Plant species compositions alleviate toxicological effects of bisphenol A by enhancing growth, antioxidant defense system, and detoxification

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Abstract
Bisphenol A (BPA), a broadly disseminated endocrine disturbing chemicals in environment, is harmful to creatures and plants. Plants can uptake and metabolize BPA, but a single plant species ability is limited. Undeniably, plant species compositions have a more vital ability to remove pollutants than a single plant species. However, the mechanisms of plant species compositions alleviating toxicological effects of bisphenol A are poorly understood. Here, we administered plant species compositions, which based on a full-factorial design of Phragmites australis (A), Typha latifolia (B), and Arundo donax (C), to unveil their role in BPA exposure. The results illustrated that the root activity, biomass, and photosynthetic pigment contents of the mixed hydroponic group (e.g., sp(ABC)) were significantly increased under concentration of BPA (1.5, 5, and 10 mg L⁻¹), which showed that the root activity, fresh weight, dry weight, chlorophyll a, and total chlorophyll contents of shoots were increased. While mixed-hydroponic culture groups (e.g., sp(AB), sp(ABC)) significantly increased antioxidant enzyme activity and antioxidant substances under concentration of BPA (5 and 10 mg L⁻¹), it astoundingly diminished responsive oxygen species (ROS) and malondialdehyde (MDA) substance, proposing that mixed-hydroponic culture groups calmed oxidative stress. Further analysis revealed that mixed-hydroponic culture groups (e.g., sp(AB), sp(AC), sp(ABC)) of 1.5, 5, and 10 mg L⁻¹ BPA exposure significantly increased detoxification enzyme activity of NADPH-cytochrome P450 reductase (CPR), glutathione S-transferase (GST), and glycosyltransferase (GT). Moreover, mixed-hydroponic culture groups (e.g., sp(AB), sp(AC), sp(ABC)) decreased the BPA substance in leaves, proposing that mixed-hydroponic culture groups advanced BPA metabolism by improving CPR, GST, and GT enzyme activities. These results demonstrated that a mixed-hydroponic culture strategy can alleviate BPA phytotoxicity and possibly offer natural and potential phytoremediation methods for BPA.

Keywords Bisphenol A · Plant species compositions · Antioxidant enzymes · Oxidative stress · Detoxification

Introduction
Bisphenol A (bisphenol A;2, 2-bis (4-hydroxyphenyl) propane) is used industrially to synthesize materials such as polycarbonate and epoxy resins (Staples et al. 1998). BPA is also applied in the production of many commodities, such as toys, water pipes, sports safety equipment, dental unit, medical equipment and pipelines, and electronic materials (Im and Loffler 2016; Wang et al. 2016a, b). Although BPA can be covalently bound to these materials, when they are washed, heated, or come into contact with an acidic or basic pH, the molecules’ ester bonds are hydrolyzed, releasing the bisphenol A monomer into the environment (Liu et al. 2013). Due to the abundant volumes and transfer of items made from BPA, BPA has brought about omnipresent within the environment (Maher et al. 2016; Wisniowska et al. 2020). Previous reports have repeatedly affirmed its presence in industrial and municipal effluents and sludge, as well as in fresh water (Lee et al. 2015). In addition, the concentration of BPA was reported in landfill leachate of hazardous waste, reaching 17.2 mg L⁻¹ (Yamamoto et al. 2001). Therefore, the BPA moves into the human body through the food chain so that human beings’ health is threatened seriously.
Previous studies have shown that BPA might cause several diseases such as childhood obesity, type II diabetes, developmental defects, and cancer (Guida et al. 2015; Dumitrescu et al. 2020; Martinez et al. 2020).

