J. Aquat. Plant Manage. 59: 57–65

Nutrients enhance the negative impact of an invasive floating plant on water quality and a submerged macrophyte

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ABSTRACT

Submerged macrophytes are an important component to the structure and function of freshwater ecosystems. Invasive, free-floating macrophytes can adversely impact native submerged macrophytes, and these impacts can be exacerbated by anthropogenic nutrient loading. Using a mesocosm study, we examined how the invasive macrophyte, giant salvinia (*Salvinia molesta* D.S.Mitchell), affected water quality and biomass of a native submerged macrophyte, coontail (*Ceratophyllum demersum* L.), under salvinia cover treatments and nutrient additions, compared with control cover and nutrient treatments. Under high nutrients, giant salvinia growth rate was ~1.0 g dry wt d^{-1}, which was five times greater than no nutrient addition. We found as giant salvinia grew and increased surface area, dissolved oxygen, pH, specific conductance, and light availability decreased. Additionally, the rate of change for these parameters were determined by nutrient availability. Coontail biomass was negatively affected by giant salvinia under increased nutrients; however, coontail persisted to the conclusion of the study, even while being covered by a complete giant salvinia mat for 3 wk. When nutrients were not added, changes to the environment due to giant salvinia were not statistically different from control treatments. Our results demonstrate how eutrophication of waterbodies enhances salvinia growth, which amplifies the rate of environmental impact. However, the ability of coontail to persist under a vegetative mat for weeks provides a time frame to control giant salvinia, while still retaining submerged macrophytes.

Key words: *Ceratophyllum demersum*, eutrophication, freshwater wetlands, giant salvinia, invasive species, *Salvinia molesta*.

INTRODUCTION

Submerged aquatic macrophytes have an important role in the structure and function of aquatic ecosystems. The diverse leaf arrangements of the plants increase habitat complexity, supporting a range of microhabitats for macroinvertebrates (Warfe and Barmuta 2006, Fisher and Kelso 2007, Fisher et al. 2012), and the surface allows for periphyton colonization and traps organic matter; both provide resources for aquatic invertebrates (Ferreiro et al. 2013, Hao et al. 2017, Hilt et al. 2018). Waterfowl and wading birds utilize freshwater habitats and submerged macrophytes for foraging, consuming roots, shoots, and seeds from submerged macrophytes, as well as invertebrates living on the plant surface (Tapp and Webb 2015, Stafford et al. 2016, Marco-Méndez et al. 2020). Fish rely on submerged macrophytes during different stages of their life cycle, utilizing the plants to evade predators and to forage for prey (Grenouillet and Pont 2001, Stahr and Shoup 2016). In addition to supporting fauna, these plants directly modify the chemistry of the water column by releasing oxygen as a biproduct of photosynthesis. (Caraco et al. 2006, Vilas et al. 2017). Submerged macrophytes assist in nutrient cycling by uptaking and releasing organic elements from the sediment. Freshwater systems dominated by aquatic macrophytes act as a carbon sink, sequestering atmospheric carbon in the sediment (Hopkinson et al. 2012, Pattison-Williams et al. 2018, Villa and Bernal 2018). Thus, submerged macrophytes are an important resource and habitat in freshwater systems—therefore, altering their communities can be consequential for the ecosystem.

The colonization of nonindigenous, free-floating plants has negative implications for submerged macrophytes and aquatic ecosystem processes. Free-floating macrophytes create a mat of vegetation on the water surface, which limits light availability under the mat, leading to a reduction of submerged macrophytes (van Gerven et al. 2015, Coetzee and Hill 2020). Successful free-floating invasive macrophytes typically have a high rate of growth, allowing them to quickly reproduce and cover the water surface when conditions are appropriate. This abrupt ecosystem reconfiguration changes habitat complexity, altering abiotic and biotic interactions, and disrupts the flow of energy through the ecosystem (Strange et al. 2018, Motitsoe et al. 2020). Giant salvinia (*Salvinia molesta* D.S. Mitchell; hereafter referred to as salvinia), is a free-floating aquatic fern, native to Brazil, and is considered highly invasive worldwide. Stems of salvinia easily break, allowing propagules to drift by wind or water current to noninfested locations (Owens et al. 2004, Heidbüchel et al. 2020). Under ideal conditions, salvinia can double its biomass in as few as 36 to 53 h (Cary and Weerts 1983, Johnson et al. 2010) and form a mat in days (Mitchell and Tur 1975). Salvinia infestations can persist for months, even years, often requiring human

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intervention, such as chemical, mechanical, or biological control methods, to reopen waterways (Martin et al. 2018).

Nutrient additions to water bodies alter the aquatic ecosystem and can promote invasions of free-floating macrophytes. Nutrients enter water bodies by various means, such as agriculture and urban runoff, wastewater discharge, atmospheric deposition, surface flow, and floodwaters receding from floodplains, with excessive nutrients causing a water body to become eutrophic (Selman and Greenhalgh 2010, Dupas et al. 2015, Wurtsbaugh et al. 2019). The increased nutrients promote algal blooms, resulting in increased turbidity and decreased light transmission through the water, and causes large die-offs of submerged macrophytes in the littoral zone (Smith et al. 1999, Chislock et al. 2013). Invasive free-floating macrophytes pose a high risk under increased nutrient environments, causing more enhanced ecosystem impacts than from algal blooms. An increase in nutrients should enhance growing conditions for these invasive plants, resulting in a faster expansion and covering of open water, potentially increasing total impact on the aquatic ecosystem.

