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# A mathematical model of biocontrol of invasive aquatic weeds

John Alford, Curtis Balusek, Kristen M. Bowers and Casey Hartnett

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In this paper we modify the classical Lotka–Volterra differential equations to analyze competition between two aquatic plant species, a submersed plant and a free-floating plant. We formulate and analyze a system of three differential equations that control the dynamics of the free-floating plant biomass and both aboveground and belowground biomass for the submersed plant. We investigate our model to understand how plant competition is affected by grass carp herbivory on the submersed plant's aboveground biomass. We analyze both a reduced model, for which the submersed plant is assumed to have constant belowground biomass, and the full model. In each case, we compute stability of equilibria and derive a minimal grass carp stocking rate such that the free-floating plant may dominate the submersed plant. For the reduced model we show that the rate at which grass carp are stocked may exhibit a hysteresis effect.

## 1. Introduction

*Hydrilla verticillata*, commonly known as hydrilla, is one of the most invasive aquatic plants in the United States. Hydrilla has a rapid growth rate (as much as 1 inch per day), is typically found in depths up of 15–20 feet, and can grow to be 25 feet long in springs, lakes, marshes, ditches, rivers and tidal zones [Gettys et al. 2009]. Hydrilla is easily spread to a new body of water by just one leaf fragment attached to a boat. Millions of dollars a year are spent on efforts to control and eliminate hydrilla, including herbivory by grass carp and insects (e.g., leaf-mining flies), mechanical harvesters, herbicides, and competition with native aquatic plants [Gettys et al. 2009; Hanlon et al. 2000]. Thus understanding the biology and control of hydrilla is a problem of great significance.

Hydrilla is a submersed plant which is attached to the ground with an extensive root system, but may grow large enough so that its branches form dense mats of plant matter on the surface of the water [Gettys et al. 2009]. A free-floating

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plant floats on the surface of the water and has roots that collect nutrients from the water and hang unanchored to the ground. An example of a free-floating plant is *Eichhornia crassipes*, commonly known as water hyacinth. Although water hyacinth is a nonnative, invasive species that must be carefully controlled, it has some desirable qualities. For example, it can be used to purify wastewater [Wolverton and McDonald 1979] and is often used as an ornamental plant for ponds and aquariums [Kay and Hoyle 2001].

When submersed plants and floating plants such as hydrilla and water hyacinth coexist they compete for light, space, and nutrients. The classic mathematical model of two species that compete for a common resource is the Lotka–Volterra differential equations [Edelstein-Keshet 2005; Zeeman 1995; Wangersky 1978]. In this paper we use the Lotka–Volterra competition model to formulate and analyze competition between a submersed plant and a free-floating plant.

Grass carp (or white amur) are fish that are native to rivers in Eastern Asia and may live up to 25 years and grow as much as 10 pounds per year [Gettys et al. 2009]. Large grass carp consume up to 30% of their body weight each day. One of the main biocontrol agents of hydrilla is the sterilized, triploid grass carp. In fact, the triploid grass carp will eat many types of aquatic weeds, but prefer submersed plants such as hydrilla when available [Cuda et al. 2008]. One study [Pine and Anderson 1991] found that given a choice of 12 different types of plants, the water hyacinth was the triploid grass carp's least preferred plant while the top three preferred plants were American pondweed, hydrilla, and elodea, each of which is a submersed plant species.

The rate at which grass carp should be stocked is an active area of research in aquatic plant management [Hanlon et al. 2000]. This rate depends on the feeding rate of the fish and the growth rate and quality of the plants, both of which are influenced by many factors [Cuda et al. 2008; Sutton et al. 2012]. Too few grass carp may be ineffective, whereas too many may completely eliminate all submersed aquatic plants. One study found that 25 to 30 grass carp per hectare of vegetation was necessary to control the undesirable vegetation while maintaining some amount of desirable vegetation [Hanlon et al. 2000]. The stocking rate of grass carp is often recommended based on the percentage of area that has been infested with the submersed plant [Hanlon et al. 2000; Sutton et al. 2012]. In our model we account for herbivory of the submersed plant by grass carp using a single parameter to control the stocking rate of grass carp. We use our model to determine the minimal stocking rate that may result in significant reduction or elimination of submersed plant biomass. The minimal stocking rate is expressed in terms of the relevant parameters that describe the ecosystem.

It is known that plant competition is influenced by herbivory [Van et al. 1998; Center et al. 2005; Tipping et al. 2009]. Our model shows that herbivory of submersed plant aboveground biomass by grass carp may allow a free-floating plant to out-compete a submersed plant and proliferate. This is an example of the *principle of competitive exclusion* [Zeeman 1995; Wangersky 1978]. We show that, at a critical grass carp stocking rate, a stable ecosystem with large amounts of submersed plant biomass and no free-floating plant biomass may shift to a stable ecosystem with large amounts of free-floating plant biomass and small or no submersed plant biomass. This sudden shift in the stability of an ecosystem has been observed in lakes, coral reefs, woodlands, deserts, and oceans [Scheffer et al. 2001].

Mathematical models of competing aquatic plants and herbivore-plant ecosystems can be found throughout the literature. A model of free-floating and submersed plant dynamics is presented in [Scheffer et al. 2003], but aboveground and belowground biomass for the submersed plant is not distinguished. Competing aquatic plants are modeled in [Shukla 1998] when an undesirable plant is subjected to removal in order to promote the growth of the desirable plant. Experimental data is used in both of these papers to support the models, but neither use Lotka–Volterra dynamics and neither consider herbivory as a plant management strategy. Mathematical models of herbivore-plant dynamics are presented elsewhere, though. For example, in [Wilson et al. 2001] a model for the biocontrol of water hyacinth by insect (weevil) herbivory is considered. In [Gurney and Nisbet 1998], a two-variable Lotka–Volterra predator-prey food chain model is considered for which the herbivore is a predator and the plant is prey. Neither of these two publications model plant competition.

