand, no sexual differences under drought stress have been found in *Acer negundo* and *Populus angustifolia* (Ward et al. 2002; Juvany and Munné-Bosch 2015). Thus, there are no general patterns about the responses of the sexes to environmental stresses. As discussed by Retuerto et al. (2018), sex-specific responses are highly dependent on species and stress types. Further research is needed to be made to elucidate the physiological, morphological and molecular mechanisms underlying sexually different responses to individual and combined environmental stresses during the whole growing season or even during the whole life-cycle of perennial plants (Retuerto et al. 2018).

In addition, sex-specific responses to rising CO₂ and temperature have been investigated in plant species to predict the potential mechanisms underlying plants' responses to the climate change (Chen et al. 2021). These studies have suggested that males benefit more from elevated CO₂ levels by increasing their leaf expansion and carbon assimilation throughout the whole growing season (Xu et al. 2008; Zhao et al. 2012). Elevated temperature leads to higher biomass in males through an increasing leaf expansion, resulting in higher carbon assimilation with higher sink activities (Tognetti 2012). The combination of CO₂ and temperature increases root growth and biomass in males to meet the enhanced photosynthetic capacities (Zhao et al. 2012). In contrast, females have a larger leaf expansion, higher reproductive mass and more investment in density growth than males under elevated CO₂ and

temperature (Huang et al. 2014). These results suggest that females and males of dioecious plants possess sex-specific strategies to cope with elevated CO₂ and/or temperature.

Biotic stresses

Sexual dimorphism is commonly associated with sexual differences in the nutritional status, growth rates and/or chemical defenses, which in turn may affect herbivory rates. In this section, we discuss sex-biased herbivory by focusing mainly on the resource allocation into growth, reproduction and defense, as well as on the effects of environmental stressors on sex-biased herbivory. Several studies have shown the presence of male-biased herbivory that is mostly derived from the cost of reproduction (Cornelissen and Stiling 2005). The resource allocation principle assumes that growth, reproduction and maintenance functions compete directly with each other, so that an increase in resource allocation to one function will result in a decrease in others (Charnov 2020; Juvany and Munné-Bosch 2015). Some studies reported that male plants have greater vegetative growth rates, more leaves and lower resource investment in physiological/chemical defenses, while females invest more nutrients into defense or reproduction (Cornelissen and Stiling 2005; Avila-Sakar and Romanow 2012). Usually, females have larger sizes and superior herbivory tolerance when compared to males in most herbaceous species (Vasiliauskas and Aarssen 1992; Bertiller et al. 2002). However, as reviewed by Avila-Sakar and Romanow (2012), it remains controversial, whether high or low growth rates favor herbivory tolerance.

Plants' nutritional quality may also affect sex-biased herbivory since herbivores are usually limited by nitrogen-compounds, such as amino acids (Mattson 1980). Rivkin et al. (2018) have suggested that the lower nitrogen content in *Sagittaria latifolia* males reduces the survival of *Listronotus appendiculatus* larvae. Moreover, nectar and pollen are important food resources for herbivores and their natural enemies (Stenberg et al. 2015). Males have increased nitrogen demands for pollen production, and they often exhibit great growth rates and nutritional qualities, as well as higher amounts of nectar per flower compared to females (Barrett and Hough 2013; Renner 2014). A quantitative analysis performed by Cornelissen and Stiling (2005) indicated that the herbivory induced by gall makers and folivores is more significant in male plants, and the herbivore damage affected by plant sex is more significant for flower predators than for browsers and folivores.

For chemical defense, plants can produce toxic chemical substances, such as secondary metabolites, to kill herbivores or elongate their development time (Fürstenberg-Hägg et al. 2013). Females have increased carbon demands for fruits and seeds. It appears that the large carbon storage in females during the non-productive period may increase the synthetic potential of carbon-containing secondary metabolites, facilitating the defense against herbivores. For example, female plants have higher levels of tannin, phenolic and quercetin-glucoside-related compounds, and better chemical defense than males in dioecious *Chlorocystis excisa* *Chamaedorea* palms, *Betula pendula* Roth and *B. pubesce* (Palo et al. 1992; Tsuji and Sota 2010; Cepeda-Cornejo and Dirzo 2010). This is consistent with the hypothesis of “sex-biased herbivory”, which assumes that females have a better defense against insect herbivores due to their increased carbon investment into reproduction and carbon-based secondary metabolisms, whereas males are mostly attracted by herbivores

because of the increased energy investment in growth (biomass) (Coley 1988; Fincher 2009; Cepeda-Cornejo and Dirzo 2010).

Most studies have reported that male-biased herbivory is common in dioecious plants studies so far (Ashman 2002; Retuerto et al. 2006; Yule and Burns 2019). However, some studies have found female-biased herbivory or similar herbivory in both sexes (McCall 2008; Espírito-Santo et al. 2012; Buckley and Avila-Sakar 2013). For example, in the Mexican ciruela, females have higher levels of herbivory associated with their nutritional content (Maldonado-López et al. 2014). In *Ilex glabra*, female-biased herbivory is found only after flowering (Buckley and Avila-Sakar 2013). The herbivory of marula trees is induced by African elephants, as the female branches are less ramified and shorter than those of male trees (Hemborg and Bond 2007). Thus, male-biased herbivory is not universal. As emphasized by Avila-Sakar and Romanow (2012), the assumption of male-biased herbivory in dioecious plants may be due to the taxonomic bias of species studied and the lack of empirical studies. Therefore, there is a need for more precise quantitative measurements of herbivore levels, growth rates and reproductive allocation in male and female plants.

Environmental conditions affect resource allocation and the content of defensive compounds in both sexes (Randriamanana et al. 2014; Yang et al. 2020). Females synthesize more condensed tannins than males under limited nutrient conditions, but less under sufficient nutrient conditions (Jiang et al. 2016). Additionally, plants' low nutritional quality can provide potential defense against herbivores (Haukioja et al. 1991; Fritz and Simms 1992; Yang et al. 2020). Overall, the sex-biased herbivory appears to be associated with trade-offs between growth, production and maintenance, although there are still uncertainties of the

mechanism (Juvany and Munné-Bosch 2015; Núñez-Farfán and Valverde 2020). The lack of a general pattern emerging from previous studies is assumed to be associated with the insufficient scope of investigations, too few plant families covered and the involvement of a single time point only (Retuerto et al. 2018; Núñez-Farfán and Valverde 2020). Therefore, further studies should be performed to have comprehensive coverage of plant species and life histories.

Overall, there is no clear pattern in the responses of different sexes to abiotic and biotic stresses. Larger scale studies encompassing multiple stress factors are needed to allow generalizations (Núñez-Farfán and Valverde 2020). These studies about sex-specific responses must consider the species in question, the nature and intensity of stresses, and life cycle stages, including also responses to combined abiotic and biotic stresses.

