



Sex-Specific Response to Stress in *Populus*

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Populus is an effective model for genetic studies in trees. The genus *Populus* includes dioecious species, and the differences exhibited in males and females have been intensively studied. This review focused on the distinctions between male and female poplar and aspen plants under stress conditions, such as drought, salinity, heavy metals, and nutrient deficiency on morphological, physiological, proteome, and gene expression levels. In most studies, males of *Populus* species were more adaptive to the majority of the stress conditions and showed less damage, better growth, and higher photosynthetic capacity and antioxidant activity than that of the females. However, in two recent studies, no differences in non-reproductive traits were revealed for male and female trees. This discrepancy of the results could be associated with experimental design: different species and genotypes, stress conditions, types of plant materials, sampling sizes. Knowledge of sex-specific differences is crucial for basic and applied research in *Populus* species.

Keywords: *Populus*, poplar, sex, dioecious species, stress, environment, drought, salinity

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INTRODUCTION

The genus *Populus* includes 29 species as per Eckenwalder's classification (Eckenwalder, 1996). Most *Populus* species are fast-growing trees, which are distributed in the Northern Hemisphere. *Populus* is one of the best-studied genera among woody plants. The genome of *P. trichocarpa* was the first tree species to be sequenced (Tuskan et al., 2006). *Populus* has become a 'model' for tree genetic studies because of its small genome size, possibility of genetic transformation, easy vegetative cloning, rapid growth, short pre-reproductive period, and potential for commercial use (Ellis et al., 2010). To date, immense and complicated data on the genetic and epigenetic characteristics of *Populus* are available in the literature, databases, and public resources, such as the plant comparative genomics portals Phytozome¹ and PopGenIE². *Populus* includes dioecious species (poplars, cottonwoods, and aspens), which have male and female reproductive organs on separate individuals. Recent studies have identified a small (about 100 kb) sex-associated genome region in *P. trichocarpa* and *P. balsamifera* (Geraldes et al., 2015). Differences between male and female individuals of *Populus* could not be restricted only to reproduction but also to their sex-specific response to different environments. For their perennial life cycle, *Populus* trees are exposed to a diversity of unfavorable conditions. Stresses, such as drought, salinity, and low temperatures,

¹<https://phytozome.jgi.doe.gov/pz/portal.html>

²<http://popgenie.org/>

dramatically affect growth, development, and productivity of trees and play an important role in the geographic distribution of species, including *Populus* spp. (Harfouche et al., 2014). In the present work, we summarized recent studies related to differences between male and female individuals of *Populus* species regarding their response to different stress conditions, including drought, salinity, heavy metals, nutrient deficiency, and elevated CO₂ concentration.

DROUGHT

Drought is among the most harmful abiotic stresses that limits plant survival and growth. Differences in the response of male and female *Populus* plants to water deficiency has been examined. Leaf area, total number of leaves, photosynthetic and transpiration rates, and efficiency of photosystem II decreased, whereas total chlorophyll concentration, carbon isotope composition, abscisic acid (ABA) and malondialdehyde contents, and peroxidase activity increased with drought both in male and female plants of *P. cathayana* in chamber and greenhouse conditions. However, female plants were more sensitive to drought environments and exhibited a more pronounced decrease in growth and photosynthetic capacity than that of male plants (Xu et al., 2008a,b). It was suggested that the differences in the response of male and female *P. cathayana* plants to drought were associated with sex-dependent protein expression related to photosynthesis, homeostasis, and stress response (Zhang et al., 2010a). Roots of *P. cathayana* male plants were less sensitive to water deficiency than those of female plants under drought stress. However, the shoots of female plants grew faster than those of male plants under well-watered conditions. Grafting of female shoots onto male roots improved the resistance of plants to drought (Han et al., 2013b). Both the sexes of *P. cathayana* demonstrated a reduction in growth and physiological functions under drought conditions; however, after inoculation with an arbuscular mycorrhizal fungus (AMF), *Rhizophagus intraradices*, male plants showed higher drought protection than female plants (Li et al., 2015a,b). In another *Populus* species, *P. yunnanensis*, female plants experienced more pronounced growth inhibition, reactive oxygen species (ROS) accumulation, and decline in the accumulation of dry matter and total chlorophyll content under water deficiency than that of male plants (Chen L. et al., 2010). The molecular basis of sex-related differences in the response of *P. yunnanensis* to drought stress was determined. Under this stress, alterations in the gene expression levels involved in photosynthesis (photosynthetic electron transport, photosystem I and II, and antenna protein biosynthesis), hormone biosynthesis (ABA biosynthesis), and ROS elimination (genes encoding ascorbate peroxidase, dehydroascorbate reductase and catalase) were more pronounced in males than females (Peng et al., 2012). Thus, it was demonstrated that compared to female plants, male plants of *Populus* species adapt to water deficiency more efficiently, and drought stress inhibits growth, photosynthesis, and ROS protection more strongly in females than in males.