Plant is an essential link in a food chain. Plants have the ability to take up BPA from their environment and translocate into above-ground parts, thus exerting severe influences on growth and development of plant (Nakajima et al. 2002, 2004). A number of studies have uncovered the effects of BPA on plant growth, seed germination, photosynthesis, reproduction, reactive oxygen, heritability, and antioxidative system in plants (Ferrara et al. 2006; Gattullo et al. 2012; Qiu et al. 2013; Ali et al. 2016, 2017; Zhang et al. 2016; Jiao et al. 2017; Xiang et al. 2018; Kim et al. 2018; Li et al. 2018a, b). The antioxidant responses and “green liver” metabolic pathways are known for their responsiveness to BPA stress (Nakajima et al. 2002, 2004; Noureddin et al. 2004; Ali et al. 2016; Ahammed et al. 2020a, b). BPA has been reported to affect the antioxidative system by reactive oxygen species (ROS), which were generated by oxidative stress of plant species (Li et al. 2008; Zhang et al. 2018). Exposure to BPA increased ROS, lipid peroxidation, and antioxidative enzymes, which scavenge ROS (Ali et al. 2016; Xiang et al. 2018). “Green liver” metabolic pathways of plant have been shown to detoxify xenobiotics (Bartha et al. 2014; He et al. 2017). Several previous studies found that xenobiotic metabolism of BPA follows three processes in plant cells. To produce more water-soluble compounds, BPA was hydroxylated in phase I via cytochrome P450 (Sasaki et al. 2008; Nakamura et al. 2011; Yu et al. 2019). In phase II, the main product of phase I was conjugated with glycosides, via GT, and glutathione, via GST, to reduce the poisoning of plant cells (Nakajima et al. 2002, 2004; Shimoda and Hamada 2009; Ahammed et al. 2020a, b). In phase III, the metabolites of phase II were compartmentalized into the vacuole. Therefore, it is necessary to conduct a complete mechanism study on the toxicity and the degradation pathway of BPA in plants.

Plants get energy from photosynthesis to absorb, retain, and assimilate pollutants. However, there are few isolated single-plant systems in nature, for in natural ecological environments, multiple-plant systems coexist (Fornara and Tilman 2008; Wang et al. 2020a, b, c). Typically, the plants’ combining serves to rectify weaknesses of each constituent when it exists alone. A variety of plant combinations have a more vital ability to remove pollutants than a single plant species (Wang et al. 2016a, b; Zhu et al. 2017). However, the plant species compositions alleviating toxicological effects of BPA have never been investigated in detail. This is because plant diversity improves the stability of ecosystem functions and enhances the effect of purifying pollutants (Zheng et al. 2016; Zhu et al. 2017). Therefore, exploring the physiological and biochemical states of various plants in various plant combinations is helpful to understand the mechanism of improving the purification efficiency of plant combinations.

Here, we picked out three macrophytes: Phragmites australis (A), Typha latifolia (B), and Arundo donax (C) who have the biotransformation and bioaccumulation capacity of environmental pollution (Bonanno 2013; He et al. 2017; Hamad 2020). Plants of Phragmites australis is the most used for BPA removal in constructed wetlands, because its root exudates can stimulate BPA-degrading bacteria activity in rhizosphere sediment under aerobic conditions (Torevlez et al. 2016, Ali et al. 2017). The Typha latifolia and Arundo donax are tolerant species to BPA and maintain a significant capacity to remove and bioaccumulate BPA in constructed wetlands (Dai et al. 2017; Campos et al. 2019; Wang et al. 2019). Three macrophytes show a high morphological plasticity and maintain a significant capacity of pollutant removal in different environmental conditions (Calheiros et al. 2009; Zhu et al. 2017; Cao et al. 2019). This study aimed to reveal a suitable plant species composition method for carrying out physiological changes in aquatic plants exposed to BPA. We checked the compositions in terms of biomass production improvement, photosynthetic system pigment content, ROS, lipid peroxidation, antioxidant enzyme activity systems, antioxidant substances, and detoxification enzymes. This study will help to understand the reaction mechanism of plant species compositions to BPA. We speculate that the alleviating effect of different plant combinations on BPA may vary with different BPA concentrations. The results of this study will provide a reference for the scientific evaluation of the ecological significance of plant species compositions and the risk of BPA pollution and formulating environmental control measures.

Materials and methods

Plant cultivation and BPA treatment

The hydroponic experiment systems were set up in April 2019, which dimension of 22 × 22 × 26 cm and total volume was 12,584 cm³. Three common large aquatic plants in China, Phragmites australis (A), Typha latifolia (B), and Arundo donax (C), were selected for the experiment. Based on a full-factorial design, three species were assembled into 7 plant combinations, including monocultures of each species (3 combinations) which were named sp(A)-(plant A, Phragmites australis), sp(B)-(plant B, Typha latifolia), and sp(C)-(plant C, Arundo donax); all possible two-species mixtures (3 combinations) which were named sp(AB)-(plant A + B, Phragmites australis + Typha latifolia), sp(AC)-(plant A + C, Phragmites australis + Arundo donax), and sp(BC)-(plant B + C, Typha latifolia + Arundo donax); and a three-species mixture of all
species which is named sp(ABC)-(plant A + B + C, Phragmites australis + Typha latifolia + Arundo donax). The plant density was settled in each hydroponic box in diverse cultured types. Each hydroponic box contained 12 individual plants, evenly distributed (i.e., 1:1 in sp(AB)/sp(AC)/sp(BC) or 1:1:1 in sp(ABC)), with each plant combination having 3 replicates (hydroponic box). In order to immobilize the pot and aquatic plants in the exposure medium, the commercially available stones were placed in each pot. All aquatic plants were allowed to acclimate in the hydroponic box of tap water for about 10 days and then Hoagland medium 10 days. The hydroponic experiment systems were fed with Hoagland medium, holding pH about 6.0 ± 0.1 using 1 M of hydrochloric acid. Next, each hydroponic box was filled with 10 L of Hoagland medium and supplemented with a total four concentrations of BPA (1.5, 5, 10, and 20 mg L⁻¹), which was renewed every 2 days for 10 days. The hydroponic test was ended at 10 days after start of BPA treatment. Shoot of plants were collected for the investigation of diverse biochemical parameters.

