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Sex-related differences in the photochemistry and in the photosynthetic electron transport chain (Z-scheme) of dioecious plants: a short review

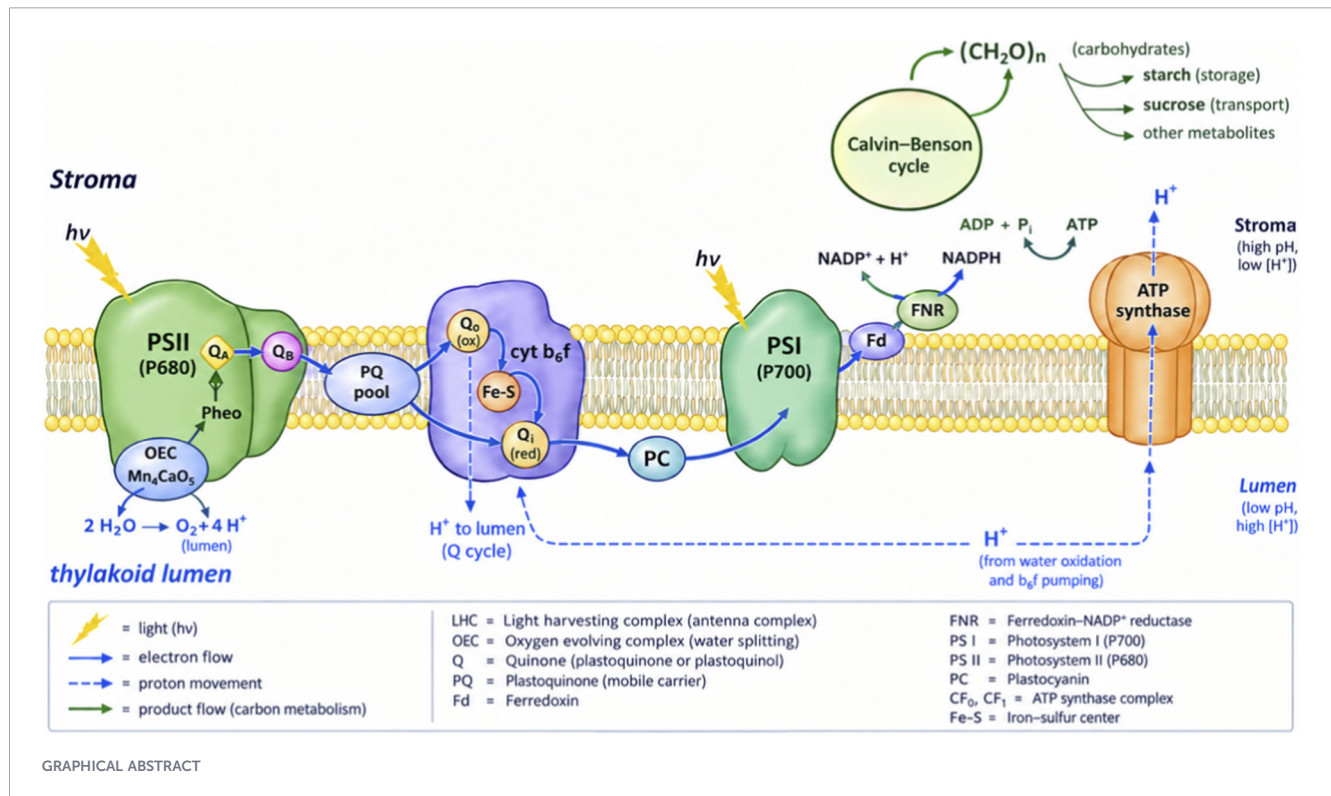
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Photosynthesis is the fundamental biological process by which light energy is converted into chemical energy, driven by the photosynthetic electron transport chain (the Z-scheme). Dioecious plant species exhibit sex-related differences in photosynthetic performance, particularly under environmental stress. Current evidence indicates that these differences are highly species-specific and strongly influenced by environmental conditions, with contrasting findings. Recent studies have revealed such differences at physiological, photochemical, and molecular levels, implicating multiple components of the photosynthetic apparatus. In *Ginkgo biloba*, for example, the male plants exhibit earlier and more pronounced limitation on the electron acceptor side of PSII during senescence, accompanied by lower oxygen-evolving complex stability and higher Q_A^- accumulation. In contrast, the female plants maintain higher cross-section-based energy fluxes and PSI end-acceptor reduction capacity. Conversely, in *Amaranthus palmeri* under high light intensity, the female plants show significantly lower PSII operating efficiency (Φ_{PSII}) and greater photoinhibition compared to the male plants, which maintain higher chlorophyll content and PSII capacity. However, in *Populus yunnanensis*, under drought stress, the male plants display more pronounced alterations in the expression of genes encoding both Photosystem I and II proteins, as well as the photosynthetic electron transport components, suggesting superior drought acclimation. These sex-specific patterns are observed through chlorophyll fluorescence parameters (F_v/F_m , Φ_{PSII} , ETR, qP , and NPQ), OJIP-derived parameters, photosynthetic pigment composition, photosynthesis-related proteins associated with both Photosystems II and I, and antioxidant defense responses. This review evaluates the current evidence and provides a photochemical overview of sex-related differences in the photosynthetic Z-scheme of dioecious plants, with particular emphasis on the function and the photochemical performance of both Photosystem II and Photosystem I.

