

Research Article

Pontederia crassipes invasiveness on Jeju island is linked to a decline in water pH and climate change-driven overwintering

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Abstract

Freshwater ecosystems are vulnerable to the invasion of exotic aquatic plant species because of the great likelihood of the introduction of exotic species, and the lack of barriers that block introduced species. Water hyacinth, *Pontederia crassipes* Mart., is one of the world's most invasive alien plant species damaging freshwater ecosystems worldwide. Here, we monitored the water hyacinth population on Jeju island, Korea, to assess current invasion risks. Furthermore, we investigated how water hyacinth affects water pH because pH is an important determinant of the distribution of other aquatic plants, and thus a good indicator of aquatic ecosystem health. Water containing water hyacinth had a pH of 5.3, while that with water hyacinth and soil had a pH of 4.8 72 hours after the start of the experiment. Water hyacinth extracts contained shikimic acid, stearic acid, and palmitic acid, which are possible compounds that caused a decline in water pH. Water hyacinth also inhibited the growth of the aquatic plant species, *Spirodela polyrhiza* and *Lemna perpusilla*. These results imply that invasion of water hyacinth adversely impacts the abiotic and biotic characteristics of aquatic ecosystems. Moreover, monitoring the water hyacinth population suggests that this invasive aquatic plant overwinters on Jeju island. Therefore, regular monitoring and subsequent control of water hyacinth population can prevent its expansion in the aquatic habitats of Jeju island and the southern region of the Korean peninsula.



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Key words: water hyacinth, water pH, climate change, overwintering

Introduction

Freshwater ecosystems across the world are threatened by human activities, such as excessive use of water resources, intensive agriculture, urbanization, water pollution, hydrological changes, and exotic species invasion (Dudgeon et al. 2005; Ormerod et al. 2010; Carpenter et al. 2011; Gozlan et al. 2019). Several invasive exotic plant species colonize new invaded aquatic habitats, altering their biotic and abiotic characteristics, and threatening the ecological stability and biodiversity of

the invaded ecosystems (Zedler and Kercher 2004; Havel et al. 2015; Stiers and Triest 2017; Hassan and Nawchoo 2020). Freshwater ecosystems are more susceptible to invasive plant species than terrestrial ecosystems because of the greater likelihood of exotic species being introduced via water transportation systems, and the lack of barriers that block introduced species (Moorhouse and Macdonald 2015). Therefore, invasive plants in freshwater ecosystems should be monitored and managed to conserve biodiversity and ecosystem function.

Water hyacinth, *Pontederia crassipes* Mart. (Pontederiaceae) [Syn. *Eichhornia crassipes* (Mart.) Solms], is a free-floating aquatic plant native to the Amazon basin of South America. It is one of the world's most invasive alien plant species (Global Invasive Species Database (2022) Species profile: *Eichhornia crassipes*. In: Global Invasive Species Database <http://www.iucngisd.org/gisd/species.php?sc=70> (accessed 04-02-2022)). Water hyacinth is currently distributed in freshwater ecosystems around the world, including Europe, Asia, Africa, Australia, North, and South America, and in many tropical islands, such as Fiji, Guam, and the Solomon Islands (Bhattacharya et al. 2015). Water hyacinth is widespread in tropical and subtropical freshwaters eutrophicated by agricultural or household wastewater and is persistent despite efforts to control it.

Water hyacinth changes the ecological function and economics of the invaded freshwater ecosystem (Villamagna and Murphy 2010; Patel 2012). Water hyacinth grows rapidly and its ability to reproduce vegetatively through stolons enables it to outcompete native aquatic plants by forming dense mats on the water surface (Bhattacharya et al. 2015). Therefore, as water hyacinth proliferates, the diversity and abundance of native aquatic plants decrease (Lolis et al. 2020). Phytoplankton communities are also negatively affected by water hyacinth invasion (Villamagna and Murphy 2010). Furthermore, the disturbance in primary producer communities by water hyacinth affects the fauna of the ecosystem. The responses of fauna to water hyacinth invasion vary depending on geological location and species composition (Villamagna and Murphy 2010). Because the population of water hyacinth is structurally and functionally different from that of native aquatic plant communities, invertebrates, and fish habitats are altered (McVea and Boyd 1975; Toft et al. 2003; Kateregga and Sterner 2009). Changes in fish communities brought about by extensive formation of water hyacinth mats hinder the fisheries industry and water transportation systems and thereby threaten local livelihoods (De Groote et al. 2003; Kateregga and Sterner 2009; Waithaka 2013; Asmare 2017; Segbefia et al. 2019). Therefore, the invasion of water hyacinth creates not only ecological damage but also socio-economic problems.