Biased sex ratios

According to the hypothesis by Fisher (1930), the sex ratios of offspring should be close to 1:1. Despite this expectation, biased sex ratios commonly exist in dioecious plants (e.g. Hardy 2002; Sinclair et al. 2012; Field et al. 2013). Based on published studies, only 29% of plant populations exhibit 1:1 sex ratios, while 59% show deviations from equality, of which almost two-thirds being male-biased (Delph 1999; Sinclair et al. 2012). It has been suggested that male-biased sex ratios are dominant in dioecious vines and trees, whereas female-biased sex ratios are generally prevalent in shrubs, herbs and annuals (Field et al. 2012). Male-biased sex ratios are associated with long-lived growth, fleshy fruits and biotic seed dispersal,

whereas female-biased sex ratios are associated with short-lived growth forms (e.g., herbs), clonality and abiotic pollen dispersal (Field et al. 2012; Sinclair et al. 2012) (Figure 3). Highly skewed sex ratios probably cause plant population declines and even extinction, potentially affecting the structure and stability of communities (Retuerto et al. 2018). Understanding the mechanism underlying sex ratio biases is necessary for predicting sex-specific responses and effects caused by environmental stresses on dioecious species.

Mechanisms driving sex ratios are often associated with unknown genetic and ecological factors, including resource allocation, vegetative vigor, sex choice/switching, pollination competition and offspring mortality (Stehlik and Barrett 2006; Harris and Pannell 2008; Field et al. 2013). The effects of environmental factors on sex ratio biases may be attributable to the manner of sexual expression. Sex ratio biases may relate to sex chromosome meiotic drive (Jaenike 2001), pollen competition (certation) (Stehlik and Barrett 2005), genotype-specific mortality (Billiard et al. 2015) or allelic/genotypic incompatibilities (Pucholt et al. 2017). Among those, the certation hypothesis assumes that competition between male- and female-determinating microgametophytes (certation) would result in variation in pollination intensity, and large pollen loads would cause female-biased offspring sex ratios, as proposed for *Rumex nivalis* (Conn and Blum 1981). The offspring sex ratios depend on the maternal pollination environment (Stehlik and Barrett 2005). Stehlik et al. (2008) have suggested that *Rumex nivalis* females positioned close to males have higher stigmatic pollen loads and produce more strongly female-biased sex ratios than females further away from males.

Meiotic drive in *Silene latifolia* assumes that the X chromosome is associated with the female-biased ratio (Taylor 1994, 1999). Allelic or genotypic incompatibilities at key loci

probably cause the genotype-specific mortality of seeds, zygotes and seedlings and, thus, sex ratio biases, such as single-locus self-incompatibility observed in the dioecious shrub species *Phillyrea angustifolia* (Billiard et al. 2015). Furthermore, female-biased sex ratios often occur in species with heteromorphic sex chromosomes, although sex chromosomes are rare in angiosperms (Charlesworth 2002; Vyskot and Hobza 2004). The “unguarded sex chromosome hypothesis” predicts that species with heterogametic sex may have higher mortalities than species with homogametic sex due to the recombination between sex-determining loci is absent, thus leading to the consequent accumulation of deleterious mutations (Stehlik and Barrett 2006; Pipoly et al. 2015).

The secondary sex ratio is usually reported to be affected by secondary sexual traits (Meagher 1992). Biased secondary sex ratios may be associated with sex-specific resource allocation, the cost of reproduction (Ortiz et al. 2002), susceptibility to environmental stressors (Varga and Soulsbury 2020), mortality and competition between sexes (Hroneš et al. 2019). Environmentally sexual determination is expected to bias sex ratios toward the sex facilitating survival and fitness in poor environments (Charnov and Bull 1977; Wade et al. 2003). The correlation of sex ratios and environmental stressors will ultimately be the consequence of the sexes experiencing environmental pressures in a sex-specific manner (Retuerto et al. 2018). Environmental factors, including light, water, temperature, CO₂ level and nutrient availability, are known to influence sex ratios in dioecious plant species (Sinclair et al. 2012; Petry et al. 2016; Retuerto et al. 2018; Mesgaran et al. 2019; Varga and Soulsbur 2020).

The sex allocation theory predicts that the environmental facilitation effect on plant growth induces female sex expression, while resource-poor conditions should favor maleness (Charnov 2020). Commonly, females exhibit greater reproductive costs than males, possibly experiencing higher mortality as well, resulting in male-biased sex ratios, especially in less favorable environments. Mesgaran et al. (2019) have suggested that the overrepresentation of male plants under stressful environments may be attributable to sex-differential mortality rather than to an actual sex change. Other studies have proposed that males produce massive amounts of pollen to successfully reproduce, and such great reproductive investment would cause female-biased sex ratios (Harris and Pannell 2008; Sinclair et al. 2012). Yet, the genetic and ecological mechanisms governing sex-ratio patterns in dioecious plant species are still unclear. Future work should attempt to elucidate in depth the effects of environmental stressors, including multiple interacting factors, on the sex-biased ratios.

Sexual interactions

Sex recognition and adaptation

Competition plays a fundamental role in determining the composition and function of biological communities (Goldberg and Barton 1992; Chen et al. 2014). Plants have evolved the ability to recognize their neighbors' identity and plastically adjust their phenotypes in response to competition (Mercer and Eppley 2014; Dong et al. 2017; Jaafry et al. 2019). Recognition of neighboring individuals includes light quality, the presence of chemical and nutrient substances, and mechanosensing of neighbors (Ballare et al. 1990; Gagliano et al. 2012; Poorter et al. 2012).

Dioecious plant species exhibit sexual dimorphism in morphology, physiology, life histories, resource allocation and defense mechanisms (Bullock and Bawa 1981; Cepeda-Cornejo and Dirzo 2010; Sánchez-Vilas et al. 2012). Some studies have suggested that females and males can recognize their neighbors' identity and exhibit sex-specific responses as a result of above- and below-ground competition, visible, for instance, as shade avoidance and root system architecture (Mercer and Eppley 2014; Dong et al. 2017; Jaafray et al. 2019).

According to the concept of a “functional equilibrium” of biomass allocation, plants would allocate more biomass to roots, if the growth-limiting factor is below ground (e.g. water and nutrients), whereas more biomass would be allocated to shoots, if the growth-limiting factor is above ground (e.g. light and CO₂) (Brouwer 1963; Thornley 1972; Poorter et al. 2012).

Some studies have suggested that males show more resource allocation to growth than do females in response to aboveground competition (Sánchez-Vilas and Pannell 2010). The study by Tonnabel et al. (2017) reported that males of *Mercurialis annua* tend to reduce aboveground biomass and canopy growth more significantly compared to females under increasing light competition. Below-ground competition is mainly driven by the availability of soil resources, such as nutrients and water (Schenk 2006). Consistently, female poplars have more root biomass than males under intersexual competition in a resource-rich environment (Chen et al. 2015). Contrarily, male poplars have higher root/shoot ratios than females when under competition with limited resources (Chen et al. 2015). As far as we know, only a few studies have investigated adaptive responses related to sex-specific below-ground competition. More studies are needed to reveal morphological, physiological and molecular differences between the sexes under competition in response to environmental stressors.