KEYWORDS

chlorophyll fluorescence, photoinhibition, photosystem I, photosystem II, sexual dimorphism



1 Introduction

Photosynthesis is a vital biological process by which light energy is converted into chemical energy (Evans, 2013). In plants, oxygenic photosynthesis utilizes light energy to oxidize water and reduce carbon dioxide into carbohydrates while releasing molecular oxygen into the atmosphere. This process occurs in chloroplasts, where photosynthetic pigments-protein complexes are organized within the thylakoid membranes (Björn et al., 2023). The light-dependent reactions involve two functionally interconnected photosystems, Photosystem II (PSII) and Photosystem I (PSI). The photosynthetic electron transport chain establishes a proton gradient across the thylakoid membrane that drives ATP synthesis through ATP synthase, whereas electron transfer through PSI results in the reduction of NADP⁺ to NADPH. Both ATP and NADPH are required for carbon fixation during the Calvin-Benson cycle (Hossain et al., 2022). Photosynthesis represents a key target for improving crop productivity and ensuring future food security (Stirbet et al., 2020).

In this context, improving photosynthetic efficiency has emerged as one of the most promising strategies for increasing biomass production and crop yield, particularly in response to the growing global demand for food and the need to enhance agricultural production while minimizing agricultural expansion (Ort et al., 2015). In addition, advances in plant breeding, genetic engineering, and synthetic biology have provided new opportunities to optimize photosynthetic performance under changing environmental conditions (Zhu et al., 2010).

The efficiency of oxygenic photosynthesis relies on the coordinated action of a highly organized photosynthetic system located within the thylakoid membranes of chloroplasts. The light-dependent reactions are driven by four major multi-subunit membrane protein complexes: Photosystem II (PSII), the cytochrome b6f complex, Photosystem I (PSI), and the ATP synthase. PSI and PSII harvest light energy through pigment-protein complexes, whereas the cytochrome b6f complex mediates electron transport between the two photosystems (Nelson and Ben-Shem, 2004; Nelson and Yocum, 2006). Linear electron transport begins with the oxidation of water in the PSII complex and ends with the reduction of NADP⁺ to NADPH in the PSI complex. Protons translocate across the thylakoid membrane, generating energy that drives ATP synthesis through the ATP synthase. The photosynthetic Z-scheme represents this sequential arrangement of these electron carriers (Björn et al., 2023). A schematic representation of the Z-scheme.

Plants have evolved mechanisms to prevent autogamy, including dichogamy, in which the male and the female reproductive organs mature at different times, and dioecy, in which the male and the female organs occur on separate individuals. Dioecy provides important ecological and evolutionary advantages (Munné-Bosch, 2015). In addition, dioecious species exhibit secondary sexual dimorphism, which refers to sex-specific differences that extend beyond reproductive organs (Munné-Bosch, 2015). These differences are not directly related to gamete production but to vegetative traits, such as morphology, growth, physiology, water-use strategies, photosynthetic performance, hormones, and phenology (Munné-Bosch, 2015). Therefore, dioecious plants are suitable for

evaluating the response of gender on plant physiological function and adaptation to environmental conditions (Munné-Bosch, 2015). Secondary sexual dimorphism may be associated with differences in reproductive investment between the male and the female plants (Juvany and Munné-Bosch, 2015). The female plants often invest more resources in reproduction than the males, because of the additional demands of fruit and seed production (Trancoso et al., 2025). Reproductive costs may vary with species, environmental conditions, and the developmental or phenological stage of the plants (Juvany and Munné-Bosch, 2015). Sex-related differences in photosynthetic performance have been reported under a wide range of stressful conditions, including drought, nutrient deficiency, extreme temperatures, ultraviolet radiation, wind erosion, and heavy metal exposure (Juvany and Munné-Bosch, 2015; Ma et al., 2022). Overall, the differences in photosynthesis are species-specific and strongly influenced by environmental factors (Juvany and Munné-Bosch, 2015). Therefore, investigating the mechanisms regulating the photosynthetic apparatus in dioecious plants is essential.

Although the present review focuses on dioecious plants, hermaphroditic sexual systems provide an important evolutionary and physiological context. Most flowering plants possess both the male and the female reproductive organs within the same individual, often within the same flower, whereas separate sexes have evolved independently many times. Separate sexes can evolve from hermaphroditic individuals either gradually, through increased reproductive investment in one sex, or more rapidly through mutations that suppress the male or the female function. Intermediate sexual systems may occur during these evolutionary transitions (Bachtrog et al., 2014). Hermaphroditic plants may also have considerable agronomic importance. Carica papaya, for example, exhibits a mixed sexual system, with male, female, and hermaphrodite plants, in which hermaphrodite plants are commercially preferred because they produce the most desirable fruit shape, making early sex identification important for reducing production costs. (Trancoso et al., 2025), investigated whether ecophysiological phenotyping could provide an alternative approach for the early segregation of the female and the hermaphrodite papaya seedlings and whether this discrimination could be improved after short-term water stress. They found that the differences between the female and the hermaphrodite seedlings were expressed in a greater number of traits under water stress than under well-watered conditions, supporting the use of ecophysiological traits for early sex segregation in papaya.

