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## Commentary

## Response to Midgley: the costs of reproduction cannot differ between the sexes

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Many studies have compared the reproductive cost and vegetative growth at a particular time point. In our review (Liu *et al.* 2021b), we summarized those results but did not compare absolute reproductive costs between the sexes (Hultine *et al.* 2016; Juvany and Munné-Bosch 2016). Moreover, we did not propose that the observed vegetative and environmental differences between the sexes were the only reasons for differences in sexual functioning, especially in the spreading and receiving of pollen (Midgley 2022). Yet, we need further evidence to support the argument. Previous studies have shown that differences in primary and physiological traits between the sexes strongly depend on the plant species and their environmental conditions, and that they may arise from a number of reasons, such as differences in trait optima of each sex along a series of resource gradients, sexual selection and sex-specific responses to sexual selection (Barrett and Josh 2013; Geber *et al.* 1999; Juvany and Munné-Bosch 2016; Kohorn *et al.* 1994; Rabska *et al.* 2021; Retuerto *et al.* 2018; Scopece *et al.* 2021; Wang *et al.* 2021).

In the comment, Midgley (2022) stated that our general argument is that 'the net reproductive costs are higher for females because they not only flower but must also produce fruits/cones/seeds (Figure 3). Midgley (2022) suggests (Figure 2) that females can ameliorate their higher costs of reproduction by maximizing resource acquisition and resource gain'. However, in our review, we summarized the general opinion and pointed out that this pattern

was not universal (see more detail in Liu *et al.* 2021b). In consistent with previous reviews, our review argues that there is no widespread rule in sex-related differences in the cost of reproduction despite the general opinion that females have higher reproductive costs than males (Darwin 1877; Liu *et al.* 2021b; Lloyd and Webb 1977). We summarized possible factors causing biased sex ratios in plants, rather than only underpinning the higher net reproductive costs in females than in males (Liu *et al.* 2021b). Similarly, we proposed possible mechanisms causing sexual differences in responses to biotic stress, rather than underpinning the higher net reproductive costs in females than in males (Liu *et al.* 2021b), which is also adapted from Núñez-Farfán and Valverde (2020).

Despite the widespread view that reproductive costs of plants are higher in females than in males, different results have also been reported in the literature (Delph and Bell 2008; Leigh 2006). In our review, we discussed the relative reproductive costs of the sexes in a specific plant species and condition, but did not compare the absolute reproductive cost of males and females throughout their life history (Liu *et al.* 2021b). Moreover, we explained that there was no uniform view of the reproductive costs of females and males (Liu *et al.* 2021b). This is different from the statement that the reproductive cost must be the same in the two sexes (Midgley 2022).

It has been proposed that the estimate of reproductive costs in males and females may differ in

their temporal allocation patterns, such that females may possess great compensation mechanisms in the production of fruits (Sánchez-Vilas 2011; Zunzunegui *et al.* 2006). For example, males may have higher reproductive costs than females during flowering due to the large cost of pollen and flowers, but the reproductive cost of females may be higher than that of males due to the great investment in the production of fruits (Sánchez-Vilas and Retuerto 2011; Zunzunegui *et al.* 2006). Additionally, females have been suggested to have larger roots in absolute terms, while males allocate more biomass towards roots at later stages of plant growth (Oñate *et al.* 2012). These studies emphasized the important roles of the absolute and relative sink and source in reproductive costs, and the timing of resource deployment in sexual dimorphism in the annual plant *Mercurialis annua* (Vilas 2011). Overall, it is important to generate large-scale data about the reproductive investment in females and males, including the roles of multiple interacting factors, taking into account sexual differences in the intensity, frequency and developmental stage of reproductive events (Juvany and Munné-Bosch 2016; Retuerto *et al.* 2018).

In addition, Midgley (2022) states that ‘the costs of reproduction may differ between the sexes is controversial because it is difficult to measure, and it is also contrary to theory’. Is it this why the author suggested that there was no difference in reproductive costs between females and males? The author cited references from Leigh and Nicotra (2003), and argued that ‘It is highly unlikely that such large direct allocation differences will have no indirect impacts such as on growth, mortality, or have no eco-physiological consequences’. Doust (1989) has proposed that, based on the resource allocation theory, reproduction can directly compete with defense responses and vegetative growth when the resources are limited, which implies that resource allocation is associated with plant species and nutrient traits (Juvany and Munné-Bosch 2016; Liu *et al.* 2021a, 2021b).