A mesocosm study was designed to examine the interaction between salvinia and nutrients, and its effect on water quality and a native submerged macrophyte, coontail (*Ceratophyllum demersum* L.). Coontail has a branching leaf structure with high surface area. It reproduces asexually by drifting of leaf and stem segments (Lombardo and Cooke 2003) and sexually with monoecious flowers that produce small nuts as fruit (Godfrey and Wooten 1981). Coontail lacks true roots, but instead uses modified leaves to uptake nutrients from the water column (Denny 1972, Best 1980). The objectives of this study were to: 1) determine how salvinia affects water quality, light availability, and coontail biomass following introduction; and 2) determine how nutrients affect the rate of salvinia growth and water quality changes. We assessed the objectives through weekly sampling, and examined nine different salvinia and nutrient interaction scenarios. We hypothesized that under low nutrients, salvinia growth would be limited and might not become established, and that changes in water quality would be minimal with coontail being able to maintain biomass through the duration of the study. When nutrients were added, we suspected that salvinia would thrive, reducing water quality and decreasing coontail biomass through the duration of the study, and result in a complete loss of submerged macrophyte biomass under high nutrient additions.

METHODS AND MATERIALS

Mesocosm design

A mesocosm study was conducted from May through June 2019 in a temperature-controlled greenhouse at the Louisiana State University (LSU) Agricultural Center in Baton Rouge, LA, USA. Mesocosms consisted of 36 black plastic containers (114 L; 0.66 by 0.44 by 0.38 m; L by W by H; surface area = 0.29 m^2) filled with local outdoor pond water (pH = ~7.0). Prior to adding coontail, mesocosms were covered with salvinia for 30 d, which depleted total nitrogen in the mesocosms. After the nutrient depletion period, salvinia from each mesocosm was discarded and fresh plants were used for the study. Mature tertiary stage salvinia was collected from outdoor ponds at the LSU Agricultural Center Reproductive Biology Center in St. Gabriel, LA (13.4 km from mesocosm site), and coontail was collected from Blind River in Ascension Parish, LA (30.103231, −90.727329; 52 km from mesocosm site). A systemic insecticide (21.4% Imidacloprid) was applied to the foliage of salvinia 30 d prior to control herbivorous insects.

Initial salvinia coverage and total nitrogen were used to test effects on coontail biomass and water quality. Total nitrogen was selected to account for all usable forms of nitrogen available to macrophytes. Three initial salvinia coverages (0, 5, and 20%) and three nutrient treatments (0, 3, and 8 mg N L^{-1}) were selected. The three salvinia treatments represent coverages observed at field locations following winter die off, where 0% is complete die off and the other two are partial die offs. Once introduced, salvinia grew undisturbed for the entirety of the study, and percent salvinia cover was measured weekly. The rate of increased salvinia cover was determined from initial coverage either until salvinia reached 100% cover or completion of the study. Nutrient regimes were maintained at those concentrations for the duration of the study. Total nitrogen was sampled weekly with a handheld colorimeter[1]. Miracle-Gro®[2] (24–8–16, N–P–K) was used to fertilize mesocosms as needed. Nitrogen concentrations were selected to mimic concentrations from a natural water source, the Mississippi River (3 mg N L^{-1}), and agricultural field runoff (8 mg N L^{-1}) (Yu et al. 2008).

Plant quality

To address our objective of how salvinia affected coontail biomass, repeated sampling of coontail biomass through time was conducted. Coontail grew in 0.65 L planting pots (9 by 8.5 by 8.5 cm) filled with 7 cm of top soil[3] then covered with 2 cm of sand; five apical shoots (10 cm) then were added to each pot. Three pots were placed in a mesocosm approximately 10 cm apart. After potting, coontail grew undisturbed for 21 d prior to treatments being implemented (Strange et al. 2018). Following this period, total nitrogen was sampled in all mesocosms to verify nutrient depletion (0.11 ± 0.31 mg L^{-1} [mean ± SD]; $n = 36$). Coontail biomass was collected weekly (108 pots = 3 nutrients by 3 salvinia coverages by 6 wk by 2 replicates), and all biomass (i.e., leaves and shoots) from a pot was removed (when sampled) then placed in a resealable plastic bag until processing. Plant matter was placed in a drying oven for 72 h at 65 C then weighed for dry biomass. To account for initial biomass, five pots were harvested immediately before treatments were implemented. Treatment location within the mesocosm array and weekly plant sampling were randomized.

Salvinia biomass and tissue nutrients were collected from both cover treatments. Initial biomass was determined with five samples of each cover treatment, and all salvinia biomass was collected at the completion of the study ($n = 4$). To account for nutrient effects on salvinia, plant tissue was sampled for percent carbon and percent nitrogen at 0, 3, and 6 wk using the Dumas dry combustion method (Matejovic 1995). Salvinia tissue samples were processed at the LSU Agricultural Center Soil Test and Plant Analysis Lab, Baton Rouge, LA. Salvinia biomass samples were dried in the same manner as coontail.

Water quality

To address our objective of how salvinia affected water quality, physico-chemical parameters and light availability were collected weekly in each mesocosm (36 mesocosms = 3 nutrients by 3 salvinia coverages by 4 replicates). Dissolved oxygen (DO), pH, and specific conductance were collected with a handheld multiprobe[4]. Temperature was recorded every 30 min using HOBO® pendant temperature loggers[5] (accuracy ± 0.53 C). Air temperature was recorded 0.5 m above the ground and a logger was placed inside a solar radiation shield[5] (mean air temperature was 26.34 ± 0.05 C; $n = 1$). Water temperature loggers were placed inside the mesocosm on the bottom to ensure consistent conditions throughout the experiment (mean water temperature was 26.84 ± 0.01 C; $n = 18$).