Despite extensive reports of sex-biased photosynthetic performance (Juvany and Munné-Bosch, 2015), the specific physiological mechanisms driving these differences remain largely unknown. Therefore, it is essential to focus on the physiological mechanisms within the photosynthetic electron transport chain. Photosynthetic performance mostly depends on the efficiency of PSII, cytochrome b6f, PSI, and ATP synthase. Understanding how these complexes function differently in male and female plants is important for studying sex-related physiological adaptations. Therefore, in this review, we summarize the current knowledge on sex-related differences in the photosynthetic electron transport chain of dioecious plants, with a particular focus on the Z-scheme and its major components.

2 Photosystem II (PSII)

2.1 Importance of PSII in photosynthesis

PSII is a multimeric pigment-protein complex located within the thylakoid membranes of chloroplasts. It represents the “first” photosynthetic complex of the Z-scheme and is widely considered one of the most important biological catalysts because it performs the most thermodynamically demanding reaction in biology, the light-driven oxidation of water. PSII catalyzes the “splitting” of water molecules into molecular oxygen and provides the electrons required to drive the entire photosynthetic electron transport chain. This unique photochemical process supports the survival of almost all forms of life on Earth (Barber, 2003). Despite the remarkable phylogenetic and ecological diversity of oxygenic phototrophs, all of them use the same PSII for the conversion of solar energy into chemical energy (Vinyard et al., 2013). The catalytic chemistry underlying water oxidation is considered one of the rarest and most remarkable biochemical processes in nature. The ability of PSII to extract electrons from water is regarded as a unique evolutionary innovation that emerged more than three billion years ago. PSII is one of the most significant biological systems in the history of life on Earth (Barber, 2003; Dau and Zaharieva, 2009). Therefore, understanding its structure and organization is essential for examining plant responses to both normal and stressful environmental conditions.

2.2 Structure and functional organization of PSII

PSII consists of a dimer, with its monomer comprising two major functional components, the PSII core and a connected light-harvesting antenna system. The PSII core contains the reaction center (RC), which is formed by the D1 (PsbA) and D2 (PsbD) proteins and harbors the redox cofactors responsible for the primary charge separation and the initiation of photosynthetic electron transport. In plants, the peripheral antenna system is mainly composed of light-harvesting complex II (LHCII), which transfers excitation energy through the inner antenna proteins CP43 (PsbC) and CP47 (PsbB) toward the PSII reaction center (Müh and Zouni, 2020; Shevela et al., 2023). The PSII core is also associated with extrinsic proteins, including PsbO, PsbP and PsbQ (Müh and Zouni, 2020; Shevela et al., 2023). The oxygen-evolving complex (OEC) of PSII contains the Mn_4CaO_5 cluster, which catalyzes the light-driven oxidation of water. After the light absorption of the reaction center, electrons are transferred through a series of electron acceptors, such as pheophytin and plastoquinones (Q_A and Q_B). The coordinated organization of these components supports the overall efficiency of oxygenic photosynthesis (Shevela et al., 2023).

2.3 Environmental stress and photoinhibition of PSII

PSII is considered the most vulnerable component of the photosynthetic apparatus and therefore represents one of the primary targets of environmental stress (Landi and Guidi, 2023). Environmental stress can affect the functioning of the

photosynthetic apparatus and modify the balance between photochemical energy conversion, heat dissipation, and chlorophyll fluorescence. Under these conditions, photoinhibition may occur either as a dynamic process, in which physiological functions are rapidly reversible, or as *chronic* photoinhibition, where the photosynthetic mechanism recovers slowly or suffers permanent damage (Ait Said et al., 2013). Since light is the driving force of photosynthesis, a certain degree of photoinhibition is unavoidable under natural conditions. However, photosynthetic organisms have developed efficient mechanisms that continuously repair damaged PSII complexes (Murata et al., 2007; Ohad et al., 1992). The severity of photoinhibition is determined by the balance between photodamage and the repair capacity of PSII rather than photodamage alone (Murata et al., 2007). Photodamage of PSII occurs through a two-step process. Initially, excessive light induces damage to the Mn_4CaO_5 cluster of the OEC, which is responsible for water oxidation. Subsequently, the absorbed light energy causes the inactivation of the PSII reaction center, resulting in impaired photochemical activity (Murata et al., 2007; Ohnishi et al., 2005). Therefore, maintaining the balance between photodamage and repair is essential for preserving PSII functionality under abiotic stress and provides information for understanding the sex-related differences in PSII performance discussed in the following sections.

2.4 Chlorophyll fluorescence analysis

Chlorophyll a fluorescence analysis is one of the most widely used techniques (Govindjee, 2004) for evaluating PSII functionality and photosynthetic performance, and has been applied to investigate sex-related differences in photosynthesis in dioecious plants (Cheng et al., 2026). The technique is based on the principle that the light energy absorbed by chlorophyll molecules can be utilized in photochemistry, dissipated as heat, or re-emitted as chlorophyll fluorescence. Therefore, measurements of chlorophyll fluorescence provide information not only on the photochemical efficiency, but also on the activation of photoprotective mechanisms. The most frequently used fluorescence parameters—directly associated with the PSII function—are the effective quantum yield of PSII (Φ_{PSII}), which represents the proportion of light absorbed by PSII that is used in photochemistry, the maximum quantum efficiency of PSII (F_v/F_m), which is determined in dark-adapted leaves and represents the maximum quantum efficiency of PSII photochemistry and the photochemical quenching coefficient (qP), which reflects the proportion of open PSII reaction centers. The electron transport rate (ETR) provides an estimate of the rate of linear electron transport through PSII (Maxwell and Johnson, 2000), whereas the maximum electron transport rate (ETR_{max}), represents the maximum apparent rate of photosynthetic electron transport through PSII and is obtained from the ETR light-response curve, at the photosynthetic photon flux where electron transport reaches saturation (Robakowski et al., 2018). Finally, the non-photochemical quenching coefficient (NPQ) describes changes in the dissipation of excess excitation energy as heat relative to the dark-adapted state and therefore provides information on photoprotective energy dissipation (Maxwell and Johnson, 2000).