In this paper, we use existing models to formulate differential equations that control the dynamics of aboveground and belowground submersed plant biomass and free-floating plant biomass. We include Lotka–Volterra type competition between the free-floating plant and the aboveground submersed plant and a parameter that controls the mortality of the submersed plant aboveground biomass due to grass carp herbivory. Our paper is outlined as follows. In Section 2 we present the model and nondimensionalize the equations. In Section 2.1 we assume the submersed plant has a constant belowground biomass and analyze a reduced (two-equation) model. In Section 2.2, we consider the full model that incorporates the dynamics for both belowground and aboveground biomass of the submersed plant. In each section we present theoretical results that show how the equilibria and stability of equilibria depend on grass carp stocking rate. In the conclusion, the results are summarized and weaknesses of the model are discussed.

## 2. The model equations

The model equations are

$$\frac{dB}{dt} = sA - cB\left(1 - \frac{A}{m_A}\right) - d_B B, \tag{2-1}$$

$$\frac{dA}{dt} = (cB + r_A A)\left(1 - \frac{A}{m_A}\right) - \alpha_1 AL - d_A A, \tag{2-2}$$

$$\frac{dL}{dt} = r_L L\left(1 - \frac{L}{m_L}\right) - \alpha_2 AL. \tag{2-3}$$

All of the parameters $s$, $c$, $d_B$, $r_A$, $m_A$, $\alpha_1$, $d_A$, $r_L$, $m_L$, $\alpha_2$ are nonnegative. Here $A$ and $B$ are (respectively) the aboveground and belowground biomass of the submersed plant species and $L$ is the free-floating species biomass. In order to ensure biologically feasible solutions, initial data must be nonnegative. The growth dynamics of the submersed plant in the absence of $L$ are given by the coupled equations (2-1) and (2-2), and for $d_A = 0$, the model is the same as the one in [Turchin 2003; Turchin and Batzli 2001]. The aboveground biomass growth equation (2-2) incorporates logistic growth in the absence of $B$ and exponential growth (regrowth) from energy supplied by the belowground biomass in the absence of $A$. The parameter $d_A$ in (2-2) controls the mortality of aboveground biomass of the submersed plant. The growth dynamics of the floating plant, given by (2-3), are logistic in the absence of $A$. Logistic growth has been experimentally verified as a good growth model for water hyacinth [Wilson et al. 2001; 2005]. Competition is modeled as the standard Lotka–Volterra type described in [Edelstein-Keshet 2005] with interaction terms proportional to $AL$. The competition coefficients $\alpha_1$ and $\alpha_2$ control the ability of each plant species to compete with the other and measure how efficient one species is compared to the other at capturing the shared resources.

The parameter $d_A$ has dimensions $(\text{time})^{-1}$ and represents the number of grass carp that are stocked per unit time. As discussed in the introduction, grass carp prefer submersed plants when available and triploid grass carp are sterilized before stocking [Hanlon et al. 2000; Cuda et al. 2008; Pine and Anderson 1991]. Fish-eating predators such as otters and other fish may reduce the number of grass carp, but large grass carp are not affected by predation [Gettys et al. 2009] and grass carp may live 20 or more years [Cuda et al. 2008]. Thus our model assumes that grass carp do not feed on the free-floating plant, there is a limited timespan for biocontrol with large grass carp, and the natality and mortality of grass carp may be ignored.

In order to reduce the number of parameters and understand the important relationships between parameters, we nondimensionalize the model equations by introducing the *dimensionless* variables and parameters

$$x_1 = d_B B(s m_A)^{-1}, \quad y_1 = A m_A^{-1}, \quad x_2 = L m_L^{-1}, \quad \tau = r_L t, \tag{2-4}$$

$$\rho = cs(r_L d_B)^{-1}, \quad \delta_2 = d_B r_L^{-1}, \quad \phi = c r_L^{-1}, \quad \psi = r_A r_L^{-1}, \quad \delta_1 = d_A r_L^{-1}, \tag{2-5}$$

$$\theta_1 = \alpha_1 m_L r_L^{-1}, \quad \theta_2 = \alpha_2 m_A r_L^{-1}. \tag{2-6}$$

After substituting (2-4)–(2-6) into (2-1)–(2-3) we get the system

$$dx_1/d\tau = \delta_2(y_1 - x_1) - \phi x_1(1 - y_1), \tag{2-7}$$

$$dy_1/d\tau = (\rho x_1 + \psi y_1)(1 - y_1) - \theta_1 y_1 x_2 - \delta_1 y_1, \tag{2-8}$$

$$dx_2/d\tau = x_2(1 - x_2) - \theta_2 y_1 x_2. \tag{2-9}$$

Here the variable $x_1$ controls the (nondimensionalized) submerged plant belowground biomass dynamics, $y_1$ controls the (nondimensionalized) submerged plant aboveground biomass dynamics, and $x_2$ controls the (nondimensionalized) floating plant biomass dynamics.