We monitored the water hyacinth population on Jeju Island, South Korea, and asked whether this invasive plant could overwinter on the island. Water hyacinth originated from the Amazon basin (Patel 2012), which has an average annual temperature of 25 to 28°C (USAID (2018) Climate Risk Profile: Amazon Basin); thus it cannot tolerate the cold winter of temperate countries. The leaves of water hyacinth die with one overnight freeze, and the plant cannot regrow with 3 weeks of continuous freezing temperature or 4 weeks of near-freezing temperature (5°C) (Owens and Madsen 1995). Therefore, water hyacinth, which is a perennial plant in its native habitat, becomes an annual plant in cold temperate habitats, including Korea. However, global warming caused by climate change could make water hyacinth overwinter in places where it typically could not. Modeling studies predicted that climate change may create opportunities for the introduction and expansion of invasive species (Rahel and Olden 2008; Chapman et al. 2016; Shrestha et al. 2018; Thapa et al. 2018). For instance, Netten et al. (2010) predicted that invasive free-floating plants could thrive more with the loss of submerged plants if global warming worsens. The

distribution of water hyacinth may expand poleward if current climate change trends continue (Kriticos and Brunel 2016) as winter temperature will increase.

It is critical to understand the invasion mechanism of water hyacinth and its effects on the environment to design effective water hyacinth control strategies. Previously, the effects of the water hyacinth population on water quality were studied at various geological locations. Such studies report changes in dissolved oxygen (DO), carbon dioxide concentration, transparency, and nutrient concentration in the water, where water hyacinth grew (Rommens et al. 2003; Mangas-Ramírez and Elías-Gutiérrez 2004). In this study, we focused on the effects of water hyacinth on water pH because it is an important determinant of aquatic plant distribution (Farmer 1990; Vestergaard and Sand-Jensen 2000; Chmara et al. 2015). Each aquatic plant species has an optimal pH for its survival and growth. If the pH of the water is affected by a dense mat of water hyacinth, native aquatic plant communities are disturbed. Therefore, we investigated whether the water hyacinth population reduces water pH in the laboratory. After confirming that the water hyacinth reduces water pH, we performed the experiment to determine the mechanism by which water hyacinth causes lower water pH and how this affects other aquatic plant species.

We established the following three hypotheses that could explain the pH reduction in water with water hyacinth: 1) water hyacinth has symbiotic microorganisms that decrease water pH, 2) water hyacinth secretes specific compounds that decrease water pH, and 3) respiration of water hyacinth and blockage of the water surface by air increases the concentration of CO₂ in the water (Ultsch and Anthony 1973; Akinbile and Yusoff 2012). We conducted detailed experiments in the laboratory to test these hypotheses. Soil was added to provide nutrition and microorganisms to the water to test the first hypothesis. The chemical composition of water hyacinth and CO₂ concentration of the water was analyzed to test the second and the third hypotheses, respectively.

The rapid decrease in water pH by water hyacinth could disturb aquatic plant communities because each aquatic plant species has an optimal range of water pH. Indeed, acidification of freshwater results in alteration of aquatic plant communities (Farmer 1990; Arts 2002). However, most studies focused on the allelopathic effects of invasive free-floating plants or the effect of oxygen blockage by plant mats (Kriticos and Brunel 2016; Villamar et al. 2018). Only a few studies probe into the effects of water pH on aquatic plants (Schuurkes et al. 1986). Therefore, we investigated whether the decreased water pH caused by water hyacinth inhibits the growth of other free-floating plants, such as *Spirodela polyrhiza*, and *Lemna perpusilla*. Both species are common free-floating plants in Korea and could be strongly affected by the rapid decrease of water pH caused by water hyacinth.

Materials and methods

Preliminary test

A previous rooftop greening study suggests that the pH of rooftop ponds declines when water hyacinth is present (Kim 2021). Therefore, a preliminary test to confirm the effects of water hyacinth on water pH was conducted. Pots (40 × 50 × 30 cm) were placed on a building's roof and filled with water at a volume of 45 liters and a depth of 25 cm. Three water hyacinth plants with an average fresh weight of 330 g were grown in each pot. Three replicates were established for control and water hyacinth treatment. The pH of water in the pots was measured at 1, 3, and 7 days after the start of the experiment with an Orion Star A329 portable multiparameter instrument (Thermo Fisher Scientific, MA, USA).