Before starting the exposure experiment, the possible residual BPA on the surface of hydroponic box and stones was considered and tested. Three hydroponic boxes with the small pots were prepared, filled with the same exposure medium as described above (concentration of 1.5, 5, 10, and 20 mg L⁻¹ for BPA) but without plants. The water concentrations of BPA in each hydroponic box were then analyzed immediately (Cw₀) and 2 days later (Cw₂). The difference between Cw₀ and Cw₂ for all the BPA was lower than 2%. The temperature of the outdoor experimental facilities ranged between 28 and 32 °C.

### Determination of root activity, biomass, and light harvesting pigments

About 0.5 g of root samples was collected and cut into 0.5–1 cm section to measured root activity. Root activity was measured using the 2,3,5-triphenyl tetrazolium chloride (TTC) reduction method (Kong et al. 2009). Fresh weights of shoots were measured and kept in an oven at 80 °C for 96 h until a constant weight. The content of chlorophyll a and total chlorophyll pigments from leaves was measured according to a method described by Arnon (Arnon 1949). Fresh leaf samples (0.10 g) were placed in 2 mL of absolute alcohol in dark. After 48 h, the ethanolic extracts were measured using UV–vis spectrophotometer (UV-2550, Shimadzu Corporation, Japan) and scanned at 645 and 663 nm for absorbance (OD). The gotten absorbance values were utilized to calculate chlorophyll a and total chlorophyll content.

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\text{Chlorophyll a content} = 13.95 \times \text{OD}663 - 6.88 \times \text{OD}645
\]

\[
\text{Total chlorophyll content} = 20.2 \times \text{OD}645 + 8.02 \times \text{OD}663
\]

### Assay of ROS levels and membrane lipid peroxidation

Superoxide anion (O₂⁻) contents were measured according to previous methods (Elstner and Heupel 1976). The absorbance was recorded at 530 nm (UV-2550 spectrophotometer, Shimadzu Corporation, Japan). Hydrogen peroxide (H₂O₂) contents were determined according to previous methods (Patterson et al. 1984). The absorbance was recorded at 412 nm (UV-2550 spectrophotometer, Shimadzu Corporation, Japan). Hydroxyl radical (·OH) contents were determined according to previous methods with slight modification (Pandey et al. 2016). The absorbance was recorded at 532 nm (UV-2550 spectrophotometer, Shimadzu Corporation, Japan).

The malondialdehyde (MDA) content was determined according to previous methods with slight modification (Heath and Packer 1965). The absorbance was recorded at 532 nm (UV-2550 spectrophotometer, Shimadzu Corporation, Japan).

### Determination of antioxidant enzyme activity

The fresh leaves (1.00 g) were homogenized in 50 mM PBS (pH 7.8) containing 5 mM EDTA, 5 mM dithiothreitol and 1% (v/v) polyvinylpyrrolidone under ice cold conditions. The homogenates were centrifuged, and the supernatants were used to perform following enzyme assays.

The superoxide dismutase (SOD) activity was assayed according to Du (Du et al. 2015). The reaction mixture reacted about 30 min in fluorescent lights. One unit of SOD activity was defined as the cause 50% inhibition of the NBT measured at 560 nm within 1 min (UV-2550 spectrophotometer, Shimadzu Corporation, Japan).

The peroxidase (POD) activity was measured by following Maehly and Chance (Maehly and Chance 1954). The reaction mixture (3 mL) contained 1 mL of 50 mM PBS (pH 6.8), 2% guaiacol, 2% H₂O₂, and 100 μL enzyme extract. The change of absorbance was recorded at 470 nm within 1 min (UV-2550 spectrophotometer, Shimadzu Corporation, Japan).