More detailed information on PSII function and the photosynthetic electron transport chain can be obtained from the

fast chlorophyll a fluorescence induction (OJIP) and its analysis using the JIP-test. The OJIP transient provides information about the functional antenna size, the photochemistry of PSII, and the functioning of the photosynthetic electron transport chain (Bussotti et al., 2010; Ferroni et al., 2022; Tsimilli-Michael, 2020). Among the OJIP-derived parameters, W_k is associated with the functional state of the OEC, whereas V_j and V_i represent the relative variable fluorescence at the J and I phase of the fluorescence induction curve, respectively. The quantum yield of electron transport (Φ_{E_o}) provides information on electron transport beyond Q_A^- , while TR_o/CS_o and ET_o/CS_o describe trapped energy and electron transport fluxes per excited cross-section, respectively (Strasser et al., 2004). PL abs and total PI provide integrated information on photosynthetic performance, while DF abs express the corresponding driving force on an absorption basis. Differential analysis of normalized OJIP kinetics, such as ΔW_oj , reveals changes in the O-J phase. These parameters provide a highly detailed characterization of PSII photochemistry and photosynthetic electron transport chain (Tsimilli-Michael, 2020), which allowed us to appropriately assess sex-related differences (Cheng et al., 2026).

2.5 Comparative analysis of sex-related differences in PSII performance

Various studies indicate that sex-related differences in PSII performance in dioecious plants do not follow a common pattern. Instead, these differences vary among species and depend strongly on environmental conditions, developmental or reproductive stage, and the specific photosynthetic parameter under investigation (Korres et al., 2023; Ma et al., 2022; Xu et al., 2008). Higher PSII performance has been reported in both male and female plants, depending on the species and the environmental conditions. In some cases, no significant sex-related differences were observed, whereas in others, they became apparent only under particular stress conditions. The main findings in the current literature are summarized in Table 1.

Although sex-related differences in PSII performance have been found to vary among species, higher photochemical efficiency has been observed in the males under specific environmental conditions. Under drought conditions, the male *Populus cathayana* maintained higher F_v/F_m and qP than the females, while Φ_{PSII} decreased significantly only in the females, showing better preservation of PSII photochemical function in the males (Xu et al., 2008). A similar tendency was observed in *Juniperus communis*, where the males generally showed higher Φ_{PSII} , ETR, and ETR_{max} at specific sampling dates. In contrast, the females exhibited higher NPQ over parts of the light-response curve, suggesting that sex-related differences involved both photochemical activity and non-photochemical energy dissipation (Rabska et al., 2021). Greater PSII stability in the males was also reported in seed-derived *Rumex thyrsoiflorus* exposed to short-term heat stress (Gozdur et al., 2023). This male advantage was dependent on the specific plant species, so sex alone did not determine PSII performance against heat stress. The importance of environmental conditions and developmental stage is particularly evident in *Amaranthus palmeri*. The males showed higher Φ_{PSII} under high light and P deficiency, whereas the females showed higher maximum fluorescence under N deficiency at a later developmental stage (Korres et al., 2023). These

TABLE 1 Sex-related differences in PSII photochemistry in dioecious plant species.

Species	Sex determination/ plant stage	Stress/environmental conditions	PSII-related parameters	Main sex-related findings and interpretation	References
<i>Populus cathayana</i>	Cuttings were collected from previously identified male and female trees. Measurements were performed on fully expanded leaves during the first growing season	Drought: (30% field capacity) vs. control (100% field capacity)	Fv/Fm, Φ PSII, qP	Under drought, Φ PSII decreased only in females, whereas males maintained higher Fv/Fm and qP, indicating better preservation of PSII photochemical function	Xu et al., 2008
<i>Juniperus communis</i>	Rooted shoots originated from previously identified mature male and female plants. One-year-old needles were collected across flowering, active growth, root allocation, and dormancy stages	Long-term nutrient availability under fertilized and non-fertilized conditions	Fv/Fm, Φ PSII, ETR, ETRmax, Φ PPFsat, NPQ	Males showed higher Φ PSII and ETR, as well as higher ETRmax at specific sampling dates, whereas females exhibited higher NPQ over parts of the light-response curve. Sex-related differences occurred independently of fertilization	Rabska et al., 2021
<i>Rumex thyrsiflorus</i>	Sex determined molecularly using PCR-based Y-chromosome-specific markers	Short-term heat stress (35°C/7days), followed by 7 days of recovery (25°C). Plants were subsequently acclimated to field conditions for 9 weeks	Minimal fluorescence (F_o), maximal fluorescence (F_m), variable fluorescence (F_v), time to maximal fluorescence (TFm), overall performance index of PSII (PI), Fv/Fm	Among seed-derived plants, males were less affected by short-term heat stress and showed more stable PSII activity than females	Gozdur et al., 2023
<i>Amaranthus palmeri</i>	Sex determination method was confirmed phenologically based on the inflorescence's characteristics. Cuttings originated from F1 male and female plants produced male and female plants, respectively. Measurements were performed from early growth to later-maturing stages	Three light intensities (150, 450 and 1300 $\mu\text{mol photons m}^{-2}$) combined with N, P, K deficiencies	Steady-state fluorescence ($F'S$), maximum fluorescence ($F'M$), Φ PSII	Under high light intensity (1300 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), the males exhibited higher Φ PSII (22.5%) than females between 35–42 DAT. Under P deficiency, the males showed higher Φ PSII (7.3%–10.5%) from 28 DAT, whereas under N deficiency, the females exhibited higher $F'm$ (5.5%) at 42 DAT. Sex-related differences in PSII performance depended on both stress condition and developmental stage	Korres et al., 2023
<i>Litsea cubeba</i>	Sex determination method not reported. Two-year-old female and male plants were used	Pb stress: 1,2 or 3 mmol Pb kg^{-1} dry soil vs. untreated control soil	Fv/Fm, $F'v/F'm$, NPQ, Y(II) (effective quantum yield of PSII photochemistry), Y(NO) (quantum yield of non-regulated energy dissipation in PSII)	At P1, the females showed a significant decrease in Fv/Fm and $F'v/F'm$ compared with males. In the males, Y(II) and NPQ increased across Pb concentrations, whereas Y(NO) decreased at P1 and P2. In the females, Y(II) decreased at P1 and P3, while NPQ and Y(NO) showed no significant changes. Overall, the males showed greater adaptability to Pb stress	Li et al., 2023