Several studies have indicated that sex-specific functional traits would be strongly affected by environmental factors (Guo *et al.* 2022; Liu *et al.* 2021c, 2022a, 2022b; Yu *et al.* 2020, 2022; Zhang *et al.* 2021). As discussed above, the observed annual growth rates are indeed equivalent in both sexes, which implies a potential compensation mechanism (Case and Ashman 2005). Therefore, it is possible that there are no indirect impacts on traits, such as growth and mortality, between females and males

when the spatial and temporal allocation dynamics, resource availability and diversity of species are taken into account over the whole growing season and even over the whole life-cycle of perennial plant species (Retuerto *et al.* 2018).

As discussed above, there may be a tradeoff between production, growth and defense in dioecious plant species (Doust 1989; Juvany and Munné-Bosch 2016). The allocation of resources in plants is considered to be affected by many factors, such as plant genotypes and environmental factors (Ackerly 1997; Bazzaz 1997; Liu *et al.* 2020b; Schultz *et al.* 2013). The higher resources of males do not represent most of the resources needed to be used for defending as proposed by Midgley (2022). If males have extra resources, why would they need extra resources to defend better? In consistent with previous reviews, there has been no generalization for sexually biased herbivores, which are associated with morphological and physiological traits, reproductive periods, food selection by the herbivores, which need to be clarified in future studies (Barriónuevo *et al.* 2021; Liu *et al.* 2021b; Pereira *et al.* 2020). In our review, we only summarized recent views about sex-specific herbivores and attempted to provide possible explanations according to existing studies (Liu *et al.* 2021b). Biased sex ratios have been reported to be associated with reproductive costs, mortality, sex choice and sex-specific responses to different environmental conditions (Field *et al.* 2013; Harris and Pannell 2008; Stehlik and Barrett 2005). Thus, sex ratios in plant populations may reflect species coexistence and resource unitization (Queenborough *et al.* 2007). At the same time, sex ratios may be biased due to potentially reproductive individuals, which may not be completely censused over several flowering seasons (Queenborough *et al.* 2007). We do not fully agree with the author’s statement ‘I suggest that the lack of studies is because populations appear to be 1:1 in size and number and are thus considered relatively uninteresting’ by Midgley (2022).

It has been reported that females and males usually exhibit sex-specific responses to abiotic and biotic stresses (Liu *et al.* 2020a, 2020b, 2021b, 2021d; Retuerto *et al.* 2018; Zhang *et al.* 2021). Of course, under certain conditions, there are no sexual differences in certain traits between females and males (Chen *et al.* 2014; de la Bandera *et al.* 2008; Varga and Kytöviita 2012). In our previous paper, we summarized that sex-specific differences were greater in response to drought stress, and that the sexes showed slight or little difference under optimal water supply (Chen *et*

al. 2014; Olano *et al.* 2017). In the study by Olano *et al.* (2017), the authors selected populations occurring in two contrasting sites, which represented the extremes of the climatic range on the Iberian Peninsula. Therefore, we cannot conclude that there are no field data to verify any net differences in moisture stress, as stated in the comment by Midgley (2022). Moreover, sexually different responses may exist at a particular point of time, but we did not emphasize the existence of absolutely unequal net allocation differences in reproduction (Liu *et al.* 2021b).

Differences in hydraulic efficiency between plants are largely dependent on the plant species, stress degree and plant growth and development periods (Barbara and Stefan 2009; Gao *et al.* 2021; Liu *et al.* 2022b). We did not make the absolute statement about the differences in hydraulic efficiency between females and males in our review (Liu *et al.* 2021b). In the commentary paper by Midgley (2022), the author argued ‘Also, because the genetic benefits of sexual reproduction are equal, the “costs” or allocation must be equal (or else one sex is cheating)’. We would suggest the author to give some evidence to support his argument. Moreover, we did not use net allocation differences to explain the interesting differences between the sexes. Instead, we reviewed previous studies for possible mechanisms behind sexual differences between the sexes (Liu *et al.* 2021b).

We noticed that the author acknowledged the difficulty to compare male and female allocation to reproduction (Midgley 2022). However, this does not exclusively mean that the costs of reproduction differ between the sexes. Moreover, we did not suggest that it was meaningless to compare male and female allocation to reproduction (Liu *et al.* 2021b). Estimates of the sex ratio and cost of reproduction in plant populations have important implications for resource use by animals, reserve design and mechanisms of species coexistence, as well as implications for potential cascading consequences of skewed sex ratios on the structure and stability of ecosystem communities (Hultine *et al.* 2016; Queenborough *et al.* 2007). However, these issues have been rarely investigated. In conclusion, consistent with our and other previous reviews, the results of the presence or lack of differences in reproductive costs between females and males are not uniform, and they are dependent on plant species, and spatial and temporal allocation patterns. Finally, we did not argue that it is meaningless to study relative reproductive costs between the sexes in plant species (Hultine *et al.* 2016; Juvany and Munné-Bosch 2016; Liu *et al.* 2021b).