Light transmission through the water column was measured with a handheld light meter[6]. Light intensity was measured directly above and below (1 cm) the water surface, then at 10-cm intervals until the bottom. In addition to measuring light intensity at depth, the rate of light loss was estimated with an exponential decay model (Madden and Kemp 1996).

Statistical analyses

Analyses and figures were developed using R statistical software version 3.4.4 (Program R; R Core Team 2019) and JMP (version 15, SAS Institute, Inc., Cary, NC, USA). Analyses examined for differences in water quality and plant characteristics among salvinia coverages and nutrients. Best-fit lines were produced for coontail biomass change during the experiment. One line was produced using the mean dry biomass per week and the linear fit line was made using smoothing spline ($\lambda \geq 100$). Slope and intercept of linear fit lines were compared for differences among coverage and nutrients using an analysis of covariance (ANCOVA). Generalized linear models (GLM; package MASS; Venables and Ripley 2002) compared coontail and salvinia plant quality among initial cover and nutrients. For all variables, the selected combination of link and distribution was determined by comparing candidates and fit statistics. Comparisons of final coontail biomass, and rate of salvinia percent cover increase, among initial cover and nutrients were performed using an identity link, Gaussian distribution GLM. Comparisons of salvinia growth and percent nitrogen in salvinia tissue were performed using gamma distribution GLMs with identity and log links, respectively. A log link, Gaussian distribution, GLM was used for percent carbon comparisons.

Linear mixed effect models (LMM; package lme4; Bates et al. 2015) and generalized linear mixed effect models (GLMM; package lme4; Bates et al. 2015) compared water quality and light availability among initial cover and nutrients. The approach allows for the evaluation between response variables and fixed effects, while accounting for measurements over time. The effect of initial cover and nutrients were of interest, and thus were selected as fixed effects in all models. The effect of time on the variation of water quality parameters can be expected to differ on a weekly basis, therefore, week was selected as a random variable. Visual inspection of the data suggests that week could be an important random effect, thus additional random effect considering the interaction between week and fixed effects (initial cover and nutrients) were added when comparing models. Multiple LMM and GLMM models were evaluated with different variable, link transformation, and probability distribution combinations, with the final models selected for interpretation based on lowest Akaike information criterion (AIC), and residual plots indicating that model assumptions were met. For the analysis of dissolved oxygen, a LMM compared initial cover and nutrients. For the analysis of pH, specific conductance, and light intensity, a log link, gamma distribution GLMM compared among initial cover and nutrients. Likelihood ratio tests were conducted to test for significance in water quality differences among nutrient and initial cover treatments. Estimated marginal means (package emmeans; Lenth 2020) were used to examine significant interactions between initial cover and nutrient treatments.

RESULTS

Plant quality

Initial salvinia coverage and nutrients affected coontail biomass over time. Initial coontail dry biomass, before cover and nutrient treatments were implemented, was 5.12 g (± 0.45). Coontail was present in all treatments at the end of the experiment. Comparison of linear fit lines indicated differences in slope and intercept among treatments and week ($P = 0.01$). Coontail biomass increased in the low nutrients with 5% initial salvinia cover treatment ($P = 0.01$), whereas biomass decreased in high nutrient treatments with initial 5% ($P = 0.03$) and initial 20% coverage ($P = 0.04$; Figure 1). Nutrients ($P < 0.01$) and initial cover ($P = 0.048$) significantly decreased coontail biomass at the conclusion of the experiment. Coontail biomass differed between the 0% and 20% initial cover treatments ($P = 0.04$), and between low and high nutrient treatments ($P < 0.01$).

Salvinia growth rate and percent cover increase both were affected by nutrients. The rate of salvinia growth was enhanced by initial cover ($P < 0.01$) and nutrients ($P < 0.01$; Table 1). Growth rate for initial cover of 5% was lower than 20% ($P < 0.01$), and rate for low nutrients was less than medium nutrients ($P < 0.01$) and high treatments ($P < 0.01$). Additionally, the rate of salvinia growth for medium nutrients was lower than high nutrients ($P = 0.049$). The rate of salvinia percent cover increase varied among the nutrient regimes ($P < 0.01$). The rate of salvinia percent cover increase for low nutrients was less than medium ($P = 0.01$) and high treatments ($P < 0.01$), additionally, percent cover increase in medium nutrients was less than high ($P =$

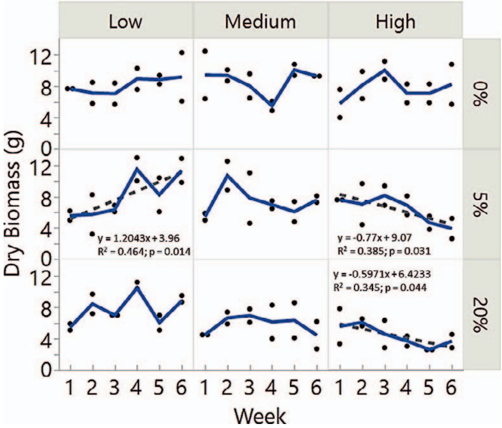

Figure 1. Coontail biomass change over time for 0%, 5%, and 20% initial salvinia cover, and low nitrogen (N) (0 mg N L^{-1}), medium (3 mg N L^{-1}), and high (8 mg N L^{-1}) nutrient treatments. Blue line represents mean dry biomass change and dashed line represents line of best fit for the study duration. Initial coontail biomass before implementing treatments was 5.12 g (± 0.45[SE]). Line of best fit equation was added for each significant treatment.