SALINITY

Salinity is a major abiotic stress that suppresses plant growth and development. Cuttings of male *P. cathayana* plants were observed to be less sensitive to salinity than those of females, in which the negative effects on growth and photosynthesis were more pronounced. The Na⁺ and Cl⁻ concentrations in female plants were higher in leaves and stems, but lower in roots than those in the respective organs in males. It was speculated that males have a better capacity to restrict Na⁺ transport from roots to shoots (Chen F. et al., 2010). The effect on female cuttings was more negative than that on the male cuttings and resulted in reduced growth and photosynthetic rates as well as greater Na⁺ accumulation. In males, lower degradation and higher abundance of proteins involved in photosynthesis, hydrogen peroxide scavenging, and stress response was observed (Chen et al., 2011). The growth rate of *P. deltoides* females was higher than that of males in the absence of salinity under intersexual competition. However, under salinity stress, males showed a higher capacity for osmotic adjustment and antioxidant activity than that of females (Li et al., 2016). Higher sensitivity to salinity and a combination of drought and salinity was also observed in *P. yunnanensis* females than in males. The female plants showed a more pronounced reduction in growth rate, higher ROS accumulation, and greater cell organelle damage than that of males (Chen L. et al., 2010). The *P. yunnanensis* female plants were found to be less tolerant to salinity than the males; the female plants exhibited less growth and lower photosynthetic rates than the male plants. Moreover, elevated CO₂ levels enhanced the negative effects of salinity in females (Li et al., 2013). Transcription profiling revealed that mainly the genes involved in photosynthesis (photosystem II and antenna system) were upregulated in males, but downregulated in *P. yunnanensis* females, under salt stress (Jiang et al., 2012). Additionally, the role of AMF in the sex-associated response of *Populus* to salt stress was investigated. *P. cathayana* plants had increased antioxidant activity and decreased growth and efficiency of photosystem II under salt stress. However, AMF alleviated the negative effects of salt on these plants. Males inoculated with AMF showed improved growth and development parameters, physiological functions, and antioxidant activities under salt stress than that of females (Wu et al., 2016). Thus, salinity has a similar effect on *Populus* to drought, with males being more adaptive to salt stress than females, with a higher growth rate, photosynthetic capacity, and antioxidant activity.

METAL-ASSOCIATED STRESSES

Although appropriate concentrations of some metals are essential for plants, high concentrations of heavy metals inhibit their growth and development. The effects of lead (Pb) on *P. cathayana* plants were studied. Pb treatment negatively affected both sexes; however, males showed higher plasticity in their photosynthetic activity than females. Moreover, drought increased the sensitivity to Pb, especially in females (Han et al., 2013a). It was shown that AMF increased the Pb uptake and accumulation in the