**2.1.** ***Constant belowground biomass.*** In this section we assume that $B$ is constant and analyze the regrowth model for the submersed plant in the absence of logistic growth as in [Gurney and Nisbet 1998]. Here we replace $\rho x_1$ with a constant $\beta$ to get

$$dy_1/d\tau = \beta(1 + \psi\beta^{-1} y_1)(1 - y_1) - \theta_1 y_1 x_2 - \delta_1 y_1,$$

for (2-8). We will make the additional assumption that there is a significant amount of belowground biomass and $\psi \ll \beta$. Then these simplifications with (2-8), (2-9) give the system

$$y_1' = \beta(1 - y_1) - \theta_1 y_1 x_2 - \delta y_1, \quad x_2' = x_2(1 - x_2) - \theta_2 y_1 x_2, \tag{2-10}$$

where we have replaced $\delta_1$ with $\delta$, and the prime denotes differentiation with respect to the dimensionless time variable $\tau$. The equilibria are constant solutions and are found by solving the algebraic system that results by setting the right sides of each equation in (2-10) to zero. The long-term behavior of a dynamical system may be determined by equilibria and initial conditions. In general, initial conditions that are close enough to a stable equilibrium will yield solutions that evolve in time to these equilibria. In the remainder of this paper, we perform standard equilibrium and local stability analysis of nonlinear differential equations [Edelstein-Keshet 2005; Strogatz 2001].

For the equilibrium computations, it will be convenient to define the quantities

$$\gamma = 1 + \delta\beta^{-1}, \quad \alpha = \theta_1\beta^{-1}. \tag{2-11}$$

We first consider a graphical analysis of the equilibria in the $y_1$-$x_2$ phase plane. The nullclines are curves along which either $y_1' = 0$ or $x_2' = 0$. These curves are

$$x_2 = (1 - \gamma y_1)/(\alpha y_1), \quad x_2 = 0, \quad x_2 = 1 - \theta_2 y_1, \tag{2-12}$$

where the first equation is the $y_1$-nullcline (when $y_1' = 0$) and the second two equations are the $x_2$-nullclines (when $x_2' = 0$). When the $y_1$-nullcline intersects either of the $x_2$-nullclines for $y_1 \geq 0$ and $x_2 \geq 0$, the point of intersection is an equilibrium. Substituting nonnegative values of $y_1$ and $x_2$ into the right side of (2-10) results in a vector field that describes the flow of (2-10) in the phase plane (that is, the direction of increase or decrease of either $y_1$ or $x_2$). The flow along the $y_1$-nullcline is vertical and the flow along the $x_2$-nullcline is horizontal.

Figure 1 depicts example phase-plane plots. Each phase plane depends on parameter values. As can be seen from these plots, either one, two, or three equilibria exist. The free-floating plant extinction equilibrium along the $x_2 = 0$-nullcline when $y_1 = \gamma^{-1}$ exists for all parameter values. There may also be one or two equilibria where $x_2 > 0$ and $y_1 > 0$. These are the coexistence equilibria. Note that there are no submersed plant extinction equilibria when $y_1 = 0$. This is clear as we assumed that the belowground biomass is constant and positive.

Motivated by the phase-plane plots we will analyze the equilibria algebraically. We denote the equilibria as $(\hat{y}_1, \hat{x}_2)$. Substituting $\hat{x}_2 = 0$ from (2-12) into the first equation from (2-12) yields the free-floating plant extinction equilibrium

$$(\hat{y}_1, 0) = (\gamma^{-1}, 0). \tag{2-13}$$

Substituting $\hat{x}_2 = 1 - \theta_2 \hat{y}_1$ from (2-12) into the first equation from (2-12) gives a quadratic equation in $\hat{x}_2$ that yields

$$\hat{x}_2^{\pm} = (2\theta_1)^{-1}\big(\hat{\delta} - \delta \pm \sqrt{(\hat{\delta} - \delta)^2 + 4\theta_1(\delta - \delta_0)}\big), \quad \hat{y}_1^{\pm} = \theta_2^{-1}(1 - \hat{x}_2), \tag{2-14}$$

where

$$\hat{\delta} = \theta_1 - \beta \quad \text{and} \quad \delta_0 = \beta(\theta_2 - 1). \tag{2-15}$$

After substituting (2-15) into the radicand in (2-14), simple algebra yields

$$(\hat{\delta} - \delta)^2 + 4\theta_1(\delta - \delta_0) = (\delta + \theta_1 + \beta)^2 - 4\theta_1\theta_2\beta,$$

which is zero for two values of $\delta$, one of which is negative as $\theta_1$, $\theta_2$, and $\beta$ are positive. The radicand in (2-14) may have a positive zero for $\delta = \delta_c$, in which case we get that $\hat{x}_2^c = \hat{x}_2^+ = \hat{x}_2^-$, where

$$\delta_c = 2\sqrt{\theta_1\theta_2\beta} - \theta_1 - \beta, \quad \hat{x}_2^c = (2\theta_1)^{-1}(\hat{\delta} - \delta_c). \tag{2-16}$$

The constants $\hat{\delta}$, $\delta_0$, and $\delta_c$ will be used to characterize the stability and existence of equilibria for (2-10). We consider all parameters except $\delta$ fixed and positive and $\delta \geq 0$. First, the floating plant equilibria $\hat{x}_2^{\pm}$ may be nonnegative and real-valued if and only if $\delta \geq \delta_c$ and $\hat{x}_2^+ = \hat{x}_2^-$ when $\delta = \delta_c$ and the radicand is zero. If $\delta > \delta_c$, $\hat{x}_2^+$ increases with $\delta$ while $\hat{x}_2^-$ decreases with $\delta$. It is easy to show that $\delta_c \leq \delta_0$. If $\delta = \delta_0$, then either $\hat{x}_2^+$ or $\hat{x}_2^-$ equals zero depending on the sign of $\hat{\delta} - \delta_c$.

The dependence of $\hat{x}_2^{\pm}$ on $\delta$ may be plotted in the $\delta$-$\hat{x}_2$ plane with all other parameters fixed. The resulting curve has the general shape of a parabola which opens to the right. Figure 2 depicts such curves for $\delta_0 > 0$ and two cases where $\delta_c < 0$, $\hat{x}_2^c < 0$ and $\delta_c > 0$, $\hat{x}_2^c > 0$.