The activity of catalase (CAT) was assayed according to previous methods with little modifications (Jiang and Zhang 2001). The reaction mixture contained 200 mM PBS (pH 7.8), 100 mM H₂O₂, and 50 μL of enzyme extract. The change of absorbance was recorded at 240 nm within 1 min (UV-2550 spectrophotometer, Shimadzu Corporation, Japan).

### Determination of non-enzymatic antioxidant substance content

The ascorbic acid (AsA) content was measured in accordance with previous methods (Singh et al. 2006). The fresh
leaves (0.20 g) were homogenized in 5% TCA and centrifuged. The reaction mixture stored 0.1 mL supernatant, 0.9 mL PBS (pH 7.4), and 1 mL deionized water. The absorbance was recorded at 525 nm (UV-2550 spectrophotometer, Shimadzu Corporation, Japan).

The glutathione (GSH) content was assayed by according to previous methods with slight modification (Devos et al. 2010). The fresh leaves (0.20 g) were homogenized in 5% TCA and centrifuged 15 min at 4 °C. The reaction mixture contained 0.1 mL supernatant, 2.6 mL PBS (pH 7.7), and 0.18 mL 5, 5-dithiobis-(2-nitrobenzoic acid). The absorbance was recorded at 412 nm (UV-2550 spectrophotometer, Shimadzu Corporation, Japan).

The free proline (Pro) content was estimated according to previous methods with slight modification (Troll and Lindley 1955). The fresh leaves (0.20 g) were homogenized in 10 mL of 3% sulfosalicylic acid and centrifuged for 10 min at 4 °C. The reaction mixture contained supernatant, ice acetic acid and 2.5% ninhydrin (1:1:1 V/V). The absorbance was recorded at 520 nm (UV-2550 spectrophotometer, Shimadzu Corporation, Japan).

**Determination of detoxification enzyme activity**

The microsomes are extracted according to that previously reported with slight modification (Tan et al. 2015). The fresh leaves about 5 g were homogenized in 2 volumes of 50 mM PBS (pH 7.8) and then was centrifuged at 10,000×g for 10 min at 4 °C. The supernatant was centrifuged at 100,000×g for 60 min and then the pellet was resuspended in 100 mM PBS (pH 7.8), containing 25% (v/v) glycerol and 10 mM mercaptoethanol.

The NADPH-cytochrome P450 reductase (CPR) activity was determined by the method described previously with slight modification (Guengerich et al. 2009). The reaction mixture (2 mL) contained 0.05 mL microsomal suspension, 5 mg mL⁻¹ cytochrome c, 50 mM PBS (pH 7.8), 10 mM NADPH. The absorbance was recorded at 550 nm (UV-2550 spectrophotometer, Shimadzu Corporation, Japan). The enzyme activity was expressed as nmol min⁻¹ mg⁻¹ protein using a millimolar extinction coefficient of 21.1 cm⁻¹.

The glutathione S-transferase (GST) activity was determined by a modified protocol as described previously (Fuerst et al. 1993). The fresh leaves (about 1.00 g) were homogenized in 100 mM PBS (pH 7.8) and centrifuged at 4 °C for 30 min. The reaction mixture was contained 100 μL supernatant, UDP-glucose, and p-nitrophenol. The reaction mixture was added with 250 μL methanol and chilled at −20 °C for 0.5 h. The reaction mixture was analyzed using high-performance liquid chromatography (LC-20A HPLC, Shimadzu Corporation, Japan) with an ultraviolet (UV) detection. One unit of the GT activity was defined as the consumption of 1 μmol p-nitrophenol per minute.

**Measurement of BPA content**

Leaves of BPA content were estimated by high-performance liquid chromatography (HPLC) as described previously with slight modification (Loffredo et al. 2010). The fresh leaves were dried until a constant weight. The dried leaves (1.00 g) were homogenized in 5 mL methanol and shaken on an oscillator for 4 h. The supernatant was evaporated off using a rotary vacuum evaporator (40 °C). The residual product was homogenized in 5 mL of 60% (v/v) acetonitrile. The supernatant was filtered through a 0.45-μm Millipore™ filter and analyzed using HPLC (LC-20A, Shimadzu Corporation, Japan) with UV detection under the following conditions: Inertsil ODS-3 column (4.6×250 mm, 5 μm), 217 nm wavelength, 70% methanol mobile phase, 0.6 mL min⁻¹ flow rate, 20 μL of the injection volume. Residual BPA content was calculated by standard curve which uses BPA samples with known concentration.