roots of female *P. cathayana* plants, but not male plants (Chen L. et al., 2015). *P. deltoides* females were found to be more susceptible to cadmium (Cd) stress than males, and showed leaf symptoms, lipid peroxidation, and altered cellular ultrastructures. Inoculation with *R. intraradices* decreased the toxic effect of Cd in females via an increase in antioxidant activity and limiting Cd transfer to shoots. However, such effects were not detected in males inoculated with AMF (Chen L. et al., 2016). Different responses of *P. cathayana* males and females in single-sex cultivation or sexual competition under Cd stress were also demonstrated. Females exposed to Cd stress had more serious damage and higher Cd accumulation under intrasexual than intersexual competition. On the contrary, males were less affected under intrasexual competition (Chen J. et al., 2016). *P. cathayana* males showed higher antioxidant activity and chlorophyll contents and were more resistant to aluminum (Al) stress than females (Li et al., 2012). *P. cathayana* males were also more tolerant to copper (Cu) stress because they accumulated higher amounts of Cu in leaves than females (Chen et al., 2013). *P. yunnanensis* female plants had higher ROS levels and less effective protection against high zinc (Zn) concentrations than males (Jiang et al., 2013). *P. cathayana* females were more sensitive to iron (Fe) deficiency and had higher growth inhibition and more serious damage of photosynthesis system II than males (Zhang et al., 2016a). Thus, *Populus* female plants were more sensitive to all the examined metal-associated stresses than the male plants.

NUTRIENTS

Plant growth is often inhibited by nutrient deficiency. *P. cathayana* males had higher antioxidant activities and less damage of photosystem II under nitrogen (N) and phosphorus (P) deficiency. (Zhang et al., 2014). *P. cathayana* male and female plants showed different responses to N and P deficiency at the proteome level. Most of the changes observed were for proteins involved in the stress response and gene expression regulation, with alterations being greater in females than in males. It was suggested that compared to males, *P. cathayana* females were more sensitive to N and P deficiency and had a more rapid metabolic response (Zhang et al., 2016b). Under limited N and P concentrations, *P. tremula* females produced more flavonoids and condensed tannins and invested more in mineral nutrient acquisition, whereas males had higher growth rates (Randriamanana et al., 2014). The growth of *P. cathayana* females was stimulated more significantly than that of males in intersexual competition under high N concentrations. However, males were more adaptive to low N concentrations in intersexual competition (Chen J. et al., 2015). The effect of potassium (K) deficiency on *P. cathayana* was also investigated; it was observed that females had a significantly lower K content in leaves and stems as well as increased sucrose content than that of males. Therefore, males were less sensitive to K deficiency (Yang et al., 2015). Plant growth is linked to soil nutrients and atmospheric CO₂, which is necessary for photosynthesis. *P. cathayana* photosynthetic capacities and growth were

stimulated by elevated CO₂ levels, and males had greater biomass production than females (Zhao et al., 2012). Besides, the effects of N supply and elevated CO₂ levels on *P. cathayana* plants were investigated. Both N deposition and elevated CO₂ levels individually increased the leaf mass and photosynthetic rate in both sexes; however, the effects were weaker when these conditions were present simultaneously. Moreover, males were more adaptive to the combined conditions imposed by elevated CO₂ levels and N deposition than females (Zhao et al., 2011).