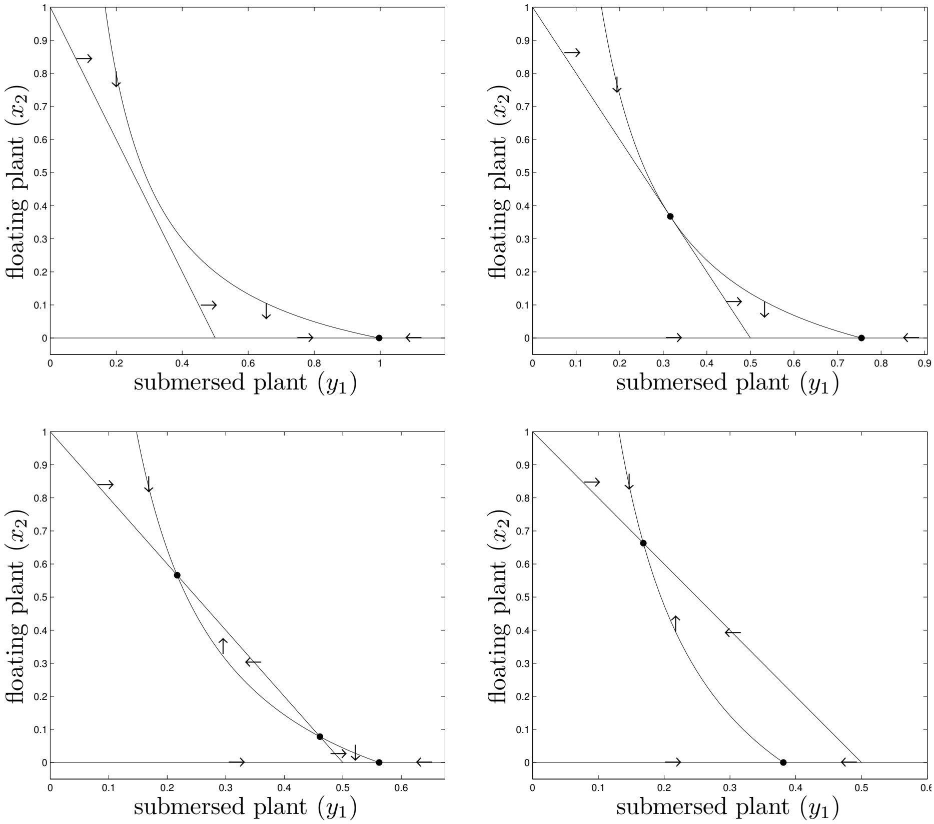

**Figure 1.** Plots of the $y_1$-$x_2$ phase plane for (2-10). The $y_1$-nullcline (curve) and $x_2$-nullclines (lines) are from (2-12). The arrows indicate the direction of flow of (2-10) along each nullcline. Equilibria are depicted at the dots where the $y_1$-nullcline intersects either of the $x_2$-nullclines. Each phase plane shows the free-floating plant extinction equilibrium at $(\gamma^{-1}, 0)$. There are no other equilibria in the top-left. The phase plane in the top-right shows a coexistence equilibrium for which the nonzero $x_2$-nullcline is tangential to the $y_1$-nullcline. The phase planes in the bottom show two (left) and one (right) coexistence equilibria where the $x_2$-nullcline intersects the $y_1$-nullcline.

The phase planes plotted in Figure 1 can be explained (qualitatively) by observing the equilibrium curve depicted in the right panel of Figure 2. First, recall that $\gamma = 1 + \beta^{-1}\delta$ defines the free-floating plant extinction equilibrium. Define the functions $f_1(y_1) = (1 - \gamma y_1)/(\alpha y_1)$ and $f_2(y_1) = 1 - \theta_2 y_1$ so that the $y_1$-nullcline is $x_2 = f_1(y_1)$ and the (nonzero) $x_2$-nullcline is $x_2 = f_2(y_1)$ from (2-12). If

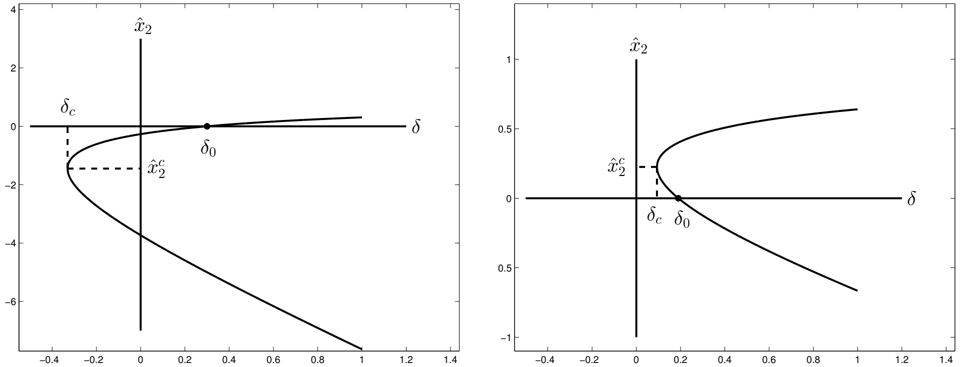

**Figure 2.** Plots of $\hat{x}_2^{\pm}$ as a function of $\delta$ from (2-14). The knee of the curve is $(\delta_c, \hat{x}_2^c)$ from (2-16). For the curve on the left, $\hat{\delta} < \delta_c < 0$, and for the curve on the right, $0 < \delta_c < \hat{\delta}$. The top half of each curve ($\hat{x}_2 > \hat{x}_2^c$) is $\hat{x}_2 = \hat{x}_2^+$ while the bottom half of each curve ($\hat{x}_2 < \hat{x}_2^c$) is $\hat{x}_2 = \hat{x}_2^-$.