0.01). For low nutrients, 5% salvinia cover growth rate was 8.5% (± 1.5) wk^{-1} and growth rate for 20% salvinia cover was 12% (± 2.2; Figure 2A). Growth rate in medium nutrients for 5% and 20% salvinia cover was 17.2% (± 3.0) and 18.8% (± 2.6) per week, respectively (Figure 2A). In high nutrients with 5% salvinia cover, growth rate was 27.1% (± 5.4) per week and salvinia growth rate for 20% cover was 26.6% (± 3.8; Figure 2A). Percent nitrogen in salvinia tissue was enhanced by nutrients ($P < 0.01$; Figure 3). Percent nitrogen in high nutrients was greater than medium ($P < 0.01$) and low treatments ($P < 0.01$); additionally, percent nitrogen in medium nutrients was higher than low nutrients ($P < 0.01$). Percent carbon in salvinia tissue was enhanced by nutrients ($P < 0.01$; Figure 3), and percent carbon in high nutrients was greater than low nutrients ($P < 0.01$). Percent nitrogen and percent carbon did not vary between initial salvinia cover.

Water quality

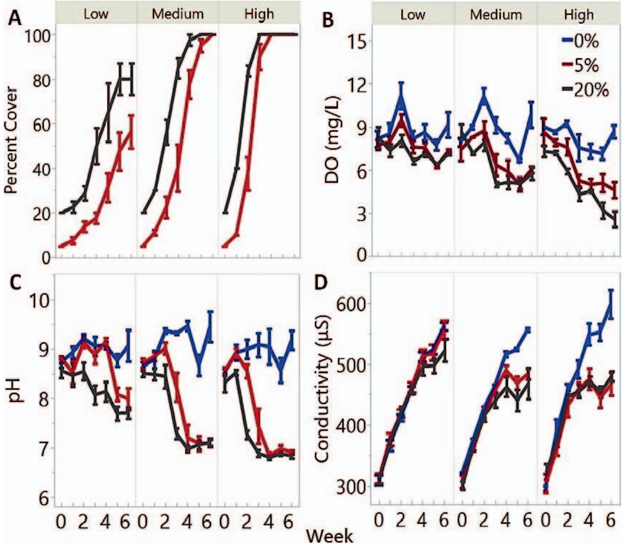

Figure 2. Weekly sampling of (A) salvinia percent cover, (B) dissolved oxygen, (C) pH, and (D) specific conductance in mesocosms. Treatments are: three initial salvinia covers, 0% (blue), 5% (red), and 20% (grey); and three nutrient (nitrogen [N]) levels, low (0 mg N L^{-1}), medium (3 mg N L^{-1}), and high (8 mg N L^{-1}]. Samples of water quality at week zero were recorded immediately before salvinia and nutrient treatments were implemented. Lines represent mean values, ± SE.

Table 1. Mean dry weight (± SE) of salvinia initially introduced to mesocosms (initial weight [wt]; $n = 5$), removed at study completion (final wt; $n = 4$), and change in mass per day (Δ wt d^{-1}; $n = 4$) among initial salvinia cover, 5%, and 20%; and nutrients (N), low (0 mg N L^{-1}), medium (3 mg N L^{-1}), and high (8 mg N L^{-1}). Study duration following salvinia introduction was 42 d.

Nutrients	Salvinia cover (%)	Initial wt (g)	Final wt (g)	Δ wt d^{-1} (g)
Low	5	2.16 ± 0.08	9.95 ± 1.02	0.19 ± 0.02
	20	5.10 ± 0.04	18.38 ± 2.04	0.32 ± 0.04
Medium	5	2.16 ± 0.08	26.88 ± 4.03	0.59 ± 0.09
	20	5.10 ± 0.04	43.13 ± 4.36	0.91 ± 0.10
High	5	2.16 ± 0.08	42.10 ± 4.31	0.95 ± 0.10
	20	5.10 ± 0.04	47.18 ± 2.49	1.00 ± 0.05

Dissolved oxygen varied among nutrient and salvinia cover treatments. In the presence of salvinia, DO decreased over the duration of the study, with nutrients influencing the rate of change (Figure 2B). In the 5% salvinia cover treatments, DO at the conclusion of the study was 1.25 (±0.90) and 1.63 times (± 0.92) lower than the 0% cover treatment for low ($\bar{X}_{5\%\text{-low}} = 7.32 \pm 0.12$ mg L^{-1}; $\bar{X}_{0\%\text{-low}} = 9.14 \pm 0.89$ mg L^{-1}) and medium nutrients ($\bar{X}_{5\%\text{-medium}} = 6.02 \pm 0.22$ mg L^{-1}; $\bar{X}_{0\%\text{-medium}} = 9.84 \pm 0.89$ mg L^{-1}), respectively. Under high nutrients, DO ended 1.88 (± 0.70) and 3.37 times (± 0.70) lower in the 5% ($\bar{X}_{5\%\text{-high}} = 4.62 \pm 0.54$ mg L^{-1}) and 20% ($\bar{X}_{20\%\text{-high}} = 2.57 \pm 0.54$ mg L^{-1}) salvinia cover treatments, relative to the 0% ($\bar{X}_{0\%\text{-high}} = 8.67$