Sexual competition

Females and males exhibit many kinds of morphological and physiological responses to optimize their performance and competitive ability (Chen et al. 2017). Consistently, many studies have suggested that female-biased sex ratios are favored under a better availability of resources to meet the greater reproductive cost of females, while male-biased sex ratios are favored in lower-resource habitats with a better stress tolerance of males (Dawson and Geber 1999; Correia and Barradas 2000; Chen et al. 2017). According to the maximum growth theory, plants with a maximum vegetative growth rate would be superior in competition, whereas the minimum resource requirement theory suggests that plant species with lower resource requirements are more competitive (Grace and Tilman 1990). Consistently, females with larger sizes exhibit a greater competitive ability than males in most herbaceous species (Vasiliauskas and Aarssen 1992; Bertiller et al. 2002; Zhang et al. 2009). In some woody dioecious perennials, males with larger sizes are expected to be competitively superior in growth (Obeso 2002). Hawkins et al. (2009) have shown that females and males exhibited similar competitive abilities in *Lindera melissifolia* (Lauraceae). Thus, it is evident that the competitive ability and intensity between the sexes vary among species and are probably related to life-history stages, reproductive costs, resource demands and environmental factors.

The two-phase resource dynamics hypothesis of plant interactions assumes that the resources are temporally variable. Consequently, most growth occurs under high-resource conditions, while most mortality takes place under poor resources (Deborah and Ariel 1997). In *Populus*

cathayana, females show a greater competitive ability than do males under well-watered, high phosphorus and nitrogen conditions, but the opposite occurs under drought and nutrient deficiency conditions (Xia et al. 2020; Wu et al. 2021). Therefore, the sex-specific utilization of resources may be decisive for the intensity and direction of competition in dioecious plants. Niche complementarity predicts that species differing in their use of resources have reduced competition and they are more likely to coexist, even in highly variable environments (Pacala and Tilman 1994). Many different kinds of coexistence mechanisms are reported, such as differential responses to spatial and temporal environmental variation (Chesson 1994, 2000), resource partitioning (Tilman 1982) and species-specific natural enemies (Janzen 1970; Connell 1971). These all lead to niche differences (Adler et al. 2010).

Dioecious plant species exhibit sexual differences in reproductive morphology, which may cause sexual specialization to different habitats leading to niche differentiation (Rogers and Eppley 2012; Mizuki et al. 2018). Further analyses have suggested that competition for limited resources would be the main results of the evolution of the sexual dimorphism in the utilization of resources and niche occupancy (Slatkin and Anderson 1984; Eppley 2005). The proposed hypothesis of the evolution of sexual niche partitioning assumes that niche differences are derived from natural selection for decreasing intersexual competition (Cox 1981). Such a hypothesis is expected to be valid only if the resulting distances in time and space are not so great that the chances for reproduction would reduce greatly (Cox 1981). Some studies have suggested that intersexual competition is greater than intrasexual one in dioecious plants, such as in *Antennaria dioica* and *Osyris quadripartite* (Herrera 1988; Varga and Kytöviita 2011), thus supporting the niche partitioning hypothesis. In turn, as a result of niche partitioning, intersexual competition between males and females may be expected to be alleviated compared with that between plants of the same sex (e.g. Zhang et al. 2009).

As we discussed above, the space segregation in patchy habitats may be attributable to the sexual specialization and competition in habitat and/or resource utilization, thus allowing the coexistence of sexes in dioecious species. The stress gradient hypothesis assumes that facilitative interactions are predominant under the most severe environmental conditions, whereas competition is common when the stress level is lower (Brooker et al. 2008; Maestre et al. 2009). Intrasexual competition is stronger in response to drought and heavy metals in *P. cathayana* (Chen et al. 2014, 2017; Li et al. 2016). However, the intersexual competition of poplars is slightly alleviated by nitrogen deficiency and drought (Chen et al. 2014, 2015) but increased by salt stress (Li et al. 2016). Therefore, environmental factors, such as nutrient availability, can significantly modify the strength and direction of competition. However, more research is needed to explore the intensity and direction of competition (including aboveground and underground competition) based on reproductive allocation and spatial sex differentiation.

Conclusions and perspectives

Sexual differences and sex-ratio biases of dioecious plant species have been explored for many decades, given the prevalence of sex ratio biases in dioecious flowering plants. Generally, females have higher reproductive costs and, consequently, reduced abiotic stresses tolerance when compared to males in most trees and vines. Conversely, males show better tolerance to biotic stresses in some studies. However, the general patterns are still lack related to sex-specific responses to stresses (abiotic and biotic stresses). Sexually different tolerances largely depend on the tradeoff between growth, reproduction and defense, requiring taking

consideration of plant reproductive frequency and intensity, life history and developmental stages. Further studies are needed to reveal the strategies and mechanisms adopted by different sexes to cope with environmental stresses (abiotic stress, biotic stress and combination of them).

Patterns of sex ratios largely depend on sex choice/switch, mortality, reproductive costs and sexual competition, which may cause spatial segregation of the sexes along environmental gradients. More studies are needed on the impact of environmental changes on population structures, especially under changing climate conditions. Moreover, the exploration of physiological and molecular mechanisms of sexual recognition and adaptation under sexual competition (including shoot and root competitions) could help to integrate the key factors determining sexual dimorphism and sex ratios under environmental changes.

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References

- Adler PB, Ellner SP, Levine JM (2010) Coexistence of perennial plants: an embarrassment of niches. *Ecol Lett* 13:1019-1029.
- Alvarenga LD, Pôrto KC, Zartman CE (2013) Sex ratio, spatial segregation, and fertilization rates of the epiphyllous moss *Crossomitrium patrisiae* (Brid.) Müll. Hal. in the Brazilian Atlantic rainforest. *J Bryol* 35:88-95.
- Ashman TL (2002) The role of herbivores in the evolution of separate sexes from hermaphroditism. *Ecology* 83:1175-1184.
- Avila-Sakar G, Romanow C (2012) Divergence in defence against herbivores between males and females of dioecious plant species. *Int J Syst Evol Micr* 897157.
- Ballare CL, Scopel AL, Sanchez RA (1990) Far-red radiation reflected from adjacent leaves— an early signal of competition in plant canopies. *Science* 247:329-332.
- Bañuelos MJ, Sierra M, Obeso JR (2004) Sex, secondary compounds and asymmetry. Effects on plant–herbivore interaction in a dioecious shrub. *Acta Oecol (Montrouge)* 25:151-157.