$0 \le \delta < \delta_c < \hat{\delta}$, then $f_1(y_1)$ does not intersect $f_2(y_1)$ and the free-floating plant extinction equilibrium is unique. In this case, $0 < \delta < \delta_c$ so that $\delta$ is below the knee of the curve in the right panel of Figure 2.

If $\delta$ is then increased until $\delta = \delta_c$, then $f_2(y_1)$ is tangent to $f_1(y_1)$ and $f_1(y_1) = f_2(y_1)$ for exactly one value of $y_1$. This is displayed in the phase plane in the top-right in Figure 1 and corresponds to the knee of the curve in the right panel of Figure 2 where $\delta = \delta_c$ and $\hat{x}_2^- = \hat{x}_2^+ = \hat{x}_2^c$. As $\delta$ is increased further, both $\hat{x}_2^+$ and $\hat{x}_2^-$ are real and positive with $\hat{x}_2^- < \hat{x}_2^+$. This corresponds to the phase plane in the bottom-left in Figure 1 and the interval $\delta_c < \delta < \delta_0$ in the right panel of Figure 2. As $\delta$ continues to increase until $\delta > \delta_0$ and $\hat{x}_2^- < 0$, there is a single feasible positive equilibrium given by $\hat{x}_2^+$. This corresponds to the phase plane in the bottom-right in Figure 1 and the interval $\delta > \delta_0$ in the right panel of Figure 2.

In order to analyze local stability of the equilibria we compute the linearized stability (Jacobian) matrix for (2-10) which is given by

$$J(\hat{y}_1, \hat{x}_2) = \begin{pmatrix} -\beta - \theta_1 \hat{x}_2 - \delta & -\theta_1 \hat{y}_1 \\ -\theta_2 \hat{x}_2 & 1 - \theta_2 \hat{y}_1 - 2\hat{x}_2 \end{pmatrix}. \tag{2-17}$$

The eigenvalues $\lambda$ of this matrix satisfy the characteristic equation

$$\lambda^2 - \operatorname{tr}(J(\hat{y}_1, \hat{x}_2))\lambda + \det(J(\hat{y}_1, \hat{x}_2)) = 0.$$

Standard theory [Edelstein-Keshet 2005; Strogatz 2001] is that a necessary and sufficient condition for stability of $(\hat{y}_1, \hat{x}_2)$ is that the eigenvalues of the Jacobian have negative real parts or

$$\mathrm{tr}(J(\hat{y}_1,\hat{x}_2)) < 0 \quad \text{and} \quad \det(J(\hat{y}_1,\hat{x}_2)) > 0. \tag{2-18}$$

Substituting the free-floating plant extinction equilibrium $\hat{y}_1 = \gamma^{-1}$ and $\hat{x}_2 = 0$ into (2-17) gives

$$\mathrm{tr}(J(\gamma^{-1},0)) = 1-\beta-\delta-\theta_2\gamma^{-1}, \tag{2-19}$$

$$\det(J(\gamma^{-1},0)) = -(1-\theta_2\gamma^{-1})(\beta+\delta). \tag{2-20}$$

Comparing (2-18) and (2-19), (2-20) shows that $(\gamma^{-1},0)$ is stable if and only if $\theta_2 > \gamma$ which is equivalent to $\delta < \delta_0$ from (2-15).

We next consider stability of the equilibria $(\hat{y}_1^+,\hat{x}_2^+)$ and $(\hat{y}_1^-,\hat{x}_2^-)$ where we assume $\hat{x}_2^- > 0$. Substitute $\hat{x}_2 = 1-\theta_2\hat{y}_1$ and (2-17) reduces to

$$J(\hat{y}_1,\hat{x}_2) = \begin{pmatrix} -\beta-\theta_1\hat{x}_2-\delta & -\theta_1\hat{y}_1 \\ -\theta_2\hat{x}_2 & -\hat{x}_2 \end{pmatrix}, \tag{2-21}$$

so that

$$\mathrm{tr}(J(\hat{y}_1,\hat{x}_2)) = -\beta-\delta-\hat{x}_2(1+\theta_1), \tag{2-22}$$

$$\det(J(\hat{y}_1,\hat{x}_2)) = \hat{x}_2[\beta+\delta-\theta_1\theta_2\hat{y}_1+\theta_1\hat{x}_2]. \tag{2-23}$$

It is clear in this case that $\mathrm{tr}(J(\hat{y}_1,\hat{x}_2)) < 0$ as $\hat{x}_2$, $\delta$, $\beta$, and $\theta_1$ are all positive. Substitute $\theta_2\hat{y}_1 = 1-\hat{x}_2$ and, after some algebra, we get that a necessary and sufficient condition for $\hat{x}_2 > 0$ and $\det(J(\hat{y}_1,\hat{x}_2)) > 0$ is $\hat{x}_2 > (1-\gamma\beta\theta_1^{-1})/2 = (2\theta_1)^{-1}(\hat{\delta}-\delta)$. Thus, if $\delta > \delta_c$ from (2-16), then $\hat{x}_2^+$ is stable and $\hat{x}_2^-$ is unstable.

Table 1 summarizes the conditions on $\delta > 0$ for the existence of equilibria for (2-10) and their (linearized) stability properties. The pair $(\delta_c, \hat{x}_2^c)$ describes the point in the $\delta$-$\hat{x}_2$ plane at the knee of the equilibrium curve when $\hat{x}_2^\pm$ is plotted as a function of $\delta$, as in Figure 2. The first three rows correspond to $\delta_c > \hat{\delta}$ so that the knee of the equilibrium curve is below the $\delta$-axis in the $\delta$-$\hat{x}_2$ plane as depicted in the left panel in Figure 2. The middle three rows correspond to $0 < \delta_c < \hat{\delta}$ and the knee of the equilibrium curve is in the top-right quadrant of the $\delta$-$\hat{x}_2$ plane as in the right panel in Figure 2. For the last three rows $\delta_c < \hat{\delta}$ and $\delta_c < 0$ so that the knee of the equilibrium curve is in the top-left quadrant of the $\delta$-$\hat{x}_2$ plane.