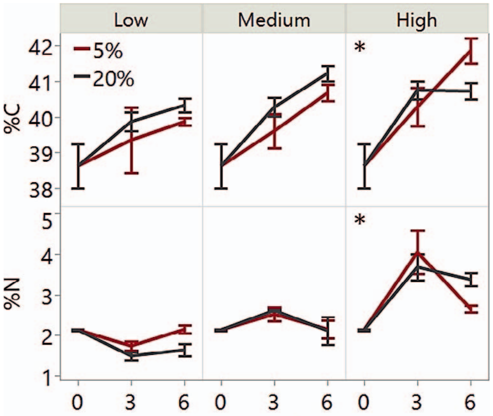

Figure 3. Line graph tracking percent carbon (% C) and percent nitrogen (% N) in salvinia tissue for the initial salvinia cover, 5%, and 20%; and for nutrient (N) levels, low (0 mg N L^{-1}), medium (3 mg N L^{-1}), and high (8 mg N L$^{-1)}$ treatments. Samples were collected initially (0 wk), halfway (3 wk) and at completion of the study (6 wk). Lines connect mean values (± SE; $n = 4$). Asterisk identifies statistically different nutrient treatment ($P < 0.01$). Initial salvinia cover treatments were statistically similar for percent carbon and percent nitrogen.

Table 2. Linear mixed model and generalized linear mixed model estimates of mean values for dissolved oxygen (DO; mg L^{-1}), pH, specific conductance (Sp Cond; µS), and light intensity (lux) at 10 cm depth with lower and upper 95% confidence limits (CL) among salvinia cover, 0%, 5%, and 20%; and nutrients (nitrogen [N]), low (0 mg N L^{-1}), medium (3 mg N L^{-1}), and high (8 mg N L^{-1}). Superscript letters indicate difference between coverages within a nutrient treatment.

Treatment	DO (CL)	pH (CL)	Sp Cond (CL)	Light intensity (CL)
0%–Low	8.89^{a} (7.19–10.58)	9.01^{a} (8.09–10.02)	466^{a} (387–562)	$8{,}946^{a}$ (743–107,628)
5%–Low	7.69^{ab} (6.00–9.39)	8.62^{a} (7.75–9.60)	469^{a} (389–566)	$4{,}334^{a}$ (359–52,180)
20%–Low	7.12^{b} (5.42–8.81)	8.09^{a} (7.27–9.00)	458^{a} (380–551)	$2{,}232^{a}$ (185–26,880)
0%–Medium	8.99^{a} (7.30–10.69)	9.12^{a} (8.19–10.14)	472^{a} (391–569)	$6{,}876^{a}$ (571–82,740)
5%–Medium	6.72^{b} (5.02–8.41)	7.95^{b} (7.15–8.85)	443^{ab} (367–534)	$1{,}624^{ab}$ (135–19,536)
20%–Medium	6.01^{b} (4.32–7.71)	7.52^{b} (6.76–8.37)	431^{b} (357–519)	467^{b} (39–5,610)
0%–High	8.10^{a} (6.41–9.80)	8.96^{a} (8.05–9.97)	499^{a} (414–601)	$7{,}913^{a}$ (657–95,235)
5%–High	5.91^{b} (4.22–7.61)	7.55^{b} (6.78–8.40)	437^{b} (363–527)	606^{b} (50–7,276)
20%–High	4.62^{c} (2.93–6.32)	7.17^{b} (6.44–7.98)	445^{b} (369–536)	287^{b} (24–3,441)

± 0.43 mg L^{-1}) salvinia cover treatment, respectively. Nutrients, initial salvinia coverage, and the interaction of nutrients with initial salvinia coverage ($P < 0.01$) affected DO. The 0% salvinia cover in the medium-nutrient treatment represented the upper limit of DO, whereas 20% cover in the high nutrient treatment was the lower limit (Table 2). Dissolved oxygen decreased by 4.37 mg L^{-1} (± 0.45; $P < 0.01$) between the upper ($\bar{X} = 8.99 \pm 0.51$) and lower limits ($\bar{X} = 4.62 \pm 0.51$). Under low nutrients, DO in 20% salvinia cover was lower than 0% cover ($P < 0.01$). In medium nutrients, DO in 0% salvinia cover was higher than 5% ($P < 0.01$) and 20% ($P < 0.01$). At high nutrients, DO in 0% salvinia cover was higher than 5% ($P < 0.01$) and 20% ($P < 0.01$). Additionally, DO in the 5% was higher than 20% cover ($P = 0.03$).

Over the duration of the study, pH decreased in treatments that contained salvinia. At the completion of the study, pH in low nutrient treatments with salvinia were at least 1.10 (± 0.34) times lower than no salvinia treatments ($\bar{X}_{0\%\text{–low}} = 9.07 \pm 0.32$; $\bar{X}_{5\%\text{–low}} = 9.84 \pm 0.89$; $\bar{X}_{20\%\text{–low}} = 7.70 \pm 0.11$; Figure 2C). Final pH in medium nutrient treatments were 1.33 (± 0.36) times lower than no salvinia treatments ($\bar{X}_{0\%\text{–medium}} = 9.45 \pm 0.30$; $\bar{X}_{5\%\text{–medium}} = 7.10 \pm 0.09$; $\bar{X}_{20\%\text{–medium}} = 7.10 \pm 0.07$); similarly, final pH in high nutrient treatments containing salvinia were at least 1.32 times (± 0.22) less than treatments not containing salvinia ($\bar{X}_{0\%\text{–high}} = 9.18 \pm 0.19$; $\bar{X}_{5\%\text{–high}} = 6.91 \pm 0.04$; $\bar{X}_{20\%\text{–high}} = 6.84 \pm 0.05$). Differences in pH were explained by nutrients ($P < 0.01$) and initial salvinia coverage ($P < 0.01$). The 0% salvinia cover in medium nutrients represented the upper pH limit, whereas 20% cover in high nutrients was the lower limit (Table 2). pH changed by 1.95 units between upper ($\bar{X} = 9.12 \pm 0.35$) and lower limits ($\bar{X} = 7.17 \pm 0.28$). In low nutrients, there were no differences between salvinia cover treatments. Under medium nutrients, pH in 0% salvinia cover was higher than 5% ($P < 0.01$) and 20% ($P < 0.01$), additionally under high nutrients, pH in 0% cover was higher than 5% ($P = 0.01$) and 20% ($P < 0.01$).