Barrett SC, Hough J (2013) Sexual dimorphism in flowering plants. *J Exp Bot* 64:67-82.

Barrett SC, Yakimowski SB, Field DL, et al. (2010) Ecological genetics of sex ratios in plant populations. *Philos T R Soc B* 365:2549-2557.

Bertiller MB, Sain CL, Carrera AL (2002) Effect of fine-scale spatial variation of soil nitrogen on the performance of the sexes of *Poa ligularis* in patchy ecosystems of northern Patagonia. *Int J Plant Sci* 163:419-425.

Billiard S, Husse L, Lepercq P, et al. (2015) Selfish male-determining element favors the transition from hermaphroditism to androdioecy. *Evolution* 69:683-693.

Bisang I, Hedenäs L (2005) Sex ratio patterns in dioecious bryophytes revisited. *J Ecol* 27:207-219.

Brooker RW, Maestre FT, Callaway RM, et al. (2008) Facilitation in plant communities: the past, the present, and the future. *J Ecol* 1:18-34.

Brouwer R (1963) Some aspects of the equilibrium between over-ground and underground plant parts. *Meded Inst Biol Scheikd Onderzoek Landbouwgewassen* 1963:31-39.

Buckley NE, Avila-Sakar G (2013) Reproduction, growth, and defense trade-offs vary with gender and reproductive allocation in *Ilex glabra* (Aquifoliaceae). *Am J Bot* 100:357-364.

Bullock SH, Bawa KS (1981) Sexual dimorphism and the annual flowering pattern in *Jacaratia dolichaula* (D. Smith) Woodson (Caricaceae) in a Costa Rican rain forest. *Ecology* 62:1494-1504.

Cepeda-Cornejo V, Dirzo R (2010) Sex-related differences in reproductive allocation, growth, defense and herbivory in three dioecious neotropical palms. *Plos One* 5:e9824.

Charlesworth D (2002) Plant sex determination and sex chromosomes. *Heredity* 88:94-101.

Charnov EL (2020) The theory of sex allocation. Princeton University Press (MPB-18), Princeton, New Jersey, USA.

Charnov EL, Bull J (1977) When is sex environmentally determined? *Nature* 266:828-830.

Chen J, Dong T, Duan B, et al. (2015) Sexual competition and N supply interactively affect the dimorphism and competitiveness of opposite sexes in *Populus cathayana*. *Plant Cell Environ* 38:1285-1298.

Chen J, Duan B, Wang M, et al. (2014) Intra- and inter- sexual competition of *Populus cathayana* under different watering regimes. *Funct Ecol* 28:124-136.

Chen J, Han Q, Duan B, et al. (2017) Sex-specific competition differently regulates ecophysiological responses and phytoremediation of *Populus cathayana* under Pb stress. *Plant Soil* 421:203-218.

Chen J, Liu Q, Yu L, et al. (2021) Elevated temperature and CO₂ interactively modulate sexual competition and ecophysiological responses of dioecious *Populus cathayana*. *For Ecol Manage* 481:118747.

Chen L, Zhang S, Zhao H, et al. (2010) Sex-related adaptive responses to interaction of drought and salinity in *Populus yunnanensis*. *Plant Cell Environ* 33:1767-1778.

Chesson P (1994) Multispecies competition in variable environments. *Theor Popul Biol* 45:227-276.

Chesson P (2000) General theory of competitive coexistence in spatially-varying environments. *Theor Popul Biol* 58:211-237.

Coley PD (1988) Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* 74:531-536.

Conn JS, Blum U (1981) Sex ratio of *Rumex hastatulus*: the effect of environmental factors and certation. *Evolution* 1:1108-1116.

Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics Populations* 298:312.

Cornelissen T, Stiling P (2005) Sex-biased herbivory: a meta-analysis of the effects of gender on plant-herbivore interactions. *Oikos* 111:488-500.

Correia O, Barradas MD (2000) Ecophysiological differences between male and female plants of *Pistacia lentiscus* L. *Plant Ecol* 149:131-142.

Cox PA (1981) Niche partitioning between sexes of dioecious plants. *Am Nat* 117:295-307.

Dawson TE, Geber MA (1999) Sexual dimorphism in physiology and morphology. In: *Gender and sexual dimorphism in flowering plants*. Springer, Berlin, Heidelberg, 175-215.

Deborah G, Ariel N (1997) The relative importance of competition on unproductive environments. *J Ecol* 85:409-418.

Delph LF (1999) Sexual dimorphism in life history. In: *Gender and sexual dimorphism in flowering plants*. Springer, Berlin, Heidelberg, 149-173.

Delph LF, Bell DL (2008) A test of the differential-plasticity hypothesis for variation in the degree of sexual dimorphism in *Silene latifolia*. *Evol Ecol Res* 10:61-75.

Dong T, Li J, Liao Y, et al. (2017) Root-mediated sex recognition in a dioecious tree. *Sci Rep* 7:1-7.

Doust JL (1989) Plant reproductive strategies and resource allocation. *Trends Ecol Evol* 4:230-234.

Eppley SM (2005) Spatial segregation of the sexes and nutrients affect reproductive success in a dioecious wind-pollinated grass. *Plant Ecol* 181:179-190.

Espírito-Santo MM, Neves FS, Fernandes GW, et al. (2012) Plant phenology and absence of sex-biased gall attack on three species of *Baccharis*. *Plos One* 7:e46896.

Field DL, Pickup M, Barrett SC (2012) The influence of pollination intensity on fertilization success, progeny sex ratio, and fitness in a wind-pollinated, dioecious plant. *Int J Plant Sci* 173:184-191.

Field DL, Pickup M, Barrett SC (2013) Comparative analyses of sex-ratio variation in dioecious flowering plants. *Evolution* 67:661-672.

Fincher GB (2009) Revolutionary times in our understanding of cell wall biosynthesis and remodeling in the grasses. *Plant Physiol* 149:27-37.

Fisher RA (1930) *The genetical theory of natural selection*. Oxford University Press, Oxford, London, UK.

Fritz RS, Simms EL (1992) *Plant resistance to herbivores and pathogens: ecology, evolution, and genetics*. University of Chicago Press, Chicago, USA.

Fürstenberg-Hägg J, Zagrobelny M, Bak S (2013) Plant defense against insect herbivores. *Int J Mol Sci* 14:10242-10297.

Gagliano M, Mancuso S, Robert D (2012) Towards understanding plant bioacoustics. *Trends Plant Sci* 17:323-325.

Galen C (2000) High and dry: drought stress, sex-allocation trade-offs, and selection on flower size in the alpine wildflower *Polemonium viscosum* (Polemoniaceae). *Am Nat* 156:72-83.

Goldberg DE, Barton AM (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am Nat* 139:771-801.

Grace JB, Tilman (1990) Perspectives on plant competition. Academic Press, New York, USA.