(Continued)

TABLE 1 Continued

Species	Sex determination/ plant stage	Stress/environmental conditions	PSII-related parameters	Main sex-related findings and interpretation	References
<i>Pistacia lentiscus</i>	Sex determination method not reported (previously identified male and female individuals were selected). Mature field-grown plants were assessed using fully expanded leaves	No artificial stress treatment; seasonal variation and aridity across three mediterranean sites (superior semiarid, inferior semiarid and arid, assessed in winter, spring, summer and autumn	Fv/Fm, Φ PSII, qP, NPQ	Females exhibited higher Fv/Fm during spring at all sites, and this female advantage persisted during summer and autumn at the superior semiarid site. Differences in Φ PSII were season- and site-dependent, whereas no consistent sex-related differences were observed in qP and NPQ. Overall, sex-related differences in PSII photochemistry were season- and site- dependent	Ait Said et al., 2013
<i>Taxus baccata</i>	Rooted shoots originated from previously identified male and female donor trees. One-year-old needles were collected across seasonal and reproductive stages	Contrasting nutrient availability (fertilized and non-fertilized plants)	Fv/Fm, Φ PSII, ETRmax, quantum yield of PSII at saturating photosynthetic photon flux (Φ PPFsat), NPQ	Females exhibited higher Fv/Fm than males, whereas no significant sex differences were observed in Φ PSII, ETRmax, or NPQ. Fertilization improved PSII performance independently of sex. Most PSII parameters were more strongly affected by nutrient availability than by sex	Robakowski et al., 2018
<i>Salix gordejevii</i>	Sex identified during flower season (specific method not reported)/Established saplings had grown for approximately 3 years after planting	Natural wind erosion stress	Fv/Fm, Φ PSII	Under wind erosion, Fv/Fm decreased significantly in males but remained relatively stable in females, which also maintained higher Φ PSII than males. No significant sex-related differences were observed under control conditions. The females showed greater stability of PSII photochemical function and higher tolerance to wind erosion than the males	Ma et al., 2022

(Continued)

TABLE 1 Continued

Species	Sex determination/ plant stage	Stress/environmental conditions	PSII-related parameters	Main sex-related findings and interpretation	References
<i>Ginkgo biloba</i>	Sex determination method not reported; mature naturally grown male and female trees were monitored during seasonal development and natural leaf senescence	Natural leaf senescence under field conditions (DOY 188–332)	OJIP/JIP-test (Fv/Fm, ΔWok , Wk, Vj, Vk, ΦE_0 , TR_0/CS_0 , ET_0/CS_0 , Plabs, PI total, DFabs)	After DOY 268, the males showed an earlier and more pronounced decline in PSII function, with stronger acceptor- and donor-side limitations and faster decreases in photochemical performance and electron transport. The females maintained higher TR_0/CS_0 and ET_0/CS_0 and showed a slower decline in Fv/Fm. Overall, the females maintained greater PSII stability and photochemical performance during natural senescence than males	Cheng et al., 2026
<i>Chamaerops humilis</i>	Sex determination method not reported (mature male and female plants were selected during the reproductive stage). Mature male and female plants were examined using fully expanded mature leaves	Seasonal variation (natural conditions), sex-related comparisons were performed under field conditions during the reproductive period	Fv/Fm, NPQ	During the summer reproductive period, the females exhibited lower Fv/Fm and greater photoinhibition than males. Their sensitivity was associated with reproductive events, but did not result in irreversible damage to the photosynthetic apparatus	Morales et al., 2016
<i>Morus alba</i>	Sex determination method not reported; male and female cuttings were vegetatively propagated and grown for 2 months before transplantation and treatment	Waterlogging for 40 days with a 5-cm water layer above the soil surface. Control plants received regular irrigation	NPQ, PsbB, PsbQ, PsbD, PsbH	Under waterlogging stress, the females showed increased NPQ and upregulation of PsbB and PsbQ, whereas males showed downregulation of PsbD, PsbB and PsbH. The females showed greater stability of PSII-associated proteins and enhanced regulation of excess energy dissipation under waterlogging stress	Deng et al., 2026
<i>Salix paraplesia</i>	Sex determined phenotypically. Current-year cuttings were collected before flowering and grown before treatment	Drought (50% soil water capacity vs. well-watered control of origin 100%) and altitude (2,400, 2,600, 2,800 m)	Pn, total chlorophyll content, chloroplast ultrastructure	Under drought, the females maintained higher Pn and total chlorophyll content than males, particularly in plants originating from high altitude, together with better preservation of chloroplast ultrastructure. These responses indicate greater drought tolerance in females, especially those originating from 2,800 m	Liao et al., 2019