Evaluating the effects of water hyacinth on water pH

A plastic bucket (height 30 cm, upper diameter 28 cm, and lower diameter 23 cm) was filled with 10 L of tap water. Six treatments were established: Water only (W), Water + Plant (WP), Water + Soil (WS), Water + Soil + Plant (WSP), Water + Plant + sterilizing UV (WPUV), and Water + Soil + Plant + sterilizing UV (WSPUV). Each treatment had five replications. The plant treatment had three water hyacinth plants (total weight 300 ± 30 g) in the bucket. Water hyacinth was not cut because of the concern that fluid would flow out from the stem cross-sections and alter pH of water. Therefore, the initial weight of the plants varied slightly at the start of the experiment. A commercial light-emitting diode (LED) [Grinmax, Korea], bar-type lamp (50 cm in length with two red LEDs, and one blue LED chip located at every 5 cm, 7.2 W) was installed to provide the light required for plant growth. Six LED bars were used for every 0.66-m^2 area of the growth room. The observed photosynthetically active radiation was $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-2}$. The soil treatment consisted of a 2-cm thick layer of commercial bed soil typically used for paddy rice (Sinki, Chungyang, Korea). The sterilizing UV treatment had an aquarium ultraviolet (UV) lamp (UVC-307, 254 nm wavelength; Coospider, Jinyun, China) to sterilize microorganisms in the soil. The temperature of the growth room was maintained at 25°C .

The change of pH was measured every 24 hours for 7 days with an Orion Star A329 portable multiparameter instrument (Thermo Fisher Scientific, MA, USA). The concentration of CO_2 was measured at 0, 12, 24, and 48 hours after the start of the experiment using a dissolved carbon dioxide kit (Sechang Instruments, Seoul, Korea).

Investigating the effects of water hyacinth on other free-floating aquatic plants in the laboratory

The effects of water hyacinth on native aquatic plants were studied using two native free-floating plant species, *Spirodela polyrhiza* (Linnaeus, 1758) and *Lemna perpusilla* (Torrey, 1843). Water only (W), Water + Plant (WP), Water + Soil (WS), and Water + Soil + Plant (WSP) treatments were prepared with the same method described above. Each treatment had five replications. Ten *S. polyrhiza* and 10 *L. perpusilla* plants were placed in each plastic bucket for each treatment. Because roots are prone to damage during measurements, the initial weight of the two native aquatic plant species was not taken. After 6 weeks of growth, *S. polyrhiza* and *L. perpusilla* were harvested separately, and the number of individuals and total plant fresh weight was obtained. The conditions of the experiment were the same as in the previous pH experiment.

Preparation of water hyacinth for chemical analysis

We analyzed the extracts of water hyacinth to figure out the substance for the water pH reduction. Homogenized water hyacinth samples (20 mg) were transferred to 2 mL microcentrifuge round bottom screw cap tubes (Eppendorf). Pre-cooled (-20°C) 1400 μL of 80% High Performance Liquid Chromatography (HPLC)-grade methanol (J.T. Baker Chemical Co., Phillipsburg) was added and vortexed for 10 s. Then, 60 μL D-Sorbitol- $1\text{-}^{13}\text{C}$ (0.2 mg mL^{-1} stock in dH_2O) was added as an internal quantitative standard and vortexed for another 10 s. After shaking for 10 min (950 rpm) in a thermomixer at 70°C , samples were centrifuged for 10 min at 11,000 g . Supernatants were transferred to glass vials and pre-cooled (-20°C) 750 μL chloroform and 1500 μL dH_2O (4°C) were added sequentially prior to vortexing for 10 s. Chloroform,

D-sorbitol-1-¹³C, pyridine, methoxyamine hydrochloride, and *N*-Methyl-*N*-(trimethylsilyl) trifluoroacetamide (MASTFA) were obtained from Sigma Aldrich.

After the samples were centrifuged for 15 min at 2,200 g, the upper polar phase consisting of 150 μ L for each sample, was transferred into a fresh 1.5 mL tube and dried in a vacuum concentrator (EYELA, CVE-2000) without heating. Then, 40 μ L of methoxyamination reagent (methoxyamine hydrochloride 10 mg mL⁻¹ in pyridine) was added to the dried samples and incubated for 2 h in a thermomixer (950 rpm) at 37°C. Next, 70 μ L of *N*-Trimethylsilyl-*N*-methyl trifluoroacetamide (MSTFA) reagent was added followed by 30 min of shaking at 37°C. Finally, derivatized samples (110 μ L) were transferred into glass amber vials suitable for GC/MS analysis (Lisec et al. 2006; Cadahia et al. 2015; Lavergne et al. 2018). Five samples were extracted and analyzed.

GC/Quadrupole-MS analysis and data acquisition

The derivatized extracts were injected into a DB5-MS (30 m, 0.25 mm ID, 0.25 μ m film thickness, Agilent) for a capillary column using a gas chromatograph apparatus (Agilent, 6890N GC) equipped with a single quadrupole mass spectrometer (Agilent, 5973 inert MSD) with an autosampler (Agilent, 7683B). Injector and source were set at 280°C and 230°C, respectively. The initial temperature of the oven was set to 70°C for 5 min and the maximum temperature was 325°C. The sample (1 μ L) was injected in splitless mode with a helium flow rate of 1 mL min⁻¹. Mass spectra were recorded in electronic impact mode at 70 eV and scanned at the 40–600 *m/z* range at a rate of 0.2 s. The mass spectrometric solvent delay was set at 8 min. Alkanes, controls (without plant material), and the blank were injected at scheduled intervals to test instrument performance, tentatively identify metabolites, and monitor shifts in retention time (Lisec et al. 2006; Cadahia et al. 2015; Lavergne et al. 2018). Raw data files (.D format) of the compounds were identified based on National Institute of Standards and Technology (NIST) libraries using Automated Mass Spectral Deconvolution and Identification System (AMDIS) (www.amdis.net) and NIST Mass Spectral Search Program (ver. 2.0).