Inspection of the middle three rows of Table 1 shows that when $\delta_c$ and $\hat{x}_2^c$ are both positive, as in Figure 2, right, equilibria $(\hat{x}_2^\pm, \hat{y}_2^\pm)$ are created as $\delta$ increases through $\delta_c$. This indicates a saddle-node bifurcation [Strogatz 2001] at $\delta = \delta_c$. In this case, there is a simple zero eigenvalue for the Jacobian matrix (2-17) for which $\mathrm{tr}(J(\hat{y}_1,\hat{x}_2)) < 0$ and $\det(J(\hat{y}_1,\hat{x}_2)) = 0$. The bifurcation diagram, plotted in Figure 3, shows $\hat{y}_1$ vs. $\delta$ and $\hat{x}_2$ vs. $\delta$ and the stability properties of these equilibria.

| $(\delta_c, \hat{x}_2^c)$ | $\delta_0$ | $\delta$ | $(\gamma^{-1}, 0)$ | $(\hat{y}_1^+, \hat{x}_2^+)$ | $(\hat{y}_1^-, \hat{x}_2^-)$ |
|---|---|---|---|---|---|
| $(-,-)$ | $\delta_0 < 0$ | $\delta > 0$ | unstable | stable | not feasible |
| $(-,-)$ or $(+,-)$ | $\delta_0 > 0$ | $0 < \delta < \delta_0$ | stable | not feasible | not feasible |
| $(-,-)$ or $(+,-)$ | $\delta_0 > 0$ | $\delta > \delta_0$ | unstable | stable | not feasible |
| $(+,+)$ | $\delta_0 > 0$ | $0 < \delta < \delta_c$ | stable | does not exist | does not exist |
| $(+,+)$ | $\delta_0 > 0$ | $\delta_c < \delta < \delta_0$ | stable | stable | unstable |
| $(+,+)$ | $\delta_0 > 0$ | $\delta > \delta_0$ | unstable | stable | not feasible |
| $(-,+)$ | $\delta_0 < 0$ | $\delta > 0$ | unstable | stable | not feasible |
| $(-,+)$ | $\delta_0 > 0$ | $0 < \delta < \delta_0$ | stable | stable | unstable |
| $(-,+)$ | $\delta_0 > 0$ | $\delta > \delta_0$ | unstable | stable | not feasible |

**Table 1.** A summary of existence and stability properties of the equilibria from (2-13) and (2-14) as they depend on $\delta > 0$. *Stable* and *unstable* indicate existence of a positive equilibrium whereas *not feasible* indicates the equilibrium exists, but is negative. The constants $\delta_c$, $\hat{x}_2^c$, and $\delta_0$ are given by (2-15) and (2-16).

Figure 3 displays a hysteresis effect. If the free-floating plant is extinct so that $(\hat{y}_1, \hat{x}_2) = (\gamma^{-1}, 0)$ and $\delta$ is increased through $\delta = \delta_0$, the free-floating plant extinction equilibrium loses stability. Any small perturbation from the extinction equilibrium (for example, a small remnant of free-floating plant attached to a boat is introduced into the lake) will cause a jump in the ecosystem to the stable coexistence equilibrium $(\hat{y}_1^+, \hat{x}_2^+)$. If $(\hat{y}_1, \hat{x}_2) = (\hat{y}_1^+, \hat{x}_2^+)$ and $\delta$ is then decreased, the system does not restabilize to the free-floating plant extinction equilibrium until $\delta = \delta_c$ at the saddle-node bifurcation.

Figure 4 shows simulations of the system (2-10). The parameters obey the middle three rows of Table 1 corresponding to the bifurcation diagram that is plotted in Figure 3. In this case, solutions for $\delta < \delta_c$ quickly (approximately 30 time units) achieve equilibrium at $(\gamma^{-1}, 0)$, while solutions for $\delta > \delta_0$ achieve equilibrium at to $(\hat{y}_1^+, \hat{x}_2^+)$ after approximately 100 time units.

In order to draw meaningful biological conclusions from the analysis, the dimensional forms of the equations and parameters must be considered. The nondimensionalizations are specified in (2-4), (2-5), and (2-6). Table 1 shows that for $\delta > \delta_0$ the free-floating plant extinction equilibrium is unstable. Using (2-5), (2-6), and (2-15), this inequality becomes

$$d_A > cBr_L^{-1}(\alpha_2 m_A r_L^{-1} - 1), \tag{2-24}$$

where $\delta$ replaced $\delta_1$ in (2-5). That is, the mortality of the aboveground biomass ($d_A$) should be larger than the production of belowground biomass ($cB$) scaled by a factor which increases with the competition efficiency of the submersed plant ($\alpha_2$)