**Statistical analysis**

All assays were conducted in triplicates. The results were expressed as the mean ± standard deviation. Treatment groups and control were analyzed by variance (ANOVA); p < 0.05 was considered statistically significant (SPSS 22.0, IBM).

**Results and discussion**

**BPA concentration in water and root activity**

Residual BPA content in hydroponic culture group of water and root activity is presented in Fig. 1. To keep four concentrations of BPA (1.5, 5, 10 and 20 mg L⁻¹) over the exposure phase, the two inlet water concentrations of BPA were analyzed immediately (C-0 and C-2), and then 2 days later, residual BPA content was measured in seven hydroponic culture groups of water. Concentrations of BPA in seven hydroponic culture groups of water had no significant difference, respectively as compared to control (C-0/C-2). The difference between seven hydroponic culture groups and C-0/C-2 for all the BPA ranged from 2 to 7%, indicating that fluctuations were negligible. Therefore, it
can be assumed that 2 days of BPA filled water will maintain a constant water concentration of the chemical, and no further water sample collection is required. Moreover, seven hydroponic culture groups ensured optimum physiological and biochemical performance in a constant BPA concentration environment.

Plant roots are crucial for wetland plants growing in an anaerobic substrate (Kong et al. 2009). Plant roots can enhance the production of root exudates by transporting oxygen to the rhizosphere (Yang et al. 2020). Hence, root health is important for different plant species of synergistic effect toward plant growth, development, and stress tolerance. As shown in Fig. 1, the root activity showed significant
differences from 1.5 to 10 mg L\(^{-1}\) BPA concentrations, respectively, as compared to single species control (sp(A), sp(B), sp(C)). The root activity of sp(ABC-A), sp(ABC-B), and sp(ABC-C), which three plant species compositions formed sp(ABC), was significantly increased in 1.5 to 10 mg L\(^{-1}\) concentrations of BPA. This suggests that increasing plant species diversity will enhance root activity for higher synergistic effects.

**Mixed-hydroponic culture groups improve the shoots fresh and dry weight**

After 10 days of exposure to BPA, variation of the shoot fresh and dry weight of seven cultured groups of the single species seedlings is observed in Fig. 2. With increase of BPA concentration, the shoot fresh and dry weight increased first and then decreased respectively as compared to 0 mg L\(^{-1}\) BPA treatment. This phenomenon is in agreement with previous studies that BPA concentrations have a cytokinin-like effect, inducing plant cell elongation and proliferation, thereby promoting plant growth to a certain extent (Li et al. 2018a, b; Xiao et al. 2019). Concentrations of BPA even destroyed the cell’s structural integrity (Ali et al. 2016; Kim et al. 2018). The shoot fresh and dry weight showed significant differences from 1.5 to 10 mg L\(^{-1}\) BPA concentrations, respectively, as compared to single species control (sp(A), sp(B), sp(C)). Consequently, the shoot fresh and dry weight of sp(ABC-A), sp(ABC-B), and sp(ABC-C), in which three plant species compositions formed sp(ABC), were significantly increased in 1.5 to 10 mg L\(^{-1}\) concentrations of BPA. In detail, the shoot fresh and dry weight of sp(ABC-A), sp(ABC-B), and sp(ABC-C) were increased by a maximum of 11.66 and 21.21%, 7.90 and 22.01%, and 8.31 and 21.38%, respectively. This result recommends that upgrading plant species diversity will result in utilizing more pollutants for higher biomass production (Gross 2008; Foranara and Tilman 2009; Zhu et al. 2017).

**Effect on chlorophyll a and total chlorophyll content**

Chlorophyll plays a pivotal role in light capture and photosynthesis (Wang et al. 2020a, b, c; Wang et al. 2020a, b, c). It traps light energy and provides reducing power for carbon assimilation. To further explore the effect of BPA on chlorophyll, chlorophyll a and total chlorophyll content in seedling leaves are determined in Fig. 3. The chlorophyll a and total chlorophyll content were increased first and then decreased with increasing BPA concentration. Several studies have been reported on soybean and Vigna radiata chlorophyll content induced by bisphenol A (Qiu et al. 2013; Kim et al. 2018). It may be speculated that low concentration of BPA led to the hormesis phenomenon. High concentration of BPA increased the accumulation of ROS, which damaged the pigments and interfered with key enzyme in chlorophyll synthesis (Qiu et al. 2013; Jiao et al. 2015, 2017). Chlorophyll a and total chlorophyll content of sp(AB-A), sp(AC-A), sp(ABC-A), sp(AB-B), sp(ABC-B), sp(AC-C), and sp(ABC-C) were significantly higher from 1.5 to 10 mg L\(^{-1}\) BPA concentrations, as compared to single species control (sp(A), sp(B), sp(C)). Consequently, the chlorophyll a content of sp(AB-A), sp(AC-A), sp(ABC-A), sp(AB-B), sp(ABC-B), sp(AC-C), and sp(ABC-C) was increased by a maximum