Investigation of water hyacinth overwintering

We first monitored presence (invasion) of water hyacinth on water reserves on Jeju island in March of 2020. The geographic coordinates of the investigated sites are listed in Table 1. Then two wetlands (YR and SSR) where water hyacinth were

Table 1. List of field investigation sites.

Site	<i>Pontederia crassipes</i>	Coordinates
Yunnam Pond (YN)		33°28'6.89"N, 126°22'6.16"E
Sineom-ri (SS)		33°27'30.90"N, 126°21'59.77"E
Haga Pond (HG)		33°27'17.22"N, 126°20'50.47"E
Yerae (YR)	°	33°14'38.25"N, 126°23'29.27"E
Gwangnyeong (GY)		33°28'16.07"N, 126°25'37.15"E
Susan Reservoir (SSR)	°	33°28'13.09"N, 126°23'17.71"E
Gueom-ri (UFO)		33°29'05.97"N, 126°22'56.95"E

* * *Pontederia crassipes* was discovered at YR (March 2020, January and March 2021 and June 2022) and SSR (March 2020, January, March, July and October 2021 and March and June 2022). *P. crassipes* were found in both sites in our last field monitoring in June 2022.

found were monitored again in 2021 and 2022 to check overwintering of water hyacinth (January and March 2021 and June 2022 for YR and January, March, July and October 2021 and March and June 2022 for SSR). We checked the presence of water hyacinth and rough estimation of a number of individuals.

Statistical analysis

The difference between the two groups (preliminary field test, water hyacinth treatment and control) was evaluated by Student's t-test using the SAS 9.3 program (SAS Institute Inc., USA). Differences between multiple groups (the detailed experiments for the effects of water hyacinth on water pH, five treatments and control; the experiment for the effects of water hyacinth on other aquatic plants, three treatments and control) were evaluated by one-way ANOVA and followed by post hoc comparisons of the means by Tukey's honestly significant difference test.

Results and discussion

Preliminary field test

The water pH of the pot with water hyacinth significantly decreased to under 5 after 3 days. Low water pH was maintained until the end of the experiment (Figure 1). Unlike the pot with water hyacinth, the pot with water only had a stable pH of around 7. This data suggested that water pH could decrease in wetlands inhabited by water hyacinth. The temperature of the water at noon was 33°C and 35°C in the pot with water hyacinth and water only, respectively. Generally, the pH of water decreases as temperature increases. Therefore, temperature is not the reason for the observed pH difference between water with plants and water without plants.

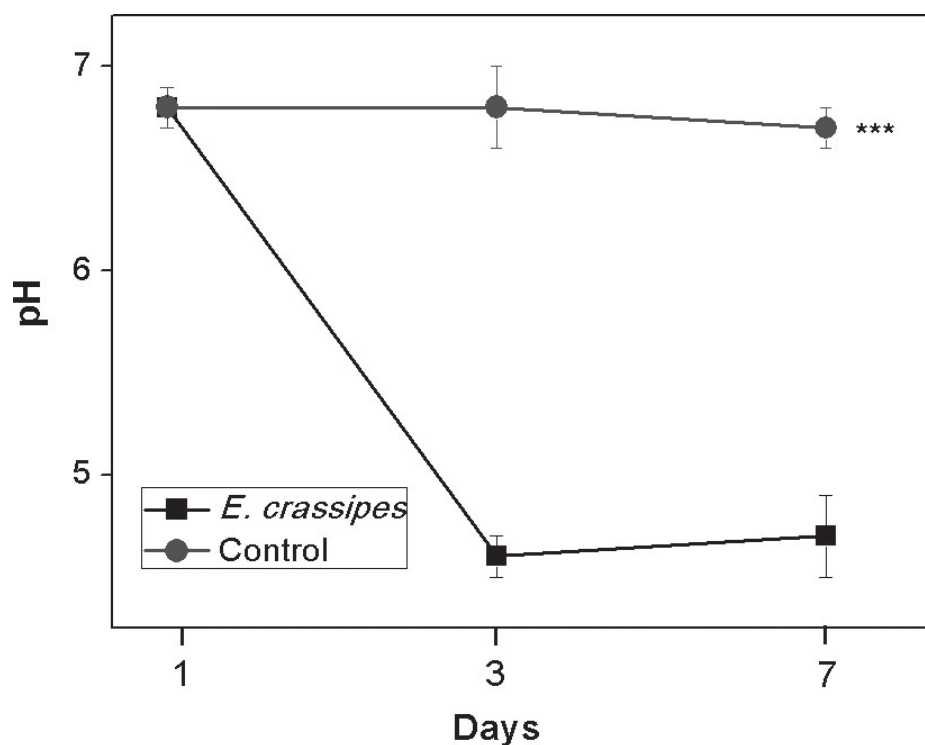


Figure 1. Preliminary experiment evaluating the effects of water hyacinth on water pH. Symbols and error bars represent means \pm S.E of five replicates. (***: $P < 0.001$).