Graff P, Rositano F, Aguiar MR (2013) Changes in sex ratios of a dioecious grass with grazing intensity: the interplay between gender traits, neighbour interactions and spatial patterns. *J Ecol* 101:1146-1157.

Han Y, Wang L, Zhang X, et al. (2013) Sexual differences in photosynthetic activity, ultrastructure and phytoremediation potential of *Populus cathayana* exposed to lead and drought. *Tree Physiol* 33:1043-1060.

Hardy IC (2002) Sex ratios: Concepts and research methods. *Am J Hum Genet* 15:229-237.

Harris MS, Pannell JR (2008) Roots, shoots and reproduction: sexual dimorphism in size and costs of reproductive allocation in an annual herb. *P Roy Soc B-Biol Sci* 275:2595-2602.

Haukioja E, Ruohomäki K, Suomela J, et al. (1991) Nutritional quality as a defense against herbivores. *For Ecol Manage* 39:237-245.

Hawkins TS, Schiff NM, Leininger TD, et al. (2009) Growth and intraspecific competitive abilities of the dioecious *Lindera melissifolia* (Lauraceae) in varied flooding regimes. *J Torrey Bot Soc* 136:91-101.

Hemborg ÅM, Bond WJ (2007) Do browsing elephants damage female trees more? *Afr J Ecol* 45:41-48.

Herrera CM (1988) Plant size, spacing patterns, and host-plant selection in *Osyris quadripartita*, a hemiparasitic dioecious shrub. *J Ecol* 76:995-1006.

Hroneš M, Macurová SH, Hradílek Z, et al. (2019) Female-biased sex ratio despite the absence of spatial and niche segregation between sexes in alpine populations of dioecious *Salix lapponum* (Salicaceae). *Alpine Bot* 129:1-9.

Huang KC, Xu X, Li XF, et al. (2014) Gender-specific characteristics of tree-ring growth and differential responses to climate change in the dioecious tree *Populus cathayana* in Xiaowutai Mountains, China. Chinese J Plant Ecol 38:270-280.

Hultine KR, Grady KC, Wood TE, et al. (2016) Climate change perils for dioecious plant species. Nat Plants 2:1-8.

Ishida TA, Hattori K, Shibata S, et al. (2005) Sex allocation of a cosexual wind-pollinated tree, *Quercus dentata*, in terms of four currencies. J Plant Res 118:193-197.

Jaafry SW, Li D, Fan Z, et al. (2019) Effect of soil nutrients, neighbor identities and root separation types on intra- and interspecific interaction among three clonal plant species. Nord J Bot 37:e02070.

Jaenike J (2001) Sex chromosome meiotic drive. Annu Rev Ecol Evol Syst 32:25-49.

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501-528.

Jiang H, Zhang S, Lei Y, et al. (2016) Alternative growth and defensive strategies reveal potential and gender specific trade-offs in dioecious plants *Salix paraplesia* to nutrient availability. *Front Plant Sci* 7:1064.

Juvany M, Munné-Bosch S (2015) Sex-related differences in stress tolerance in dioecious plants: a critical appraisal in a physiological context. *J Exp Bot* 66:6083-6092.

Kerkhoff AJ, Enquist BJ (2006) Ecosystem allometry: the scaling of nutrient stocks and primary productivity across plant communities. *Ecol Lett* 9:419-427.

Lei Y, Jiang Y, Chen K, et al. (2017) Reproductive investments driven by sex and altitude in sympatric *Populus* and *Salix* trees. *Tree Physiol* 37:1503-1514.

Leigh A, Nicotra AB (2003) Sexual dimorphism in reproductive allocation and water use efficiency in *Maireana pyramidata* (Chenopodiaceae), a dioecious, semi-arid shrub. *Aust J Bot* 51:509-514.

Leigh D (2006) The group trainer's handbook: Designing and delivering training for groups. Kogan Page Publishers, London, UK.

Li Y, Duan B, Chen J, et al. (2016) Males exhibit competitive advantages over females of *Populus deltoides* under salinity stress. *Tree Physiol* 36:1573-1584.

Liu J, Duan J (2013) *Humulus scandens* gender differences in response to water stress in the vegetative growth stage. *Acta Prataculturae Sinica* 22:243-249.

Liu M, Bi J, Liu X, et al. (2020a) Microstructural and physiological responses to cadmium stress under different nitrogen levels in *Populus cathayana* females and males. *Tree Physiol* 40:30-45.

Liu M, Liu X, Du X, et al. (2021a) Anatomical variation of mesophyll conductance due to salt stress in *Populus cathayana* females and males growing under different inorganic nitrogen sources. *Tree Physiol.* <https://doi.org/10.1093/treephys/tpab017>.

Liu M, Liu X, Kang J, et al. (2020b) Are males and females of *Populus cathayana* differentially sensitive to Cd stress? *J Hazard Mater* 393:122411.

Liu M, Wang Y, Liu X, et al. (2021b) Intra-and intersexual interactions shape microbial community dynamics in the rhizosphere of *Populus cathayana* females and males exposed to excess Zn. *J Hazard Mater* 402:123783.

Lloyd DG, Webb CJ (1977) Secondary sex characters in plants. *Bot Rev* 43:177-216.

Maestre FT, Callaway RM, Valladares F, et al. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J Ecol* 97:199-205.

Maldonado-López Y, Cuevas-Reyes P, Sánchez-Montoya G, et al. (2014) Growth, plant quality and leaf damage patterns in a dioecious tree species: is gender important? *Arthropod-Plant Inte* 8:241-251.

Mattson WJ (1980) Herbivory in relation to plant nitrogen content. *Annu Rev Ecol Syst* 11:119-161.

McCall AC (2008) Florivory affects pollinator visitation and female fitness in *Nemophila menziesii*. *Oecologia* 155:729-737.

Meagher TR (1992) The quantitative genetics of sexual dimorphism in *Silene latifolia* (Caryophyllaceae). I. Genetic variation. *Evolution* 46:445-457.

Medina-Gavilán JL, Bartual A, Ojeda F (2008) Sex-related differences in leaf traits in an androdioecious shrub under contrasting levels of soil salinity. *Plant Soil* 310:235-243.

Mercer CA, Eppley SM (2014) Kin and sex recognition in a dioecious grass. *Plant Ecol* 215:845-852.

Mesgaran MB, Matzrafi M, Ohadi S (2019) Sex lability and dimorphism in diecious *Palmer amaranth* (*Amaranthus palmeri*). *bioRxiv* 1:769935.

Mizuki I, Ishida K, Chiwa M, et al. (2018) Nutrient deficiency promotes male-biased apparent sex ratios at the ramet level in the dioecious plant *Myrica gale* var. *tomentosa* in oligotrophic environments in bogs. *J Plant Res* 131:973-985.