OTHER STRESSES

In addition to the stresses described above, the effect of other unfavorable environmental conditions on male and female *Populus* individuals was also investigated. Enhanced UV-B radiation affects plants negatively. In *P. cathayana* males, the antioxidant enzymes were more efficient and exhibited greater tolerance to the stress induced by UV-B radiation than that in females (Xu et al., 2010). Sex-related transcriptional alterations were observed in *P. cathayana* under UV-B radiation stress. Genes involved in amino acid metabolism were upregulated in males and downregulated in females. The gene regulation strategy was more effective in males than in females (Jiang et al., 2015). Skewed male:female ratios (male-biased) of *P. purdomii* were observed at high altitudes, where multifactor stress including high UV-B radiation levels is present (Lei et al., 2017). Sex-specific differences at the proteome level were noted in *P. cathayana* under conditions of high UV-B radiation. Alterations in the expression levels were higher in males than in females for proteins, which are mainly involved in translation/transcription/post-transcriptional modification, stress responses, and amino acid metabolism (Zhang et al., 2017). However, male buds of *P. tremula* were more sensitive to UV-B than female buds. Moreover, increased temperature caused more delay in bud maturation in males than in females (Stromme et al., 2015). Female floral buds of *P. tomentosa* were observed to be better adapted to heat and chilling stress than male buds. Temperature treatment resulted in increased activities of catalase, peroxidase, and superoxide dismutase in female floral buds, whereas malondialdehyde content was significantly increased in males (Song et al., 2014). In contrast to buds, *P. cathayana* female plants showed less tolerance to chilling stress than males. Disintegrated chloroplasts and numerous tilted grana stacks were identified in female plants under chilling stress, whereas a higher chlorophyll content and antioxidant activity was observed in males (Zhang et al., 2011). *P. cathayana* males had more effective protection against chilling stress at the proteome level than the females (Zhang et al., 2012). However, for *P. trichocarpa* no significant sex-specific differences in response to low and high temperatures were identified: the time from planting of exposed to stress cuttings to bud break and leaf flush was equal for genders (McKown et al., 2017). Apart from chilling, flooding is another winter stress for *Populus* trees. *P. deltoides* males were found to be more tolerant to winter flooding and demonstrated less oxidative damage than females (Miao et al., 2017). In riparian woodland,

the skewed male:female ratio (2:1) of a studied population of *P. angustifolia* was observed. Male trees had higher normalized differences in vegetation indexes than females, whereas other leaf reflectance and photosynthetic gas exchange characteristics were similar in both sexes (Letts et al., 2008). Although, the sex-specific response of *Populus* to abiotic stresses has been primarily studied, some data on the differential sensitivity of males and females to biotic stresses were also reported. Leaf rust disease, which is caused by the fungus, *Melampsora laricis-populina*, was more severe in female *P. cathayana* than in males. *M. laricis-populina* infection resulted in higher antioxidant activities, and less negative effects in males than females (Zhang et al., 2010b). Male and female trees of *P. tremuloides* had similar levels of phenolic glycosides and condensed tannins; however, the correlation of growth rate with these defense chemicals was revealed only in females. It was suggested that males are less sensitive to herbivores and need less phenolic glycosides for defense than females (Stevens and Esserb, 2009).

LACK OF SEXUAL DIMORPHISM FOR NON-REPRODUCTIVE FEATURES

Diverse stress responses in male and female *Populus* individuals were observed at genomic, epigenomic, proteomic, and physiological levels in most of the above-mentioned studies. However, recently, no differences between *Populus* sexes were revealed for non-reproductive features. *P. tremula* male and female trees from Umea and Swedish Aspen collections, which were wild-growing and not subjected to a particular experimental stress, were compared regarding morphological and biochemical characteristics, arthropod abundance, sex bias, and transcription profiles. No sexual dimorphism was found, with the exception of the expression of two genes (Potri.019G047300 and Potri.014G155300). The first gene is located in the sex-determining region (Robinson et al., 2014) and has deletion in females (Pakull et al., 2015). Sampling of

about 1,300 individuals of *P. trichocarpa* and *P. balsamifera* was tested for identification of sex-specific differences in natural conditions. Seventy functional traits and 26 wood-related traits were assessed and no significant differences between genders for non-reproductive features were revealed. Gender neutrality for non-reproductive traits was suggested in both *P. trichocarpa* and *P. balsamifera* (McKown et al., 2017). Divergence in the results of sex-specific features in *Populus* could be associated with the use of diverse plant material (cuttings, seedlings, or mature trees), conditions (natural or controlled stress), as well as sampling size and composition. Besides, in distinct populations of *Populus* species, physiology and morphology are varied, and stress responses could be associated with a particular species and genotype (Rae et al., 2007).