Effects of water hyacinth on water pH

The water pH of the treatment groups rapidly decreased in the first 24 hours of the experiment, and the differences in water pH among various treatment groups became evident 72 hours later. After 72 hours, water pH of the treatment groups stabilized. Water with plants had lower pH than that of water without plants 7 days later (WS > WSP and W > WP, Figure 2). This result confirmed that the presence of water hyacinth reduces water pH.

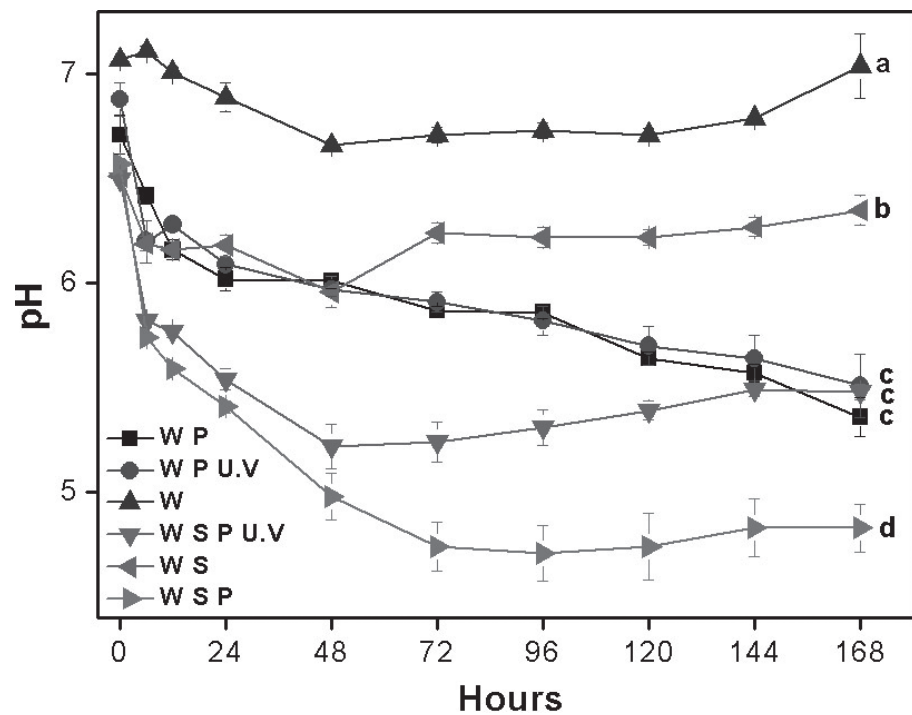


Figure 2. Time course of changes in water pH under various treatment combinations of plant, soil and UV light. Symbols and error bars represent means \pm S.E of five replicates. Symbols with different lowercase letters indicate significant differences ($p < 0.05$). W: Water only, WP: Water + Plant, WP UV: Water + Plant + UV light, WS: Water + Soil, WSP: Water + Soil + Plant, WSP UV: Water + Soil + Plant + UV light.

Soil treatments also decreased water pH. The WSP group had a significantly lower pH than that of the WP group (Figure 2), and the WS group had a significantly lower pH than that of the control (Figure 2). However, the WP group had lower pH than that of the WS group (Figure 2), implying that the effects of soil on water pH were smaller than those of the water hyacinth treatments. UV treatments only increased the pH of the group that included soil treatment. For example, WSPUV groups had a higher pH than that of WSP, whereas WPUV and WP groups had similar pH (Figure 2). This result indicates that soil-borne microorganisms are the reason for pH reduction in the groups that included soil treatments.