(Continued)

TABLE 1 Continued

Species	Sex determination/ plant stage	Stress/environmental conditions	PSII-related parameters	Main sex-related findings and interpretation	References
<i>Urtica dioica</i>	Sex determined phenotypically after sex expression. Juvenile and mature plants were examined	Combined water and nutrient deficit (withholding water for 14 days during the juvenile and/or mature reproductive stage)	Fv/Fm	Stress reduced Fv/Fm, particularly in mature plants, but no significant sex-related differences in Fv/Fm were observed, indicating similar maximum PSII efficiency under tested conditions	Oñate et al., 2011

findings demonstrate that sex-related differences in PSII performance depends on both the stress condition and the developmental stage. A male advantage was also observed in *Litsea cubeba* under lead (Pb) stress. At the lower Pb concentration, females showed significant decreases in Fv/Fm and F'v/F'm. However, in the male plants, the NPQ increased across all Pb concentrations, indicating more effective energy distribution and better adaptation to Pb exposure (Li et al., 2023).

The variability in sex-related differences across species is also supported by studies showing higher PSII efficiency or greater stability in the female plants. In *Pistacia lentiscus*, the females exhibited higher Fv/Fm during the spring, while the magnitude and persistence of the difference depended on season and aridity. Variations in ΦPSII were also season- and site-dependent, whereas no consistent sex-related patterns were observed in qP and NPQ (Ait Said et al., 2013). In *Taxus baccata*, the females maintained a higher Fv/Fm ratio than the males. However, no significant sex-related variations were detected in ΦPSII, ETRmax or NPQ. In this species, nutrient availability had a stronger influence on PSII performance than sex itself (Robakowski et al., 2018). Under a different environmental condition, a more evident female advantage was found in *Salix gordejewii* exposed to wind erosion stress. While no significant sex-related differences were observed under control conditions, Fv/Fm decreased considerably in the males under wind erosion and remained relatively stable in the females. The females also maintained higher ΦPSII than the males under stress (Ma et al., 2022). Greater PSII stability in the females was also reported in *Ginkgo biloba* during natural leaf senescence. As senescence progressed, the males showed an earlier and more pronounced decline in PSII function, including stronger donor- and acceptor-side limitations, whereas the females maintained photochemical performance and electron transport more effectively (Cheng et al., 2026).

Furthermore, reproductive investment appears to influence sex-related differences in PSII performance. In *Chamaerops humilis*, the females were more vulnerable to photoinhibition than the males during the summer reproductive period, as indicated by lower Fv/Fm. These sex-related differences disappeared during the winter, when the plants were no longer reproducing, and the photoinhibition observed in the females was reversible, suggesting an adaptive response (Morales et al., 2016). It appears that greater photoinhibition in the females was associated with their higher reproductive investment. An advantage for the female plants was also observed in *Morus alba* under waterlogging stress. The

females showed a significant increase in NPQ, indicating better regulation of excess energy dissipation. At the protein level, the female plants upregulated the PSII components PsbB and PsbQ, while the males downregulated the PSII components PsbD, PsbB and PsbH (Deng et al., 2026).

Female plants also showed greater photosynthetic tolerance in *Salix paraplesia* under drought, particularly in plants originating from higher altitudes. The females maintained higher net photosynthetic rate (Pn) and total chlorophyll content than the males, indicating greater drought tolerance, although these measurements extended beyond direct PSII fluorescence parameters (Liao et al., 2019). In contrast, sex-related differences were not detected in *Urtica dioica*. Although combined water and nutrient deficit reduced Fv/Fm, the males and the females showed similar maximum PSII efficiency under stress (Oñate et al., 2011).

Overall, the studies examined in this review do not indicate a consistent advantage of either sex in PSII performance. Instead, sex-related differences appear to depend strongly on the species and the environmental conditions. More specifically, the male and female advantages are influenced by several factors, such as the type and the level of stress, the nutrient availability, the seasonal variation, the altitude, the developmental stage, and the reproductive investment. Moreover, within the same species, sex-related differences do not necessarily follow the same pattern across all the PSII parameters. Sex does not appear to influence the PSII function independently, but it rather modifies the way PSII responds to environmental conditions in different species.