![Fig. 2](image-url)
of 14.07, 13.01, 14.89, 19.44, 19.93, 15.80, and 18.95%, respectively, and total chlorophyll content was increased by a maximum of 11.39, 11.98, 11.26, 17.42, 16.98, 13.96, 13.23%, respectively. It follows that three cultured groups of sp(AB), sp(AC), and sp(ABC) were increased in chlorophyll a and total chlorophyll content. These results suggest that plant compositions improved stress tolerance and delayed chlorophyll degradation.

### Plant compositions reduced ROS accumulation and lipid peroxidation

Environmental stress can produce the reactive oxygen species (ROS), which is residual products of various categories of metabolic pathways in plant cells (Ali et al. 2017). ROS accumulation exceeds the antioxidant scavenging capacity and created oxidative stress in chloroplasts, plasma membrane, mitochondria, and peroxisomes (Biczak et al. 2017). Malonaldehyde (MDA) characterizes the oxidative damage to lipid membranes to plants (Ali et al. 2016). Figure 4 shows the endogenous levels of $O_2^-$, $H_2O_2$, ·OH, and MDA contents in all large aquatic plants exposed to different concentrations of BPA. The levels of $O_2^-$, $H_2O_2$, ·OH, and MDA contents in the leaves increased with the increase in BPA concentration. Increases in levels of ROS indicate that the presence of BPA triggered oxidative stress responses and led to adding MDA content and lipid peroxidation (Dogan et al. 2010, Wang et al. 2015; Zhang et al. 2016; Pawlowska et al. 2019). ROS may be responsible for inhibiting biomass and making chlorophyll degradation. The levels of $O_2^-$, $H_2O_2$, ·OH, and MDA contents of all single species of sp(AB), sp(AC), and sp(ABC) groups are significantly lower than single species control (sp(A), sp(B), sp(C)), respectively, from 5 to 10 mg L$^{-1}$ BPA exposure. Compared to sp(A), sp(B), sp(C), the $O_2^-$, $H_2O_2$, and ·OH levels and MDA contents of sp(AB-A), sp(AB-B), sp(AC-A), sp(AC-C), sp(ABC-A), sp(ABC-B), and sp(ABC-C) were remarkably decreased in 5 to 10 mg L$^{-1}$ BPA. In summary, the levels of $O_2^-$, $H_2O_2$, ·OH, and MDA contents were all relieved stress in sp(AB), sp(AC), and sp(ABC) group. For example, the levels of $O_2^-$, $H_2O_2$, ·OH, and MDA contents of sp(AB-A) and sp(AB-B), which make up sp(AB), were reduced by a maximum of 13.69, 28.16, 8.66, and 6.21% and 10.83, 29.22, 13.33, and 6.13%, respectively. The levels of $O_2^-$, $H_2O_2$, ·OH, and MDA contents of sp(ABC-A) and sp(ABC-B) and sp(ABC-C), which make up sp(ABC), were reduced by a maximum of 14.90, 28.18, 10.56, and 7.19%; 11.36, 36.68, 14.10, and 7.18%; and 10.39, 27.69, 12.92, and 4.37%, respectively. It indicates that levels of $O_2^-$, $H_2O_2$, ·OH, and MDA contents were relaxed and relieved stress by mixed-hydroponic culture groups. It is well known that ROS (especially ·OH) participate in the degradation of BPA and decrease BPA (Wang and Lim 2011; Reis et al. 2014). In some certain conditions, ROS can be converted to each other (Mattila et al. 2015). Hence, this relieved phenomenon was probably correlated with the production of ROS (especially ·OH) by biological Fenton reaction, Haber–Weiss reactions, and antioxidant enzyme reaction (Halliwell 1999; Reis and Sakakibara 2012).
Observed effects were reported by previous studies (Wang et al. 2015; Inagaki et al. 2016; Zhang et al. 2018).