The decrease of water pH in the water hyacinth treatment groups did not result from the high CO_2 concentration caused by plant respiration. The control and all the treatment groups had CO_2 concentrations of under 10 ppm, which was the measurement limit of the sensor. The average alkalinity of tap water in Korea is around 55 mg/L (Korea Water Resources Corporation (2023) My water portal - Real-time Water Quality Monitoring System. In: Korea Water Resources Corporation <https://www.water.or.kr/kor/realtime/sangsudo/index.do?mode=rin->

fo&menuId=13_91_107_108 (accessed July 06, 2022)). According to Wurts and Durborow (1992), when the temperature of the water is 25°C, pH is 7, alkalinity is 55 mg/L, and the estimate of CO₂ concentration of water is 10.63 ppm. Therefore, even if there were differences in CO₂ concentration between the control and the treatment groups, 10 ppm CO₂ is not enough to decrease water pH to under 5. Previously, Ultsch and Anthony (1973) reported that CO₂ concentration in water ponds with mature water hyacinth mats was 50–60 ppm, which is higher than the results of this study. On the other hand, ponds with immature water hyacinth mats had a similar CO₂ concentration to that of open water. Therefore, the decomposition of dead water hyacinth leaves contributed more to the high water CO₂ concentration with mature mats. Our laboratory experiment setting had a relatively short time for water hyacinth to form a dense mat and have dead leaves.

Water hyacinth reduced water pH despite the addition of soil or UV treatment. Furthermore, water hyacinth-triggered reduction in water pH occurred in 24 hours and reached the lowest value in 2 to 3 days, which suggested that exudates that lowered the pH were secreted from water hyacinth roots. We therefore analyzed water hyacinth extracts to determine compounds responsible for water pH reduction. Water hyacinth extracts were mainly composed of sucrose, shikimic acid, tagatose, stearic acid, fructose, palmitic acid, galactose, and glycerol (Table 2). The most abundant compound was sucrose, which accounted for more than 80% of the extracts. The most likely metabolites that cause water pH reduction were shikimic acid, stearic acid, and palmitic acid, which accounted for 6.5%, 2.5%, and 2.0% of the extracts, respectively. Shikimic acid is an important precursor in biosynthetic processes that produce aromatic amino acids, folic acid, and a variety of other aromatic chemicals (Bochkov et al. 2012). Water hyacinth is a promising source of shikimic acid. Therefore, several studies have attempted to extract shikimic acid from the water hyacinth (Lenora et al. 2016; Ganorkar et al. 2022a; Ganorkar et al. 2022b). Shikimic acid, stearic acid, and palmitic acid have a pKa value of around 4 (National Center for Biotechnology Information (2023) PubChem Compound Summary for CID 985, Palmitic Acid. In: National Center for Biotechnology Information. <https://pubchem.ncbi.nlm.nih.gov/compound/Palmitic-Acid> (accessed June 26, 2023); National Center for Biotechnology Information (2023) PubChem Compound Summary for CID 5281, Stearic Acid. In: National Center for Biotechnology Information. <https://pubchem.ncbi.nlm.nih.gov/compound/Stearic-Acid> (accessed June 26, 2023); National Center for Biotechnology Information (2023) PubChem Compound Summary for CID 8742, Shikimic acid. In: National Center for Biotechnology Information. <https://pubchem.ncbi.nlm.nih.gov/compound/Shikimic-acid> (accessed June 26, 2023)), and therefore could acidify the water. Although shikimic acid in water hyacinth is

Table 2. The peak area of compounds detected in water hyacinth extracts.

Compound	Peak area
Sucrose	83.343 ± 6.154
Shikimic acid	6.601 ± 1.554
Tagatose	4.104 ± 0.233
Stearic acid	2.562 ± 0.249
Fructose	2.066 ± 0.114
Palmitic acid	1.722 ± 0.159
D-(+)-Galactose	0.87 ± 0.136
Glycerol	0.382 ± 0.037

Values represent the mean ± SE of five replicates.

not higher than that of other plant species (Bochkov et al. 2012), the continuous release of this compound could be sufficient to acidify the water. However, our experiments were not able to determine if shikimic acid was secreted by water hyacinth roots because we could not analyze the water that water hyacinth inhabited.

The reduction in water pH by water hyacinth could contribute to its proliferation as a noxious invasive plant by blocking the growth of other aquatic plant species. Recently, a paper has reported similar results that pH level of water where water hyacinth grows showed lower pH value compared to open water areas (Kiyemba et al. 2023). As this paper is reporting field case where the lake is over 60km², the pH altering effects can be stronger in our indoor experiments. Also, this paper implies that such effects can actually occur in other fields in other countries. There are several reports on the allelopathic effects of secreted water hyacinth chemicals, such as loliolide, on other plant species (Kato-Noguchi et al. 2014), microorganisms, and green algae (Shanab et al. 2010). However, loliolide was not detected in our analysis of water hyacinth extracts. The absence of loliolide in our samples could be due to differences in extraction methods or plant environmental conditions (Kong et al. 2002).