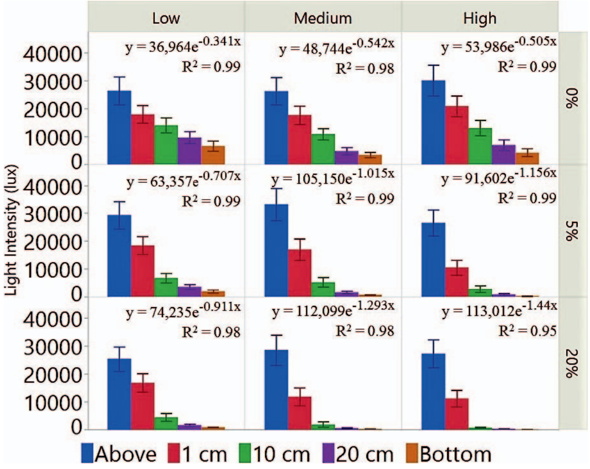

Figure 4. Mean light intensity (lux) ± SE, over the duration of the study for the low (0 mg L^{-1} N), medium (3 mg L^{-1} N), and high (8 mg L^{-1} N) nutrient (N) treatments and the three initial salvinia coverages (0%, 5%, and 20%). Light intensity was measured directly above the water surface then below surface at different depths: 1 cm, 10 cm, 20 cm, and mesocosm bottom. Exponential decay equation of mean light intensity through the water column was added for each treatment.

Specific conductance was influenced by salvinia cover and nutrients. When salvinia was not present, specific conductance (microsiemens, µS) increased over the duration of the study and was 1.06 times (± 24.42) greater in high nutrient treatments ($\bar{X}_{0\%\text{–high}} = 598.25 \pm 23.43$ µS), relative to low ($\bar{X}_{0\%\text{–low}} = 562.25 \pm 6.80$ µS) and medium nutrients ($\bar{X}_{0\%\text{–medium}} = 556.75 \pm 15.13$ µS; Figure 2D). Under the medium nutrient treatments, specific conductance for salvinia treatments were at least 1.15 times (± 9.78) less than no salvinia treatments ($\bar{X}_{5\%\text{–medium}} = 484.00 \pm 9.33$ µS; $\bar{X}_{20\%\text{–medium}} = 468.50 \pm 25.76$ µS), and salvinia treatments were at least 1.25 times (± 24.80) less than no salvinia treatments when nutrients were high ($\bar{X}_{5\%\text{–high}} = 467.25 \pm 18.90$ µS; $\bar{X}_{20\%\text{–high}} = 480.00 \pm 8.03$ µS; Figure 2D). Initial salvinia coverage and the interactions between nutrients with initial salvinia coverage were significant ($P < 0.01$). The 0% salvinia cover treatment in high nutrients represented the upper limit, whereas 20% cover in medium nutrients was the lower limit (Table 2). Specific conductance changed by 68 µS between upper ($\bar{X} = 499 \pm 33.7$) and lower limits ($\bar{X} = 431 \pm 29.1$). Specific conductance did not vary under low nutrients. Under medium nutrients, specific conductance in the 0% salvinia cover was higher than 20% cover ($P = 0.03$). Within the high nutrient treatments, specific conductance in the 0% salvinia cover was higher than 5% ($P = 0.01$) and 20% coverages ($P < 0.01$).

Light availability was limited by initial cover and nutrients. The rate of exponential decay in light availability increased with salvinia cover and nutrients (Figure 4).

Although PAR is a more precise method to measure spectral range available for photosynthesis, lux provided useful in understanding how light availability was impacted by salvinia. In the low nutrient treatment, light availability at 10 cm in 0% cover ($\bar{X}_{0\%\text{-low}} = 8{,}990 \pm 1{,}315$ lux) was 2.08 (± 3,143 lux) and 3.15 times (± 3,000) more than the 5% ($\bar{X}_{5\%\text{-low}} = 2{,}784 \pm 779$ lux) and 20% ($\bar{X}_{20\%\text{-low}} = 806 \pm 377$ lux) salvinia cover treatments, respectively. Similarly, in medium nutrients, light availability was 2.09 (± 2,637) and 5.94 times (± 2,281) less for 5% ($\bar{X}_{5\%\text{-medium}} = 206 \pm 23$ lux) and 20% ($\bar{X}_{20\%\text{-medium}} = 98.5 \pm 55$ lux) salvinia cover treatments, respectively, relative to no salvinia ($\bar{X}_{0\%\text{-medium}} = 6{,}225 \pm 1{,}435$ lux). At high nutrients, light availability was 4.67 (± 2,990) and 18.24 times (± 2,780) less in the 5% ($\bar{X}_{5\%\text{-high}} = 58 \pm 12$ lux) and 20% ($\bar{X}_{20\%\text{-high}} = 55 \pm 13$ lux) salvinia cover treatments, respectively, compared to no salvinia ($\bar{X}_{0\%\text{-high}} = 5{,}415 \pm 480$ lux). Differences in light intensity at 10 cm were explained by nutrients, initial salvinia cover, and the interaction of nutrients with initial salvinia coverage ($P = 0.04$). The model estimated that 0% salvinia cover in low nutrients represented the upper limit, whereas 20% cover in high nutrients was the lower limit (Table 2). Light availability changed by 8,659 lux between upper ($\bar{X} = 8{,}946$, $SE = 8{,}047$) and lower limits ($\bar{X} = 287$, $SE = 258$). In low nutrients, there were no differences between salvinia cover treatments. Under medium nutrients, light availability at 10 cm in 0% salvinia cover was higher than 20% ($P < 0.01$), additionally under high nutrients, light availability in 0% cover was higher than 5% ($P = 0.01$) and 20% ($P < 0.01$).