Morales M, Oñate M, García MB, et al. (2013) Photo-oxidative stress markers reveal absence of physiological deterioration with ageing in *Borderea pyrenaica*, an extraordinarily long-lived herb. *J Ecol* 101:555-565.

Núñez-Farfán J, Valverde PL (2020) Introduction: Evolutionary Ecology of Plant-Herbivore Interactions. In: *Evolutionary Ecology of Plant-Herbivore Interaction*. Springer International Publishing, Cham, Switzerland, 1-11.

Obeso JR (2002) The costs of reproduction in plants. *New Phytol* 155:321-348.

Olano JM, González-Muñoz N, Arzac A, et al. (2017) Sex determines xylem anatomy in a dioecious conifer: hydraulic consequences in a drier world. *Tree Physiol* 37:1493-1502.

Oñate M, García MB, Munné-Bosch S (2012) Age and sex-related changes in cytokinins, auxins and abscisic acid in a centenarian relict herbaceous perennial. *Planta* 235:349-358.

Ortiz PL, Arista M, Talavera S (2002) Sex ratio and reproductive effort in the dioecious *Juniperus communis* subsp. *alpina* (Suter) Čelak. (Cupressaceae) along an altitudinal gradient. *Ann Bot* 89:205-211.

Pacala SW, Tilman D (1994) Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *Am Nat* 143:222-257.

Palo RT, Bergström R, Danell K (1992) Digestibility, distribution of phenols, and fiber at different twig diameters of birch in winter. Implication for browsers. *Oikos* 1:450-454.

Petry WK, Soule JD, Iler AM, et al. (2016) Sex-specific responses to climate change in plants alter population sex ratio and performance. *Science* 353:69-71.

Pickering CM, Kirkwood A, Arthur JM (2003) Habitat and sex specific differences in the dioecious weed *Acetosella vulgaris* (Polygonaceae). *Austral Ecol* 28:396-403.

Pipoly I, Bókony V, Kirkpatrick M, et al. (2015) The genetic sex-determination system predicts adult sex ratios in tetrapods. *Nature* 527:91-94.

Poorter H, Niklas KJ, Reich PB (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol* 193:30-50.

Pucholt P, Hallingbäck HR, Berlin S (2017) Allelic incompatibility can explain female biased sex ratios in dioecious plants. *BMC Genomics* 18:1-2.

Randriamanana TR, Nybakken L, Lavola A, et al. (2014) Sex-related differences in growth and carbon allocation to defence in *Populus tremula* as explained by current plant defence theories. *Tree Physiol* 34:471-487.

Renner SS (2014) The relative and absolute frequencies of angiosperm sexual systems: dioecy, monoecy, gynodioecy, and an updated online database. *Am J Bot* 101:1588-1596.

Retuerto R, Fernández-Lema B, Obeso JR (2006) Changes in photochemical efficiency in response to herbivory and experimental defoliation in the dioecious tree *Ilex aquifolium*. *Int J Plant Sci* 167:279-289.

Retuerto R, Sánchez Vilas J, Varga S (2018) Sexual dimorphism in response to stress. *Environ Exp Bot* 146:1-4.

Ribeiro-Mendes HN, Marques ES, Silva IM, et al. (2002) Influence of host-plant sex and habitat on survivorship of insect galls within the geographical range of the host-plant. *Trop Zool* 15:5-15.

Rivkin LR, Barrett SC, Johnson MT (2018) The effects of plant sexual system and latitude on resistance to herbivores. *Am J Bot* 105:977-985.

Rogers SR, Eppley SM (2012) Testing the interaction between inter-sexual competition and phosphorus availability in a dioecious grass. *Botany* 90:704-710.

Sánchez-Vilas J, Bermúdez R, Retuerto R (2012) Soil water content and patterns of allocation to below-and above-ground biomass in the sexes of the subdioecious plant *Honckenya peploides*. *Ann Bot* 110:839-848.

Sánchez-Vilas J, Pannell JR (2010) Differential niche modification by males and females of a dioecious herb: extending the Jack Sprat effect. *J Evolution Biol* 23:2262-2266.

Schenk HJ (2006) Root competition: beyond resource depletion. *J Ecol* 94:725-739.

Simancas B, Cotado A, Müller M, et al. (2018) Phosphate starvation during the transition phase increases the sex ratio and 12-oxo-phytodienoic acid contents in females of *Urtica dioica*. *Environ Exp Bot* 145:39-46.

Sinclair JP, Emlen J, Freeman DC (2012) Biased sex ratios in plants: theory and trends. *Bot Rev* 78:63-86.

Slatkin M, Anderson DJ (1984) A model of competition for space. *Ecology* 65:1840-1845.

Soldaat LL, Lorenz H, Trefflich A (2000) The effect of drought stress on the sex ratio variation of *Silene otites*. *Folia Geobot* 35:203-210.

Song H, Lei Y, Zhang S (2018) Differences in resistance to nitrogen and phosphorus deficiencies explain male-biased populations of poplar in nutrient-deficient habitats. *J Proteomics* 178:123-127.

Stark L, McLetchie N, Mishler B (2001) Sex expression and sex dimorphism in sporophytic populations of the desert moss *Syntrichia caninervis*. *Plant Ecol* 157:183-196.

Stehlik I, Barrett SCH (2005) Mechanisms governing sex-ratio variation in dioecious *Rumex nivalis*. *Evolution* 59:814-825.

Stehlik I, Barrett SCH (2006) Pollination intensity influences sex ratios in dioecious *Rumex nivalis*, a wind-pollinated plant. *Evolution* 60:1207-1214.

Stehlik I, Friedman J, Barrett SC (2008) Environmental influence on primary sex ratio in a dioecious plant. *P Natl Acad Sci USA* 105:10847-10852.

Stenberg JA, Heil M, Åhman I, et al. (2015) Optimizing crops for biocontrol of pests and disease. *Trends Plant Sci* 20:698-712.

Taylor DR (1994) The genetic basis of sex ratio in *Silene alba* (*S. latifolia*). *Genetics* 136:641-651.

Taylor DR (1999) Genetics of sex ratio variation among natural populations of a dioecious plant. *Evolution* 53:55-62.

Thornley JH (1972) A model to describe the partitioning of photosynthate during vegetative plant growth. *Ann Bot* 36:419-430.

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA

Tognetti R (2012) Adaptation to climate change of dioecious plants: does gender balance matter? *Tree Physiol* 32:1321-1324.

Tonnabel J, David P, Pannell JR (2017) Sex-specific strategies of resource allocation in response to competition for light in a dioecious plant. *Oecologia* 185:675-686.

Tsuji K, Sota T (2010) Sexual differences in flower defense and correlated male-biased florivory in a plant-florivore system. *Oikos* 119:1848-1853.

Varga S, Kytöviita MM (2011) Sex ratio and spatial distribution of male and female *Antennaria dioica* (Asteraceae) plants. *Acta Oecol* 37:433-440.