The effects of water hyacinth on other free-floating plants in the laboratory

Both free-floating plant species (*Spirodela polyrhiza* and *Lemna perpusilla*) were strongly affected when co-cultured with water hyacinth (Table 3). The number of *S. polyrhiza* increased by more than 10-fold, and the number of *L. perpusilla* increased by 38-fold in the WS treatment. The total biomass of the two free-floating plant species also increased, which corresponded to the increased number of plants. However, plant number of the two species in the WSP treatment was half of that of the WS treatment. The difference in total biomass between the WSP and WS treatment was even larger, showing one-fifth for *S. polyrhiza* and one-tenth for *L. perpusilla*. This result provided evidence that water hyacinth inhibits the growth of other free-floating plants. The water pH for this particular experiment was not measured because of miscommunication among members of the investigation team. The parameters for this experiment were identical to those of the water pH experiments described above, except for the presence of *S. polyrhiza* or *L. perpusilla*, which had relatively small biomass. The maximum fresh weight of *S. polyrhiza* and *L. perpusilla* was 5.3 g and 1.94 g, respectively, while that of water hyacinth was about 300 g. Therefore, it was assumed that the water pH of this experiment was similar to that of the previous water pH experiments. Both the species did not grow well in the treatment without soil (W and WP) because of the lack of water nutrients (Table 3).

Table 3. Harvested number of plants and biomass of *Spirodela polyrhiza* and *Lemna perpusilla* grown with *Pontederia crassipes* for 6 weeks.

Species	<i>Spirodela polyrhiza</i>		<i>Lemna perpusilla</i>	
	Number	Weight	Number	Weight
W	5.2 ± 0.2 ^b	0.1 ± 0.0 ^b	24.2 ± 3.1 ^b	0.02 ± 0.01 ^b
W P	12.8 ± 3.1 ^b	0.1 ± 0.0 ^b	25.8 ± 8.3 ^b	0.03 ± 0.01 ^b
W S	108.6 ± 16.8 ^a	5.3 ± 1.5 ^a	377.6 ± 64.1 ^a	1.94 ± 0.41 ^a
W S P	67.2 ± 25.5 ^{ab}	0.9 ± 0.3 ^b	116.2 ± 36.7 ^{ab}	0.18 ± 0.04 ^b

Values represent the mean ± SE of five replicates.

Different lowercase letters within a column indicate significant differences ($p < 0.05$).

W: Water only, W P: Water + Plant, W S: Water + Soil, W S P: Water + Soil + Plant

Results confirmed that the reduction in water pH caused by water hyacinth could affect the growth of other aquatic plant species. Many studies report on the impacts of water hyacinth on the abiotic and biotic environments (Villamagna and Murphy 2010; Patel 2012; Wang and Yan 2017; Degaga 2018). Water hyacinth decreases light intensity beneath its dense mat (Rommens et al. 2003), reduces dissolved oxygen (McVea and Boyd 1975; Rommens et al. 2003; Mironga et al. 2012), increases CO₂ concentration in water (Rommens et al. 2003; Mironga et al. 2012), and changes nutrient levels in the water (Zhang et al. 2009). Therefore, the proliferation of water hyacinth disturbs native aquatic plants, phytoplankton, invertebrates, and fish communities (McVea and Boyd 1975; Toft et al. 2003; Kateregga and Sterner 2009; Villamagna and Murphy 2010; Wang and Yan 2017; Lolis et al. 2020). Here, a new mechanism that explains how water hyacinth adversely affects the aquatic plant environment is reported. The reduction of water pH could also negatively affect the aquatic animal community (Rago and Wiener 1986; Rosemond et al. 1992; Locke et al. 1994). Therefore, water hyacinth must be controlled to protect the structure and function of aquatic ecosystems.

Monitoring of overwintering water hyacinth

In this study, we found a population of water hyacinth that overwintered on Jeju island. This is the first study showing that water hyacinth overwinters in Jeju.

Seven wetlands on Jeju Island were monitored in 2020. Among the seven wetlands surveyed, water hyacinth was found in the Yerae stream (YR) and Susan Reservoir (SSR) in March 2020. Then two wetlands (YR and SSR) where water hyacinth were found were monitored again in 2021 and 2022 to monitor overwintering of water hyacinth (January and March 2021 and June 2022 for YR and January, March, July, and October 2021 and March and June 2022 for SSR). In March of 2021, the plants were small and had floating leaves and thus readily recognized as water hyacinth. A temperature above 10°C is needed for water hyacinth seeds to germinate (Tomihisa 1989). Therefore, water hyacinth seeds start to germinate in May in similar latitudes to Jeju island (Wm and Earle 1948). It takes more than 40 days from seed germination for water hyacinth to reach the size of the plant we found in March 2021 (Wm and Earle 1948). Therefore, the water hyacinth populations from YR and SSR in March 2021 were assumed to regrow from overwintered individuals, not germinated from seeds.