3 Photosystem I (PSI)

3.1 Importance of PSI in photosynthesis

PSI is an essential component of the photosynthetic electron transport chain and represents an efficient system for the conversion of light energy into chemical energy (Nelson, 2009). It uses absorbed light energy to drive electron transfer through a series of redox centers. Light absorbed by the antenna pigments is transferred to the P700 reaction center, initiating photochemical reactions of PSI. Functionally, PSI acts as a light-driven plastocyanin-ferredoxin oxidoreductase and holds a central role in chloroplast metabolism. Therefore, PSI plays a critical role not only in photosynthetic electron transport but also in metabolic networks and physiological responses in plants (Chitnis, 2001). PSI occupies a

particularly important position within the photosynthetic system between the harvesting of light energy and its utilization through cellular metabolism. Although PSII is generally considered the primary target of photoinhibition, PSI can also become inactivated due to an imbalance in photosynthetic energy. The recovery of PSI activity is slower than that of PSII, highlighting the importance of maintaining PSI functionality for the overall stability of the photosynthetic system (Lima-Melo et al., 2021).

3.2 Structure and functional organization of PSI

In plants, PSI is a large multiprotein complex organized as a monomer. It consists of two major functional components, the PSI core complex and the peripheral light-harvesting complex I (LHCI). The core complex contains components needed for charge separation and electron transfer reactions. It also comprises chlorophyll molecules that form a light-harvesting antenna. The central region of the PSI core is composed of the PsaA and PsaB subunits, which are associated with the reaction center P700 and several components of the electron transport chain. In higher plants, LHCI mainly consists of four Lhca proteins, which transfer excitation energy to the PSI core (Busch and Hippler, 2011; Jensen et al., 2007).

3.3 Environmental stress and PSI photoinhibition

Light energy is essential for photosynthetic electron transport, but it can damage the photosynthetic machinery when electron pressure within the photosystems exceeds the capacity of chloroplast electron acceptors. PSI is generally protected against photoinhibition through several mechanisms, but damage can occur under excessive excitation or electron pressure (Lima-Melo et al., 2021). PSI photoinhibition can be induced by the combined effects of light and environmental stress, such as low temperature, drought, and salinity. In addition, PSI becomes vulnerable when the capacity of its acceptor side is exceeded by excessive electron flow (Lima-Melo et al., 2021). Photoinhibition can disturb the operational balance of the chloroplast, while excessive electron pressure may damage the iron-sulfur clusters of PSI. Several protective mechanisms reduce the risk of PSI photoinhibition by decreasing electron flow toward the donor side of PSI or by increasing the electron-consuming capacity of its acceptor side (Kılıç et al., 2023).

3.4 Assessment of PSI activity

PSI activity can be evaluated through changes in the redox state of P700. Oxidation of P700 induces an absorbance change around 820 nm. This change can be used for monitoring P700 oxidation and reduction *in vivo* (Harbinson et al., 1989).

Modulated reflection at 820 nm (MR820) can be measured together with prompt chlorophyll fluorescence (PF) and delayed chlorophyll fluorescence (DF), providing information about different parts of the photosynthetic electron transport chain (Wang et al., 2022). PF is emitted rapidly when excited Chl *a* returns to the ground state, whereas DF is emitted later, after

backward electron transfer and charge recombination re-excite chlorophyll molecules following the initial photochemical reactions. Therefore, PF and DF provide complementary information on PSII-related photochemical and electron-transfer processes, whereas MR820 provides information on PSI-related redox changes (Goltsev et al., 2009; Guo and Tan, 2013; Wang et al., 2022).

The kinetics of MR820 can be expressed as the normalized MR/MR₀ transient. In Wang et al. (2022), MR₀ was defined as the first reliable MR measurement, recorded at 0.7 m. The MR/MR₀ ratio was calculated using the modulated reflection signal at 820 nm and reflects changes in the redox status of P700 and plastocyanin (Pc). Upon illumination, an initial oxidation of P700 and Pc is followed by their reduction. The maximum decreasing slope of the MR/MR₀ transient is defined as VPSI, whereas the maximum increasing slope is defined as VPSII-PSI. These parameters reflect changes in the oxidation and reduction rates of P700 and Pc (Wang et al., 2022).

In addition, the OJIP-derived parameters can provide information about electron transport toward the terminal electron acceptors of PSI. RE₀/CS₀, for example, represents the electron flux reducing terminal electron acceptors at the PSI acceptor side per cross section and therefore provides information on electron transport toward the PSI acceptor side (Cheng et al., 2026).

3.5 Comparative analysis of sex-related differences in PSI performance

Sex-related differences in PSI have been reported under different environmental and developmental conditions, although the available evidence remains more limited than that for PSII. The main findings about sex-related differences in PSI performance and PSI-associated components are summarized in Table 2.

In *G. biloba*, sex-related differences in PSI activity changed during autumnal senescence. During the early stage of senescence, the males showed higher PSI electron transport activity than the females, whereas the females maintained higher activity during later stages (Shi et al., 2012). This shift indicates that the relative performance of the two sexes may change during development. Cheng et al. (2026), also reported greater maintenance of electron transport toward PSI terminal acceptors in the females during natural leaf senescence. Together, these studies suggest that the females may preserve PSI-related electron transport more effectively during advanced senescence. *Torreya grandis* also displayed differences in PSI-related electron transport between the sexes under progressive drought. After 20 days of drought, the efficiency of electron transport from the intersystem carriers to the PSI end-electron acceptors (ΔR_0) decreased by 27.1% in the males compared with 12.7% in the females, suggesting that the females maintained electron transfer toward PSI end acceptors much more effectively than the males. Changes in MR820 kinetics, reflecting changes in the redox state of P700 and plastocyanin, were greater in the males, as the maximum falling slope of the MR/MR₀ curve (VPSI) increased by 23.3% in the males and 8.2% in the females, whereas the maximum rising slope of the MR/MR₀ curve (VPSII-PSI) decreased by 22.9% in the males and 5.8% in the females (Wang et al., 2022).