DISCUSSION

Our study shows that nutrients were an important factor when determining the impact of salvinia on coontail and water quality. Our hypothesis was supported in that under low nutrients, coontail was able to persist and its biomass seemed unaffected by salvinia. The data did not support the prediction that salvinia at higher levels of nutrients would result in the complete loss of coontail biomass, and this was presumably due to duration of the study. Given more time, however, the complete loss of coontail biomass might have occurred. Under low and medium nutrients, coontail biomass did not decrease; however, under high nutrients, coontail biomass decreased when salvinia was present. Despite weeks of being under a salvinia mat, coontail persisted through the duration of the study. Changes in water quality were evident in salvinia when nutrients were added, and these changes were enhanced as salvinia cover increased.

The inclusion of specific conductance in our parameter collection allowed us to examine nutrient changes in the water. Specific conductance is a useful proxy for determining salinity or total salt concentration of water (Ratnayake et al. 2018). Nutrient addition in 0% salvinia cover was consistent over the study duration with adding 0 to 2 mg N L^{-1} each week. The 5% and 20% salvinia coverages required similar amounts for the first week or two but required more nitrogen, 2 to 4 mg N L^{-1}, as the study progressed, with salvinia depleting most nitrogen in both nutrient addition treatments by week 4. This change in water nutrients could be observed in the reduction of specific conductance over time in treatments with salvinia, relative to no salvinia (Figure 2D). This suggests that nutrients were being reduced at faster rates from treatments containing salvinia. Both coontail and salvinia have previously shown the ability to uptake substantial amounts of nutrients from the water column (Foroughi et al. 2010, Ng and Chan 2017). However, additional research is needed to examine nutrient absorption of total nitrogen from both species.

Shading from salvinia is the most likely explanation of reduced coontail biomass at a high nutrient concentration. Salvinia did not completely cover the no-nutrient addition treatments, thus light was not completely cut off and coontail biomass was not affected. It appears that high shading, near 100% salvinia coverage, was necessary to reduce coontail biomass. A 10-wk study examining the effects of filamentous algal mats on coontail performance found that biomass of coontail was significantly lower under 100% cover mat; however, biomass under no mat and 50% mat did not vary (Liu et al. 2012). A similar study examined the effects of shading on three submerged macrophytes, including coontail, over 8 wk and found that shading $\geq 90\%$ was needed to reduce biomass, and the highest accumulation of coontail biomass was 65% shading (Kankanamge et al. 2019). Leaf and stem fragments of coontail can overwinter in deep water and under ice for months at low light conditions (Stuckey et al. 1978, CABI 2019). Coontail has a low light compensation point, the point on the light curve where the rate of photosynthesis matches the rate of cellular respiration, of 7.2 μmol m^{-2} s^{-1} (Sand-Jensen and Madsen 1991). This might explain why the plant is able to tolerate high shading, thrive in deeper water, and survive long periods under ice (Van et al. 1976, Spencer and Wetzel 1993, Gross et al. 2003). The increased growth under low to moderate levels of shading has been observed for *Vallisneria natans* L., *Myriophyllum spicatum* L., and *Elodea nuttallii* (Planch.) H. St. John (Lu et al. 2013, Zefferman 2014). Coontail is a canopy-forming species, and the shading provided by its floating canopy might create more favorable growing conditions for itself. Because of the duration of the study, we were unable to determine how much time under full salvinia coverage would be needed to eliminate coontail biomass. The plant persisted in our study for 3 wk under 100% salvinia cover and has been reported to persist after 10 wk of shading (Liu et al. 2012), suggesting coontail is tolerant shaded environments.

The rate of change in dissolved oxygen by salvinia was directly related to nutrient levels. Nutrient additions increased the rate of salvinia growth, which exacerbated the impact to DO. The observation of decreased DO in the presence of salvinia was expected (Oliver 1993, Tipping et al. 2008). Decreased DO can be attributed to a reduction of photosynthesis by submerged macrophytes and phytoplankton, limited atmospheric gas exchange due to mat presence, and the decomposition of organic matter (Owens et al. 2005). In field locations, decreases in DO might also be explained by the salvinia mat reducing windblown disturbance of the water surface, thus limiting the diffusion of oxygen through the water surface (Liss 1973, Doeleman

1989). The extensive formation of a salvinia mat can lead to near anoxic conditions, potentially causing internal nutrient loading of the water body (Wahl et al. 2020). Previous research has found that DO concentrations $\leq$ 1 mg L^{-1} results in increased sediment nutrient release of ammonium (Zhang et al. 2014) and phosphorus (Wu et al. 2014). During the study, DO concentrations remained above stressful or lethal levels for freshwater warmwater stream and wetland fish and invertebrates (Killgore and Hoover 2001, Kaller and Kelso 2007, Justus et al. 2014). However, salvinia decomposition and concurrent hypoxic ($<$ 2 mg L^{-1}) and anoxic conditions have been associated with fish mortality (Flores and Carson 2006).