Varga S, Soulsbury CD (2020) Environmental stressors affect sex ratios in sexually dimorphic plant sexual systems. *Plant Biol* 22:890-898.

Vasiliauskas SA, Aarssen LW (1992) Sex ratio and neighbor effects in monospecific stands of *Juniperus virginiana*. *Ecology* 73:622-632.

Vyskot B, Hobza R (2004) Gender in plants: sex chromosomes are emerging from the fog. Trends Genet 20:432-438.

Wade MJ, Shuster SM, Demuth JP (2003) Sexual selection favors female-biased sex ratios: the balance between the opposing forces of sex-ratio selection and sexual selection. Am Nat 162:403-414.

Ward JK, Dawson TE, Ehleringer JR (2002) Responses of *Acer negundo* genders to inter-annual differences in water availability determined from carbon isotope ratios of tree ring cellulose. Tree Physiol 22:339-346.

Wheelwright NT, Logan BA (2004) Previous-year reproduction reduces photosynthetic capacity and slows lifetime growth in females of a neotropical tree. P Natl Acad Sci USA 101:8051-8055.

Wu X, Liu J, Meng Q, et al. (2021) Differences in carbon and nitrogen metabolism between male and female *Populus cathayana* in response to deficient nitrogen. Tree Physiol 41:119-133.

Xia Z, He Y, Yu L, et al. (2020) Sex-specific strategies of phosphorus (P) acquisition in *Populus cathayana* as affected by soil P availability and distribution. New Phytol 225:782-792.

Xu X, Yang FA, Xiao X, et al. (2008) Sex-specific responses of *Populus cathayana* to drought and elevated temperatures. *Plant Cell Environ* 31:850-860.

Yang G, Xu Q, Li W, et al. (2020) Sex-related differences in growth, herbivory, and defense of two *Salix* species. *Forests* 11:450.

Yang Y, Jiang H, Wang M, et al. (2015) Male poplars have a stronger ability to balance growth and carbohydrate accumulation than do females in response to a short-term potassium deficiency. *Physiol Plant* 155:400-413.

Yu L, Dong H, Li Z, et al. (2020) Species-specific responses to drought, salinity and their interactions in *Populus euphratica* and *P. pruinosa* seedlings. *J Plant Ecol* 13:563-573.

Yule KJ, Burns KC (2019) Parasite-offspring competition for female resources can explain male-biased parasitism in plants. *Biol Lett* 15:20180761.

Zhang C, Zhao X, Gao L, et al. (2009) Gender, neighboring competition and habitat effects on the stem growth in dioecious *Fraxinus mandshurica* trees in a northern temperate forest. *Ann Forest Sci* 66:812.

Zhang S, Jiang H, Zhao H, et al. (2014) Sexually different physiological responses of *Populus cathayana* to nitrogen and phosphorus deficiencies. *Tree Physiol* 34:343-354.

Zhang S, Tang D, Korpelainen H, et al. (2019) Metabolic and physiological analyses reveal that *Populus cathayana* males adopt an energy-saving strategy to cope with phosphorus deficiency. *Tree Physiol* 39:1630-1645.

Zhao H, Li Y, Zhang X, et al. (2012) Sex-related and stage-dependent source-to-sink transition in *Populus cathayana* grown at elevated CO₂ and elevated temperature. *Tree Physiol* 32:1325-1338.

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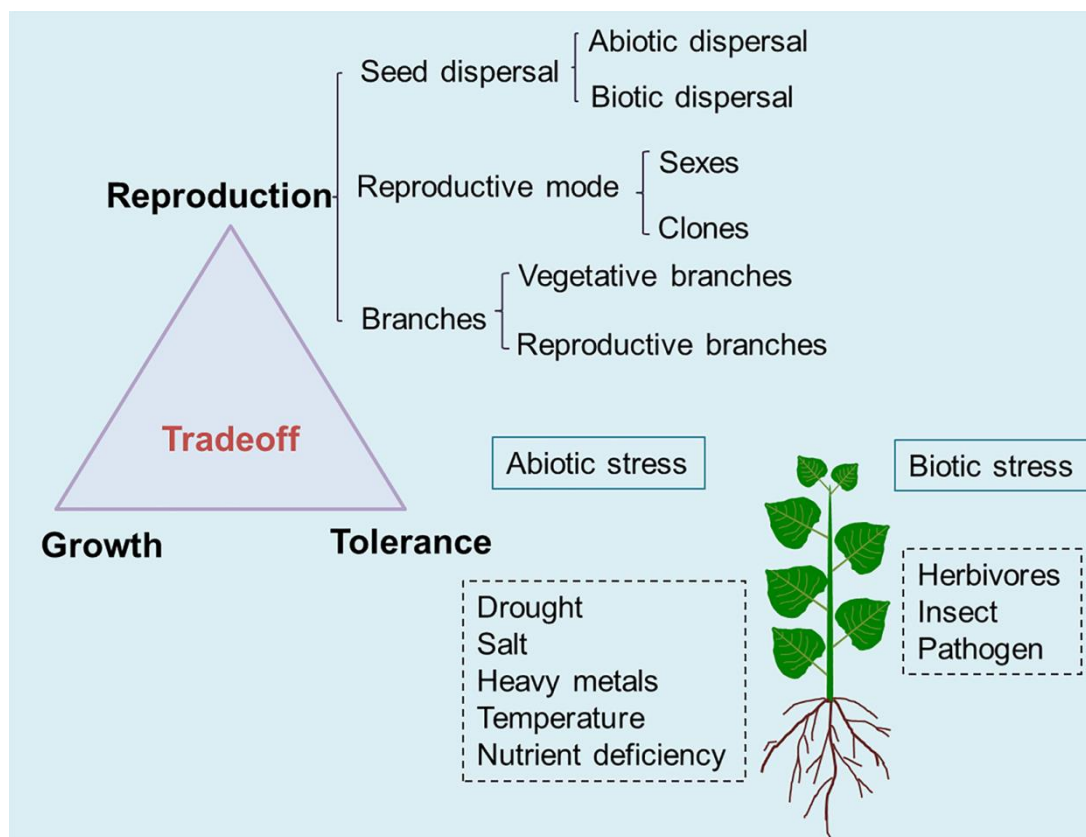


Figure 1 Determining factors of secondary sexual dimorphism in dioecious plants (adapted from Juvany and Munné-Bosch (2015)). Secondary sexual dimorphism can be modified by tradeoffs among vegetative growth, reproduction and stress tolerance. Sexual differences in reproductive costs determine reproductive fitness, growth and defense. Reproductive costs are affected by the type of seed dispersal, reproduction and branches.