We investigated whether water hyacinth previously existed in YR and SSR. We confirmed that water hyacinth did not inhabit in SSR from 2014 to 2019 because SSR is a regular vegetation monitoring site of our research team. Water hyacinth first appeared in SSR in the spring of 2020 and was also found in March, July, and October 2021. Because no data is available on YR before 2020, satellite pictures from the Korea map service (Kakao map) were used to investigate the water hyacinth population in this location. According to the satellite pictures, water hyacinth was absent in YR until 2014. However, satellite images of YR streams, in which water hyacinth typically thrives, from 2015 to 2016 were not available. Water hyacinth only appeared in satellite images of YR streams in 2017 and was observed to grow continuously since then. Therefore, the water hyacinth population in YR overwintered at least since 2017.

The winter temperature of Jeju island was not cold enough to kill water hyacinth in 2020 and 2021. The average air temperature of Jeju in January was 8.9°C in 2020 and 6.8°C in 2021. Days of below freezing temperatures were 0 days in 2020 and 3 days in 2021. The mild winter and elevated water temperature of SSR and YR likely enabled water hyacinth to survive. Although water temperature of SSR in January 2020 and January 2021 was not measured, we found that it was 6.9°C on the coldest day of January 2022 when the air temperature was -2.9°C, which was the lowest temperature

recorded in the past 3 years. This observation led to the assumption that water temperature in January 2020 and 2021 was more than 6°C. YR streams have a consistent temperature throughout the year because it comes from underground spring water. The average annual temperature of spring water on Jeju Island ranges from 14°C to 18°C (Kang et al. 2018). The average temperature of Gangjeongdong (33°13'59.15"N, 126°29'56.63"E), which is another spring water-fed wetland in the southern part of Jeju island, was 13.5°C in January 2021. The water temperature of YR was assumed to be similar to this temperature. Seventy percent of water hyacinths could survive for 4 months under conditions, in which the air and water temperature is 4.8°C and 6.1°C, respectively (You et al. 2013). Moreover, all the plants could survive for 4 months, in which air and water temperature is 8 to 9°C (You et al. 2013). Water hyacinth could withstand temperatures of 0°C for 48 hours (Owens and Madsen 1995). However, from 2020 to 2022, the lowest recorded temperature on Jeju island was -3.1°C, and temperatures below zero persisted for less than 48 hours. Therefore, the winter temperature of Jeju was mild enough for water hyacinth to overwinter. In January 2022, about 20 water hyacinth individuals were found at SSR when water temperatures were measured. By June 2022, the population had increased to over 1000 individuals. This result indicates that overwintering of water hyacinth happens every year in Jeju, making the monitoring and management of this invasive species urgent.

For three decades, Jeju island could have been a habitat supporting the overwintering of water hyacinth based on past temperature records. The winter temperature of Jeju shows an increasing trend beginning in the 1960s. The average temperature increased by 1.2°C in January, 1.7°C in February, and 2.0°C in March from the 1960s to the 2010s (KMA (2021) Weather archive. Available at: <https://www.weather.go.kr/w/obs-climate/land/past-obs/obs-by-elementdo?st-n=184&yy=2020&obs=07>). The average minimum temperature in January also increased by 1.7°C from the 1960s to the 2010s. Thus, short periods of extreme cold are less likely to occur. The average January temperature of Jeju in 2020 was 8.9°C, which was the highest temperature recorded since 1961. However, water hyacinth also overwintered in 2021, when the average temperature in January 2021 (6.8°C) was similar to previous years. Therefore, it is believed that overwintering of newly introduced individuals gave rise to the current water hyacinth population in YR and SSR, which was made possible by climate change.

Conclusions

The location of Jeju island in the southern part of the Korean Peninsula makes it prone to the effects of global warming caused by climate change. Water hyacinth is expected to spread its distribution if current climate change trends continue. Moreover, because water hyacinth grows faster from the overwintered individuals after experiencing a warm winter, it could flourish more in Jeju because of upward trends in temperature. Water hyacinth caused a decrease in the water pH, which hindered the growth of other aquatic plants. Furthermore, a survey of wetlands on Jeju island revealed overwintering in water hyacinth, which could cause serious damage to aquatic ecosystems in the Korean Peninsula if climate change continues. Extensive research on how water hyacinth influences ecosystems and the development of ecologically friendly management methods are needed to minimize ecosystem damage by this noxious weed. It is likely that water hyacinth is not the only invasive plant species that overwinters in Jeju and the Korean Peninsula. As such, it is expected that the damage inflicted by invasive plant species will increase. Research on efficient monitoring systems for invasive species that could potentially overwinter in the Korean Peninsula should enable the implementation of sound aquatic ecosystem conservation strategies.

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Author contribution

Uhram Song: Conceptualization, Methodology, Investigation, Data curation, Writing - original draft, SeokHyeon Oh: Investigation, Data curation, Byoung Woo Kim: Investigation, Seonah Jeong: Investigation, Hojun Rim: Conceptualization, Methodology, Investigation, Writing - review & editing.

Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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