**Effect of BPA on antioxidant enzymes activities**

To defend plant organisms from oxidative stress, plants have an antioxidant defense mechanism that can scavenge ROS in cells (Xiao et al. 2020). The production and cleanup of ROS exists in homeostasis in vivo, and the excessive ROS can damage the plant organism (Czarnocka and Karpinski 2018). Hence, antioxidant enzymes play a key role in clearing up excess ROS or changing them, which include SOD, POD, and CAT. Protecting cells from $O_2^-$ toxicity, SOD catalyzes the disproportionation of $O_2^-$ to $O_2$ and $H_2O_2$. $H_2O_2$ is further converted to non-toxic oxygen and water by CAT and POD (Xu et al. 2008). In order to investigate the response of all large aquatic plants to BPA stress, the activities of SOD, POD, and CAT in leaves were measured (Fig. 5). It was
found that SOD, POD, and CAT activities were increased after BPA exposure. This result indicated that BPA stress induced enhanced antioxidant enzyme activities, which effectively eliminated ROS to protect normal physiological functions of the plant. In comparison to single species control (sp(A), sp(B), sp(C)), the SOD, POD, and CAT activities of all single species of sp(AB), sp(AC), sp(BC), and sp(ABC) groups were significantly increased after 10 days of 5 mg L\(^{-1}\) and 10 mg L\(^{-1}\) BPA exposure. For example, the SOD, POD, and CAT activities of sp(AB-A) and sp(AB-B), which formed sp(AB), were significantly increased by a maximum of 13.63 and 14.35\%, 32.68 and 28.00\%, and 31.03 and 71.98\%, compared with single species control (sp(A), sp(B)), respectively. Meanwhile, the SOD, POD, and CAT activities of sp(ABC-A), sp(ABC-B), and sp(ABC-C), in which three plant species compositions formed sp(ABC), were significantly increased by a maximum of 12.91, 13.72, and 40.16\%; 36.08, 29.57, and 45.21\%; and 34.53, 64.01, and 77.22\%, compared to single species control (sp(A), sp(B), sp(C)), respectively. These observations suggest that SOD, POD, and CAT activities were further enhanced by mixed-hydroponic culture groups. This result indicated that antioxidant enzyme activities further effectively eliminated ROS to increase biomass and inhibit chlorophyll degradation by mixed-hydroponic culture groups.

**Effects of BPA on the content of antioxidant substances**

Ascorbic acid (AsA) has antioxidant functions, which is an effective scavenger for hydroxyl radicals and superoxide (Li et al. 2020). Glutathione (GSH) is a key antioxidant copiously distributed in plants and animals (Ma et al. 2019; Ahammed et al. 2020a, b). GSH is a low-molecular-weight thiol, which can directly remove ROS (Geu-Flores et al. 2011). At the same time, GSH is also involved in the detoxification of xenobiotics (Ahammed et al. 2020a, b). Free proline (Pro) regulates cell membrane osmosis and responses to salinity, drought, and other osmotic environmental stresses (Stein et al. 2011). Figure 6 depicts the effects of BPA on antioxidant substances in all large aquatic plant leaves. With the increase in concentration of BPA, the ASA, GSH,
and Pro contents were increased in leaves. This result indicated that BPA stress induced an increase in antioxidant substance contents, which effectively eliminated ROS and reduced BPA contents and mediated osmotic adjustment in leaves. The ASA, GSH, and Pro contents of the single species of sp(AB), sp(AC), sp(BC) (without GSH), and sp(ABC) cultured groups were significantly increased from 5 to 10 mg L\(^{-1}\) BPA, as compared to single species control (sp(A), sp(B), sp(C)), respectively. For example, the ASA, GSH, and Pro contents of sp(AB-A) and sp(AB-B), which formed sp(AB), were significantly increased by a maximum of 44.09 and 54.35%, 16.43 and 13.11%, and 24.43 and 76.22%, compared with single species control (sp(A), sp(B)), respectively. Meanwhile, the ASA, GSH, and Pro contents of sp(ABC-A), sp(ABC-B), and sp(ABC-C), in which three plant species compositions formed sp(ABC), were significantly increased by a maximum of 54.12, 53.89, and 40.52%; 16.03, 15.07, and 12.53%; and 28.16, 73.67, and 50.99%, compared to single species control (sp(A), sp(B), sp(C)), respectively. These observations indicated that the ASA, GSH, and Pro contents were further enhanced by mixed-hydroponic culture groups. These results suggest that antioxidant substance contents further effectively eliminated ROS-reduced BPA contents and mediated osmotic adjustment for protecting normal physiological functions by mixed-hydroponic culture groups.