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## REFERENCES

- Ackerly DD (1997) Allocation, leaf display, and growth in fluctuating light environments. In Bazzaz FA, Grace J (eds). *Plant Resource Allocation*. New York: Academic Press, 231–264.
- Barbara B, Stefan M (2009) Intraspecific differences in drought tolerance and acclimation in hydraulics of *Ligustrum vulgare* and *Viburnum lantana*. *Tree Physiol* **29**:765–776.
- Barrett SCH, Josh H (2013) Sexual dimorphism in flowering plants. *J Exp Bot* **64**:67–82.
- Barrionuevo CN, Benitez-Vieyra S, Sazatornil F (2021) Floral biology of *Salvia stachydidifolia*, a species visited by bees and birds: connecting sexual phases, nectar dynamics and breeding system to visitors’ behaviour. *J Plant Ecol* **14**:580–590.
- Bazzaz FA (1997) Allocation of resources in plants: state of the science and critical questions. In Bazzaz FA, Grace J (eds). *Plant Resource Allocation*. New York, NY: Academic Press, 1–37.
- Case AL, Ashman TL (2005) Sex-specific physiology and its implications for the cost of reproduction. In Reekie EG, Bazzaz FA (eds). *Reproductive Allocation in Plants*. Amsterdam: Elsevier Inc, 129–157.
- 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.
- Darwin C (1877) *The Different Forms of Flowers on Plants of the Same Species*. London, UK: John Murray.
- de la Bandera MC, Traveset A, Valladares F, *et al.* (2008) Gender, season and habitat: patterns of variation in photosynthetic activity, growth and fecundity in *Thymelaea velutina*. *Acta Oecol* **34**:294–302.
- 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.
- Doust JL (1989) Plant reproductive strategies and resource allocation. *Tree* **4**:230–233.
- Field DL, Pickup M, Barrett SC (2013) Comparative analyses of sex-ratio variation in dioecious flowering plants. *Evolution* **67**:661–672.
- Gao S, Cai ZY, Yang CC, *et al.* (2021) Provenance-specific ecophysiological responses to drought in *Cunninghamia lanceolata*. *J Plant Ecol* **14**:1060–1072.
- Geber M, Dawson T, Delph L (1999) *Sexual and Gender Dimorphism in Flowering Plants*. Heidelberg: Springer, 1–31.
- Guo Q, Liu L, Liu J, *et al.* (2022) Plant sex affects plant-microbiome assemblies of dioecious *Populus cathayana* trees under different soil nitrogen conditions. *Microbiome* **10**:191.
- Harris MS, Pannell JR (2008) Roots, shoots and reproduction: sexual dimorphism in size and costs of reproductive allocation in an annual herb. *Proc R Soc Lond B* **275**:2595–2602.