GENETIC DETERMINATION OF SEX IN *Populus*

Populus has an XY sex-determining system, and males and females differ at the genome level by 650 SNPs, which are significantly associated with sex. The sex-associated region in *Populus* is relatively small—about 100 kb (Gerald et al., 2015). It contains a gene encoding METHYLTRANSFERASE1 (MET1), which is involved in DNA methylation – an important mechanism of plant adaptation to stress (Ashapkin et al., 2016). Gender-specific methylation of the *PbRR9* gene, which is also located in the sex-associated region and encodes cytokinin signaling orthologs of ARABIDOPSIS RESPONSE REGULATOR 16 and 17 (ARR 16 and 17), was revealed in xylem tissues of *P. balsamifera* (Brautigam et al., 2017). Thus, genetic differences between males and females influence not only reproductive organs, but also secondary sex characteristics, and therefore, could lead to gender differences in non-reproductive features.

Further studies will show what role in response to unfavorable environments belongs to gender differences in *Populus*, and data received to date have been summarized in **Table 1**.

TABLE 1 | *Populus* sex-specific response to environments.

Stress	Species	Sex-specific response
Drought	<i>Populus cathayana</i> <i>P. yunnanensis</i>	Females were more sensitive: had more pronounced decrease of growth, physiological functions, hormone biosynthesis, and photosynthesis, but higher accumulation of reactive oxygen species (ROS).
Salinity	<i>P. cathayana</i> <i>P. deltoides</i> <i>P. yunnanensis</i>	Females were more sensitive: had less capacity to restrict Na ⁺ transport from roots to shoots, more reduction of growth and photosynthesis, greater damage of cell organelles, but higher accumulation of ROS.
Metals	<i>P. cathayana</i> <i>P. deltoides</i> <i>P. yunnanensis</i>	Females were more sensitive to Pb, Cd, Al, Cu, Zn stress and Fe deficiency: had higher growth inhibition, more damage of photosynthesis system and less antioxidant activity.
Nutrients	<i>P. cathayana</i> <i>P. tremula</i>	Females were more sensitive to nutrient deficiency: had higher growth inhibition. Males had greater biomass production under elevated CO ₂ conditions.
UV-B	<i>P. cathayana</i> <i>P. purdomii</i> <i>P. tremula</i>	Female trees were more sensitive to UV-B: had less antioxidant activity and amino acid metabolism. However, female buds had less damage under UV-B than male buds.
Temperature	<i>P. tremula</i> <i>P. tomentosa</i> <i>P. cathayana</i> <i>P. trichocarpa</i>	Females were more sensitive to chilling stress: had more damage of photosynthesis system and less antioxidant activity. However, female buds had increased antioxidant activity and less damage under heat and chilling stress. In <i>P. trichocarpa</i> , no sex-specific response to temperature stress was revealed.

CONCLUSION

Considerable information on gender differences of *Populus* species, especially under unfavorable conditions, has been accumulating. Most research has shown that male *Populus* plants tend to be more tolerant to environmental stresses, such as drought, salinity, heavy metals, and nutrient deficiency, than female plants. Under unfavorable conditions, males exhibit less reduction in growth rate and photosynthetic activity, as well as less cellular damage and higher antioxidant activities than females. The inverse situation was observed for floral buds – females had less damage than males under temperature stress and high UV-B radiation. Thus, it can be suggested that under unfavorable conditions, the strategy of male trees is to maintain their growth and vegetative mass, whereas females aim to preserve their reproductive organs. However, some recent studies showed no differences between *Populus* sexes for non-reproductive traits and adaptation strategies. Controversial results could be associated with genotype differences, definite stress conditions, types of plant material, sampling sizes,

etc. Understanding sex-specific differences is crucial for basic research and effective practical applications in dioecious species. Further studies are needed to conclude whether there is a difference in secondary sex characteristics between *Populus* sexes.

AUTHOR CONTRIBUTIONS

NM, EB, AS, AK, and AD wrote the manuscript. All the authors revised the work critically for important intellectual content, approved the version to be published, and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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