Salvinia reduced overall pH and the rate of change was determined by nutrients. The reduction in pH associated with salvinia have been reported previously (Julien et al. 2009, Coetzee and Hill 2020). In the mesocosms, pH declined until 100% salvinia cover occurred, stabilizing around 7. Although unmeasured in this experiment, the reduction in pH could be due to the accumulation of carbon dioxide in the water. Photosynthesis of submerged macrophytes removes carbon dioxide, and a reduction in submerged macrophytes should reduce photosynthesis, thus limiting carbon dioxide uptake. The salvinia mat acts as a barrier between the atmosphere and water surface, limiting gas exchange and accumulating carbon dioxide in the water (Mitchell 1969, Doeleman 1989, McFarland et al. 2004).

The reduced pH also might be due to localized habitat modification by salvinia to create more ideal growing conditions. Previous research in greenhouse settings have found the highest rate of salvinia growth occurred when pH was around 6.0 (Cary and Weerts 1984, Madsen and Wersal 2008). Sediment release of ammonium has been found to be greatest when pH was at 6 (Zhang et al. 2014), and this might explain why salvinia prefers slightly acidic conditions. The slightly acidic conditions have been found to negatively affect the metabolism of submerged macrophyte hydrilla (*Hydrilla verticillata* L.f.) (Song et al. 2018); thus, the modified environment might reduce competition from other plants. Decreased pH under free-floating macrophyte mats also has been observed for water hyacinth (*Pontederia crassipes* Mart. Solms) (Mahmood et al. 2005), mosquito fern (*Azolla filiculoides* Lam.) (Janes et al. 1996), and water lettuce (*Pistia stratiotes* L.) (O'Farrell et al. 2011). Submerged macrophytes also modify local pH. Frodge et al. (1990) found that pH in canopies of coontail exceeded 10 and was two units higher than the adjacent open water, potentially due to release of phosphorus from the sediment. The rate of phosphorus release from the sediment starts to increase around pH of 8 and continues to increase as the water becomes more alkaline (Jin et al. 2006, Wu 2014). In this experiment, coontail might have modified the local environment by increasing pH. The pond water used to fill the mesocosms had a pH of 7.0; after the 21-d acclimation period, mean pH across all mesocosms was 8.6 (± 0.03).

Nutrient addition amplified the rate of increase in salvinia coverage and exacerbated effects to water quality. Salvinia has been shown to respond positively to modest and high nutrient additions (Cary and Weerts 1984, Oliver 1993, Madsen and Wersal 2008). Nutrient additions to water bodies, through agriculture or urban runoff, create favorable conditions for salvinia to proliferate and create a mat on the water surface. Management actions in coastal zones (e.g., diversion for wetland enhancement and restoration) or flood control efforts that route nutrient-rich water into wetlands (Day et al. 2018) also might enhance salvinia at the expense of native aquatic vegetation.

To help lessen the impact from invasive floating macrophytes, aquatic resource managers should focus on reducing nutrients entering water bodies. We found that moderate nutrient additions can result in rapid aquatic habitat degradation; thus, limiting nutrients entering aquatic systems is essential. Practices to reduce inputs from agricultural and urban sources, such as buffer zones around stream and river corridors, and properly functioning septic and wastewater systems, should be implemented to limit nutrient loading. Identification of point and nonpoint nutrient sources, and estimated input from those sources, would help determine how nutrients are entering water bodies. Additionally, monitoring of nutrients near point sources would inform resource managers if proper nutrient reduction practices were being conducted.

Maintaining abundant and diverse community of native submerged macrophytes is critical for land managers. However, invasion from salvinia quickly alters environmental conditions, requiring management efforts to maintain submerged macrophytes. Within weeks, salvinia created low DO conditions, decreased pH, and reduced light availability. We demonstrated that nutrients determine the rate at which salvinia degrades the aquatic environment. Coontail persisted after salvinia covered the water surface, which suggests that an opportunity exists for immediate management to control salvinia to maintain native submerged macrophytes and environmental quality. More research is needed to determine the time until submerged macrophytes are completely absent, and how long is necessary for those communities to recover following control of salvinia.

SOURCES OF MATERIALS

[1] LaMotte Smart 3, LaMotte Company, 802 Washington Ave., Chestertown, MD 21620.

[2] Miracle-Gro®, The Scotts Miracle-Gro Co., 14111 Scottslawn Rd., Marysville, OH 43040.

[3] Organic Valley®, Garick LLC, 13600 Broadway Ave., Cleveland, OH 44125.

[4] Pro-DS5, YSI Incorporated, 1700 Brannum Ln., Yellow Springs, OH 45387.

[5] HOBO®, Onsite Computer Corporation, 470 MacArthur Blvd., Bourne, MA 02532.

[6] MW700, Milwaukee Instruments, Rocky Mount, NC 27804.

ACKNOWLEDGEMENTS

We would like to thank the following people for helping with study design, and also with field and laboratory assistance: Louisiana State University AgCenter employees, William Kelso, Seth Spinner, and Fatima Nguyen; and US Army Corps of Engineers employee, Christopher Mudge. Thanks to Louisiana Department of Wildlife and Fisheries, Delta Waterfowl, and Mid-South Aquatic Plant Management

Society for providing funds. This material is based upon work that also was partially supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, Hatch and McIntire-Stennis Programs under as project number LAB-94345 and LAB-94335.

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