TABLE 2 Sex-related differences in PSI photochemistry in dioecious plant species.

Species	Sex determination/plant stage	Stress/environmental conditions	PSI-related parameters	Main sex-related findings and interpretation	References
<i>Ginkgo biloba</i>	Sex determination method not reported. Fully expanded leaves from 30-year-old male and female trees were sampled	Natural autumn senescence under field conditions, monitored from day 259 to day 317	PSI electron transport activity	During the early stage of senescence, males showed higher PSI electron transport activity, whereas at later stages, females maintained higher activity. Thus, the relative advantage shifted from the males to the females as senescence progressed	Shi et al., 2012
<i>Ginkgo biloba</i>	Sex determination method not reported; mature naturally grown male and female trees were monitored during seasonal development and natural leaf senescence	Natural leaf senescence under field conditions (DOY 188–332)	RE_0/CS_0	During senescence, RE_0/CS_0 decreased by 67.94% in the females and 73.11% in the males. The females-maintained electron flow toward the end electron acceptors of PSI more effectively during natural senescence	Cheng et al., 2026
<i>Torreya grandis</i>	Sex determination method not reported. Two-year-old male and female seedlings were used	Progressive drought for 20 days, after irrigation, with measurements at 0, 6, 12, and 20 days	ΔR_0 , MR820 kinetics (VPSI, VPSII-PSI)	After 20 days of drought, ΔR_0 decreased by 27.1% in males and 12.7% in females; VPSI increased by 23.3% in males and 8.2% in females, whereas VPSII-PSI decreased by 22.9% in males and 5.8% in females. Changes in MR820 kinetics were greater in males. Overall, the females-maintained electron transport toward PSI end acceptors more effectively than males under drought	Wang et al., 2022
<i>Litsea cubeba</i>	Sex determination method not reported; two-year-old female and male plants were used	Pb stress: 1,2 or 3 mmol Pb kg ⁻¹ dry soil vs. untreated control soil	PSI-related gene expression	Transcriptomic analysis revealed higher expression levels of PSI-related genes in the males than in the females under both control and Pb stress conditions	Li et al., 2023
<i>Populus deltoides</i>	Sex determination method not reported. Male and female cuttings were collected from trees and were grown for approximately 2 months	Infection with <i>Alternaria alternata</i> applied to fully expanded leaves	PsaN, Lhca3	Following infection, PsaN was upregulated in the males, which also showed a higher abundance of Lhca3 than the females	Tian et al., 2024
<i>Morus alba</i>	Sex determination method not reported; male and female cuttings were vegetatively propagated and grown for 2 months before transplantation and treatment	Waterlogging for 40 days with a 5-cm water layer above the soil surface. Control plants received regular irrigation	PsaA, PsaB, and Lhca proteins	Under waterlogging stress, PsaA, PsaB and Lhca3 were downregulated in the males, whereas Lhca1-6 remained stable in the females, which maintained greater stability of PSI-associated proteins	Deng et al., 2026

Sex-related differences can also be observed at the molecular level. In *L. cubeba*, transcriptomic analysis revealed higher expression levels of PSI-related genes in the males than in the females under both control and Pb stress conditions ([Li et al.,](#)

2023). Biotic stress also resulted in sex-specific regulation of PSI-associated proteins. In *Populus deltoides*, following *Alternaria alternata* infection PsaN, a PSI subunit involved in efficient electron transfer from PQ to the PSI reaction center, was

upregulated in the males, which also showed a higher Lhca3 abundance than the females (Tian et al., 2024). In contrast, under waterlogging stress in *M. alba*, several PSI-associated components PsaA, PsaB, and Lhca3 were downregulated in the males, whereas Lhca1-6 remained stable in the females (Deng et al., 2026).

Overall, the studies examined in this review do not indicate a consistent advantage of either sex in PSI performance. Instead, sex-related differences appear to depend on species, environmental condition, and developmental stage. The female plants-maintained electron transport toward the PSI terminal acceptors much more effectively under drought and during natural leaf senescence, while the PSI electron transport activity was higher in the males during the early stages of senescence. Expression of the PSI-related genes and the proteins under Pb stress, infection and waterlogging also demonstrated differences between the sexes. Further studies using direct PSI-specific measurements are needed to determine sex-related patterns. The sex of the plant appears to influence PSI activity combined with environmental stress or developmental stage (see Table 2 for details).

4 Conclusion

This short review provides evidence that sex-related differences occur in both PSII and PSI of dioecious plants, without following a general pattern across the species. Neither the males nor the females exhibit a universal advantage in photosynthetic performance. Environmental conditions, as well as the developmental stage and the reproductive stage, have a significant influence on these differences. While sex-related variations have been reported for PSII and PSI, information about the other major components of the Z-scheme remains limited. Further studies focusing on the cytochrome b_6f and ATP synthase are needed to obtain a complete understanding of sex-related variations across the entire photosynthetic electron transport chain. Further investigations at both physiological and molecular levels are expected to provide a deeper insight into sex-related photosynthetic responses in dioecious plants.

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