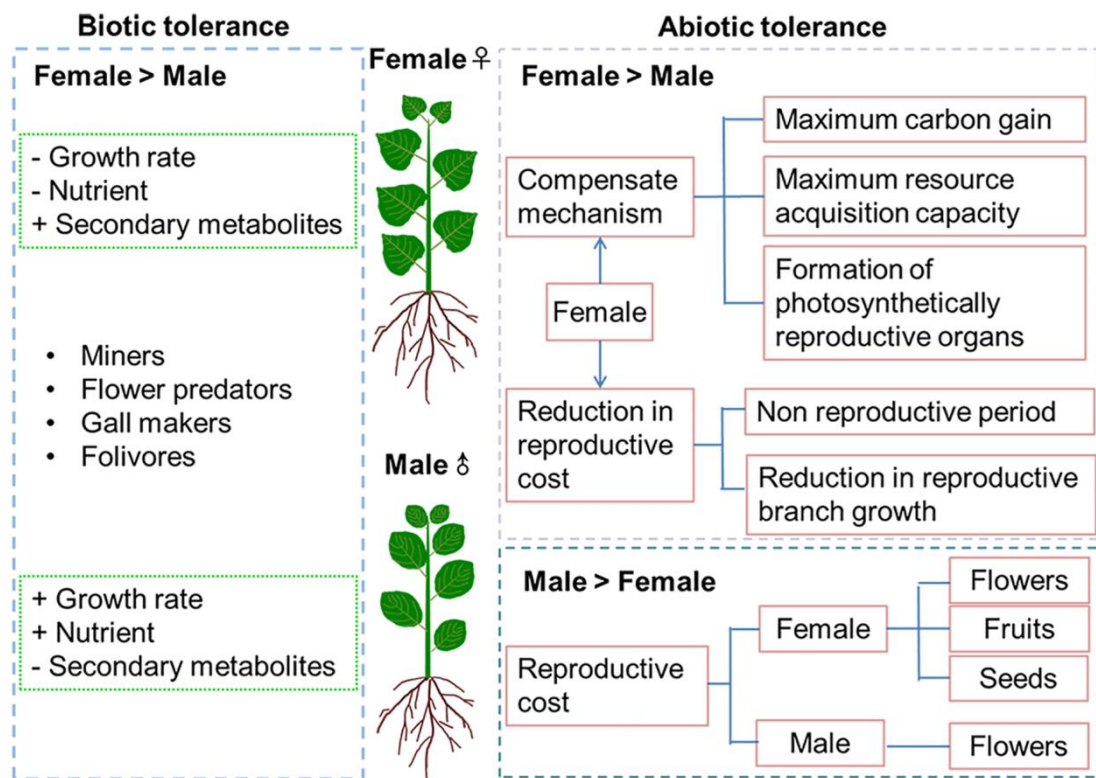


Figure 2 Sexually different tolerances to abiotic stress and biotic stress. Sexual difference in response to biotic stress was adapted from Núñez-Farfán and Valverde (2020). Female > male means that the stress tolerance (abiotic stress and biotic stress) is usually higher in females than in males. A higher biotic stress tolerance in females is often associated with lower rate of growth, lower content of nutrients and higher secondary metabolites. A lower abiotic stress tolerance in females is often associated with higher reproductive costs for producing flowers, fruits and seeds. Male > female means that the stress tolerance (abiotic stress) is usually higher in males than in females. A higher tolerance to abiotic stress in females is usually associated with reduced reproductive costs and compensation mechanisms.

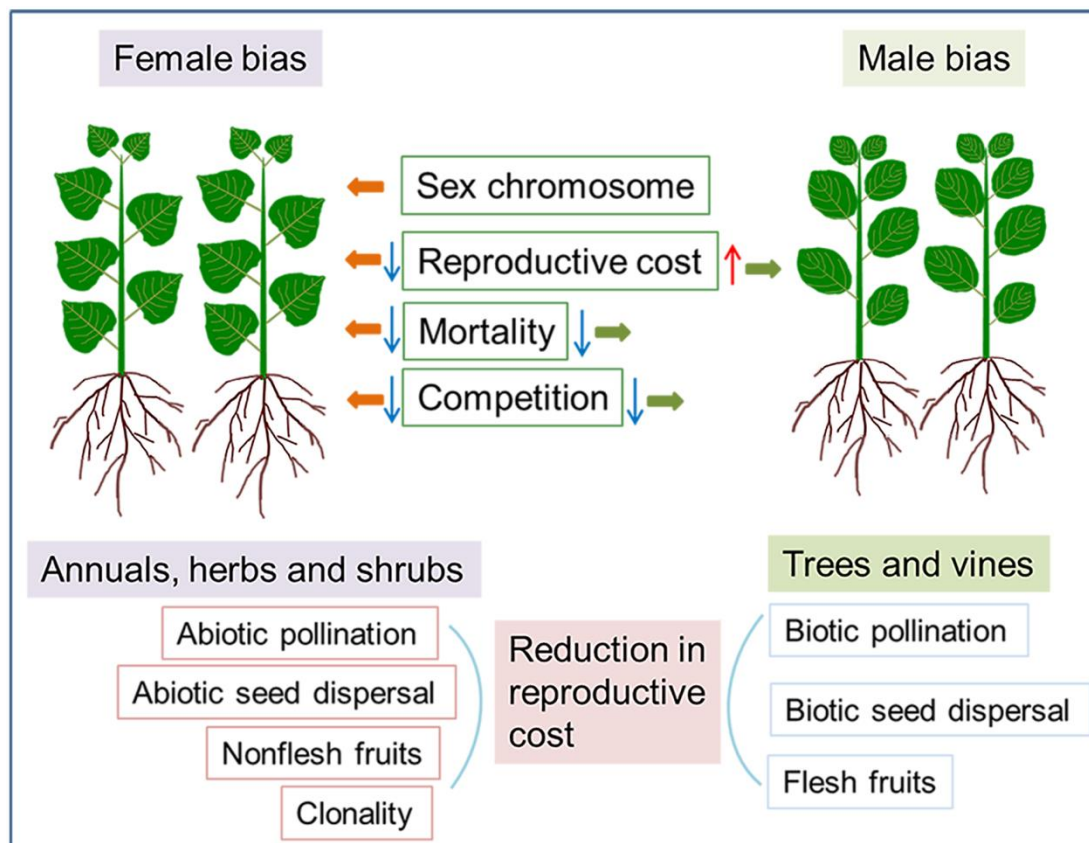


Figure 3 Factors causing biased sex ratios in plants. Biased sex ratios are usually determined by sex chromosomes, reproductive costs, mortality and sexual competition. Female-biased sex ratios are common in annuals, herbs and shrubs, being associated with sex chromosomes, reduced reproductive costs (such as abiotic pollination, abiotic seed dispersal and nonfleshy fruits), clonality, and low mortality and competition. Male-biased sex ratios are common in trees and vines, being associated with lower mortality and sexual competition.