- Hultine KR, Grady KC, Wood TE, *et al.* (2016) Climate change perils for dioecious plant species. *Nat Plants* **2**:1–8.
- Juvany M, Munné-Bosch S (2016) Sex-related differences in stress tolerance in dioecious plants: a critical appraisal in a physiological context. *J Exp Bot* **66**:6083–6092.
- Kohorn LU, Goldstein G, Rundel PW (1994) Morphological and isotopic indicators of growth environment: variability in  $\delta^{13}\text{C}$  in *Simmondsia chinensis*, a dioecious desert shrub. *J Exp Bot* **45**:1817–1822.
- Leigh D (2006) *The Group Trainer's Handbook: Designing and Delivering Training for Groups*. London, UK: Kogan Page Publishers.
- 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.
- Liu Y, Bachofen C, Lou Y, *et al.* (2021a) The effect of temperature changes and K supply on the reproduction and growth of *Bolboschoenus planiculmis*. *J Plant Ecol* **14**:337–347.
- Liu M, Bi JW, Liu XC, *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, Korpelainen H, Li CY (2021b) Sexual differences and sex ratios of dioecious plants under stressful environments. *J Plant Ecol* **14**:920–933.
- Liu M, Liu XC, Du XH, *et al.* (2021c) Anatomical variation of mesophyll conductance due to salt stress in *Populus cathayana* females and males growing under different inorganic nitrogen sources. *Tree Physiol* **41**:1462–1478.
- Liu M, Liu XC, Zhao Y, *et al.* (2022a) Sex-specific nitrogen allocation tradeoffs in the leaves of *Populus cathayana* cuttings under salt and drought stress. *Plant Physiol Biochem* **172**:101–110.
- Liu W, Sun S, Zhang C, *et al.* (2020b) Linking plant spatial aggregation with reproductive traits and near-source seed dispersal: ecological adaptation to heavy grazing. *J Plant Ecol* **13**:489–498.
- Liu X, Wang Y, Liu S, *et al.* (2021d) Sex-specifically responsive strategies to phosphorus availability combined with different soil nitrogen forms in dioecious *Populus cathayana*. *J Plant Ecol* **14**:730–748.
- Liu M, Zhao Y, Wang Y, *et al.* (2022b) Stem xylem traits and wood formation affect sex-specific responses to drought and re-watering in *Populus cathayana*. *Tree Physiol* **42**:1350–1363.
- Lloyd D, Webb C (1977) Secondary sex characters in plants. *Bot Rev* **43**:177–215.
- Midgley JJ (2022) The costs of reproduction cannot differ between the sexes. *J Plant Ecol* **15**:1308–1311.
- Núñez-Farfán J, Valverde PL (2020) Introduction: evolutionary ecology of plant-herbivore interactions. In Núñez-Farfán J, Valverde P (eds). *Evolutionary Ecology of Plant-Herbivore Interaction*. Cham, Switzerland: Springer International Publishing, 1–11.
- 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.
- Pereira CC, Boaventura MG, de Castro GC, *et al.* (2020) Are extrafloral nectaries efficient against herbivores? Herbivory and plant defenses in contrasting tropical species. *J Plant Ecol* **13**:423–430.
- Queenborough SA, Burslem DFRP, Garwood NC, *et al.* (2007) Determinants of biased sex ratios and inter-sex costs of reproduction in dioecious tropical forest trees. *Am J Bot* **94**:67–78.
- Rabska M, Warwick NWM, Iszkulo G, *et al.* (2021) Intersexual differences in leaf size and shape in dioecious *Adriana tomentosa*. *J Plant Ecol* **14**:67–83.
- Retuerto R, Sánchez Vilas J, Varga S (2018) Sexual dimorphism in response to stress. *Environ Exp Bot* **146**:1–4.
- Sánchez-Vilas J, Retuerto R (2011) Reproduction reduces photosynthetic capacity in females of the subdioecious *Honckenia peploides*. *Acta Oecol* **37**:155–163.
- Schultz JC, Appel HM, Ferrieri AP, *et al.* (2013) Flexible resource allocation during plant defense responses. *Front Plant Sci* **4**:324.
- Scopece G, Criscuolo N, Cozzolino S (2021) In nomen omen: the effect of flower distance on female reproductive success of the lax-flowered orchid *Anacamptis laxiflora* (Orchidaceae). *J Plant Ecol* **14**:451–464.
- Stehlik I, Barrett SCH (2005) Mechanisms governing sex-ratio variation in dioecious *Rumex nivalis*. *Evolution* **59**:814–825.
- Varga S, Kytöviita MM (2012) Differential competitive ability between sexes in the dioecious *Antennaria dioica* (Asteraceae). *Ann Bot* **110**:1461–1470.
- Vilas JS (2011) Sexual dimorphism in resource acquisition and deployment: both size and timing matter. *Ann Bot* **107**:119–126.
- Wang LL, Yang NC, Chen MY, *et al.* (2021) Polyploidization and sexual dimorphism of floral traits in a subdioecious population of *Dasiphora glabra*. *J Plant Ecol* **14**:229–240.
- 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.
- Yu L, Huang Z, Li Z, *et al.* (2022) Sex-specific strategies of nutrient resorption associated with leaf economics in *Populus euphratica*. *J Ecol* **110**:2062–2073.
- Zhang C, Zhu J, Liu G, *et al.* (2021) The sexual dimorphism displayed by the roots of mulberry (*Morus alba*) saplings depends on the sex of the neighboring plants. *J Plant Ecol* **14**:1037–1046.
- Zunzunegui M, Barradas M, Clavijo A, *et al.* (2006) Ecophysiology, growth timing and reproductive effort of three sexual forms of *Corema album* (Empetraceae). *Plant Ecol* **183**:35–46.