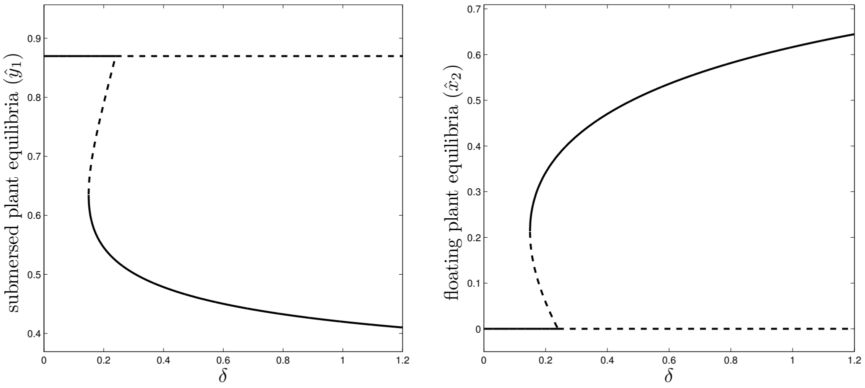

**Figure 3.** Bifurcation curves in the $\delta$-$\hat{y}_1$ plane (left) and $\delta$-$\hat{x}_2$ plane (right) for $\delta \geq 0$, $\hat{y}_1 \geq 0$, and $\hat{x}_2 \geq 0$ where $\beta = 1$, $\theta_1 = 2$, and $\theta_2 = 1.24$. Stable equilibria are plotted solid whereas unstable equilibria are plotted dashed. The submersed plant carrying capacity equilibria $\hat{y}_1 = (1 + \beta^{-1}\delta)^{-1}$ is the top curve in the left panel and the free-floating plant extinction equilibria $\hat{x}_2 = 0$ is the horizontal line in the right panel. The coexistence equilibria $\hat{y}_1 = \hat{y}_1^{\pm}$ make up the bottom curve (solid $\hat{y}_1^{+}$ and dashed $\hat{y}_1^{-}$) in the left panel and $\hat{x}_2 = \hat{x}_2^{\pm}$ make up the top curve (solid $\hat{x}_2^{+}$ and dashed $\hat{x}_2^{-}$) in the right panel. The coexistence equilibria coalesce when $\hat{y}_1^{+} = \hat{y}_1^{-}$ and $\hat{x}_2^{+} = \hat{x}_2^{-}$ at a saddle-node bifurcation for $\delta = \delta_c = 0.15$ from (2-16). Here $\delta_0 = 0.24$ and there is a region of bistability for $\delta_c < \delta < \delta_0$.

and the carrying capacity of aboveground biomass ($m_A$) and decreases with the growth rate of the free-floating plant ($r_L$). The minimal stocking rate is quantified by (2-24). Any plant management strategy that can reduce the right side of (2-24) results in a smaller number of grass carp necessary to destabilize the ecosystem towards free-floating plant dominance. If the quantity in parentheses can be made negative, for example by increasing the growth rate of $r_L$, grass carp will not be needed at all as the free-floating plant extinction equilibrium is stable for $\delta_A = 0$ (corresponding to row 1 and row 7 in Table 1 where $\delta_0 < 0$).

**2.2.** ***Nonconstant belowground biomass.*** In the previous section, the belowground biomass was assumed positive. This precludes the existence of a submersed plant extinction equilibrium. In this section we investigate the full model (2-7), (2-8), (2-9) and show that there is a stable submersed plant extinction equilibrium. As in the case for constant belowground biomass, there are multiple equilibria which will be denoted by $(\hat{x}_1, \hat{y}_1, \hat{x}_2)$ and which depend on the various parameters. Setting the

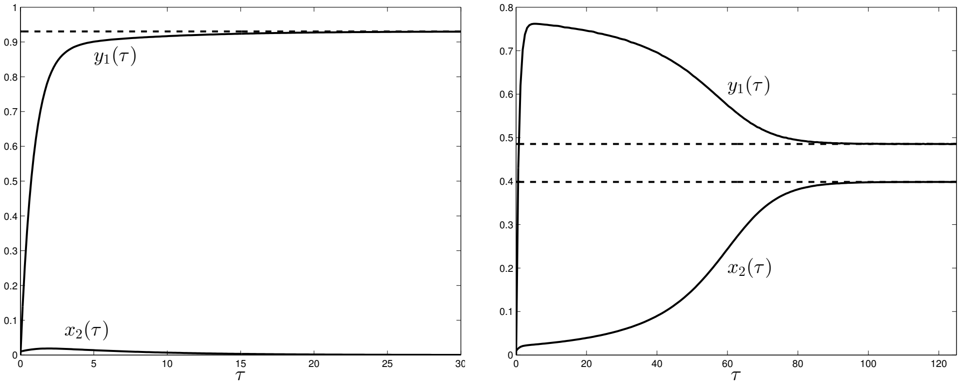

**Figure 4.** Simulations of the system (2-10) where the parameters are as in Figure 3 with $\beta = 1$, $\theta_1 = 2$, and $\theta_2 = 1.24$. For both plots the initial conditions are $(y_1(0), x_2(0)) = (0, 0.01)$. In the left panel, $\delta = 0.0748 < \delta_c$, and in the right panel, $\delta = 0.264 > \delta_0$. The dashed horizontal lines are the stable equilibria at $y_1 = (1+\beta^{-1}\delta)^{-1}$ and $x_2 = 0$ in the left panel and $y_1 = \hat{y}_1^+$ and $x_2 = \hat{x}_2^+$ in the right panel.

right side of (2-7) to zero yields

$$\hat{x}_1 = \hat{\delta}_2 \hat{y}_1 (1 + \hat{\delta}_2 - \hat{y}_1)^{-1}, \quad \hat{\delta}_2 = \phi^{-1}\delta_2. \tag{2-25}$$

If we next substitute (2-25) into the right side of (2-8) and use (2-9), then we get that the equilibria $\hat{y}_1$ and $\hat{x}_2$ obey

$$\hat{y}_1\big([\psi(1-\hat{y}_1) - \delta_1 - \theta_1 \hat{x}_2](\phi + \delta_2 - \phi \hat{y}_1) + \rho\delta_2(1-\hat{y}_1)\big) = 0, \tag{2-26}$$

$$\hat{x}_2(1 - \hat{x}_2 - \theta_2 \hat{y}_1) = 0. \tag{2-27}$$

We first consider the case $\hat{y}_1 = 0$ and the submersed plant is extinct. This yields two possibilities. The case $(0, 0, 0)$ is extinction of both species and the case $(0, 0, 1)$ is extinction of the submersed plant with the free-floating plant at carrying capacity.