**Effect of BPA dosage on detoxification enzyme activity**

NADPH-cytochrome P450 reductase (CPR) is part of cytochrome P450s system, which transfers the reduced xenobiotics from NADPH to the cytochrome P450 (Chen et al. 2021). Glutathione S-transferase (GST) and glycosyltransferase (GT) catalyzed conjugation of toxicants with GSH and sugar, respectively, and the complex was further delivered to sub-cellular apartment for catabolism (Zhang et al. 2017; Chen et al. 2021). Figure 7 illustrates the effects of BPA dosage on CPR, GST, and GT activities and BPA contents in seven cultured groups of the single species seedlings leaves. Previous
studies show that BPA catalyzed the hydroxylation, epoxidation by cytochrome P450s system in phase I (Hamada et al. 2002; Sasaki et al. 2005; Gabriel et al. 2007). In phase II, BPA or BPA-hydroxylated was catalyzed synthesis reactions with GSH and sugar by GST and GT (Nakajima et al. 2002, 2004; Kanwar et al. 2020). Hence, the activities of CPR, GST, GT, and BPA contents in leaves were increased with increasing BPA dosage, implying that BPA-degraded and residual BPA content were closely related to the enhanced plant detoxification of the enzymes. The CPR, GST, and GT activities of all the single species of sp(AB), sp(AC), sp(BC) (only in 1.5 mg L⁻¹ BPA) and sp(ABC) cultured groups were significantly increased from 1.5 to 10 mg L⁻¹ BPA, respectively, as compared to single species control (sp(A), sp(B), sp(C)), respectively. For example, the CPR, GST, and GT activities of sp(AB-A) and sp(AB-B), which formed sp(AB), were
significantly increased by a maximum of 34.32 and 59.16%, 22.88 and 15.66%, and 65.51 and 55.79%, compared with single species control (sp(A), sp(B)), respectively. Meanwhile, the CPR, GST, and GT activities of sp(ABC-A), sp(ABC-B), and sp(ABC-C), in which three plant species compositions formed sp(ABC), were significantly increased by a maximum of 35.39, 75.38, and 74.98%; 21.55, 16.04, and 33.41%; and 69.47, 64.73, and 53.40%, compared to single species control, respectively.

We also measured BPA contents in leaves. The BPA contents of all the single species of sp(AB), sp(AC), and sp(ABC) cultured groups significantly decreased from 1.5 to 10 mg L⁻¹ BPA, respectively, as compared to single species control (sp(A), sp(B), sp(C)), respectively. For example, the sp(AB-A), sp(AB-B), sp(AC-A), sp(AC-C), sp(ABC-A), sp(ABC-B), and sp(ABC-C), which formed sp(AB), sp(AC), and sp(ABC) cultured groups, were significantly decreased by a maximum of 28.38, 12.61, 25.82, 24.14, 33.30, 15.20, and 30.33%, compared with single species control (sp(A), sp(B)), respectively. These results suggest that BPA contents were further effectively reduced by mixed-hydroponic culture groups in leaves.

Conclusions

In conclusion, we found that BPA can be harmful to *Phragmites australis* (A), *Typha latifolia* (B), and *Arundo donax* (C) through the induction oxidative stress in leaves, which eventually inhibited biomass production and chlorophyll content. However, the mixed-hydroponic cultures (sp(AB), sp(ABC)) alleviate toxicological effects of BPA. This conclusion is supported by a proposed model depicting the plant species compositions (Fig. 8). Firstly, BPA contents were further reduced by biotransformation and degradation of detoxification enzymes and biological Fenton reaction in the mixed-hydroponic cultures (sp(AB), sp(ABC)). BPA-induced oxidative stress ability was severely weakened. Secondly, ROS levels which were produced by oxidative stress of BPA were further lowered by antioxidant enzymes and antioxidant substance content in the mixed-hydroponic cultures (sp(AB), sp(ABC)). Thirdly, root activity, biomass production reduction, and chlorophyll degradation were relieved due to the reduction of ROS levels in the mixed-hydroponic cultures (sp(AB), sp(ABC)). These results have already illustrated that reasonable plant richness and sort play a vital part in alleviating BPA stress. This study gives valuable data on how to create artificial floating island and constructed wetland with tall working BPA expulsion.

Author contribution All the authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Xianguang Nie. The first draft of the manuscript was written by Xianguang Nie; all the authors commented on previous versions of the manuscript. All the authors read and approved the final manuscript.

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Data availability The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate Not applicable.

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