We now consider the equilibria such that $\hat{x}_1 > 0$, $\hat{y}_1 > 0$ and the submersed plant is not extinct. First, note that (2-25) implies that $\phi + \delta_2 - \phi\hat{y}_1 > 0$ and from (2-26) we see that the feasible equilibria must obey $0 < \hat{y}_1 < 1$ as all of the parameters are nonnegative. For the coexistence equilibria $\hat{x}_1 > 0$, $\hat{y}_1 > 0$, $\hat{x}_2 > 0$ and neither the submersed plant nor the free-floating plant is extinct. In this case, (2-27) gives that $\hat{x}_2 = 1 - \theta_2 \hat{y}_1$ and substituting this into (2-27) yields the equation

$$\nu \hat{y}_1^2 + (\xi - 1 - \nu(1 + \hat{\delta}_2))\hat{y}_1 + 1 + \hat{\delta}_2 - \xi\kappa = 0, \tag{2-28}$$

where

$$\nu = 1 - \theta_1\theta_2\psi^{-1}, \quad \xi = \psi^{-1}(\delta_1 + \theta_1 - \rho\hat{\delta}_2), \quad \kappa = 1 + \frac{(\delta_1 + \theta_1)\hat{\delta}_2}{\delta_1 + \theta_1 - \rho\hat{\delta}_2}. \tag{2-29}$$

We will use (2-28) in Theorem 1 to examine coexistence equilibria under a constrained parameter set.

In order to analyze stability of equilibria, we consider the Jacobian matrix $J(\hat{x}_1, \hat{y}_1, \hat{x}_2)$ which is given by

$$\begin{pmatrix} -\delta_2 - \phi(1 - \hat{y}_1) & \delta_2 + \phi\hat{x}_1 & 0 \\ \rho(1 - \hat{y}_1) & -\rho\hat{x}_1 - \theta_1\hat{x}_2 - \delta_1 + \psi - 2\psi\hat{y}_1 & -\theta_1\hat{y}_1 \\ 0 & -\theta_2\hat{x}_2 & 1 - 2\hat{x}_2 - \theta_2\hat{y}_1 \end{pmatrix}. \tag{2-30}$$

We will use (2-30) and the results of the equilibria computations to show the following theorem.

**Theorem 1.** *If* $\delta_1 > \psi + \rho\hat{\delta}_2$ *and* $\theta_2 < \min\{1, \theta_1^{-1}\psi\}$, *then* $(0, 0, 1)$ *is the only feasible stable equilibrium of* (2-7), (2-8), (2-9).

*Proof.* First consider the free-floating plant extinction equilibrium $(\hat{x}_1, \hat{y}_1, 0)$ where $\hat{x}_1 \geq 0$ and $\hat{y}_1 \geq 0$. The Jacobian from (2-30) is $J(\hat{x}_1, \hat{y}_1, 0)$ whose last row is the vector $(0, 0, 1 - \theta_2\hat{y}_1)$. Thus $J(\hat{x}_1, \hat{y}_1, 0)$ has one eigenvalue equal to $1 - \theta_2\hat{y}_1$. In this case, inspection of (2-25) and (2-26) yields that $0 \leq \hat{y}_1 < 1$ as all parameters are positive and all equilibria must be nonnegative. The assumption $\theta_2 < 1$ shows that $1 - \theta_2\hat{y}_1 > 0$ so that $(\hat{x}_1, \hat{y}_1, 0)$ is unstable.

We next consider $(0, 0, 1)$, the submersed plant extinction equilibrium when the free-floating plant is at carrying capacity. Substituting this into the Jacobian (2-30) results in the matrix

$$J(0, 0, 1) = \begin{pmatrix} -\delta_2 - \phi & \delta_2 & 0 \\ \rho & \psi - \theta_1 - \delta_1 & 0 \\ 0 & -\theta_2 & -1 \end{pmatrix}, \tag{2-31}$$

and the eigenvalues obey

$$(1+\lambda)\big(\lambda^2 + (\theta_1 + \delta_1 - \psi + \delta_2 + \phi)\lambda + (\delta_2 + \phi)(\theta_1 + \delta_1 - \psi) - \rho\delta_0\big) = 0. \tag{2-32}$$

Thus $\lambda = -1$ or

$$\lambda = \big(-\gamma \pm \sqrt{\gamma^2 - 4[(\delta_2 + \phi)(\theta_1 + \delta_1 - \psi) - \rho\delta_0]}\big)/2, \tag{2-33}$$

where $\gamma = \theta_1 + \delta_1 - \psi + \delta_2 + \phi$ which is positive as it was assumed that $\delta_1 > \psi$. Therefore, nonreal eigenvalues have negative real parts. If the eigenvalues are real, they will both be negative if $(\delta_2 + \phi)(\theta_1 + \delta_1 - \psi) - \rho\delta_0 > 0$ which is equivalent to $\delta_1 > \rho\hat{\delta}_2(1 + \hat{\delta}_2)^{-1} + \psi - \theta_1$ where $\hat{\delta}_2 = \delta_2\phi^{-1}$. The assumption $\delta_1 > \psi + \rho\hat{\delta}_2$ shows that both eigenvalues are negative in this case and $(0, 0, 1)$ is stable.

Coexistence equilibria obey $\hat{x}_1 > 0$, $\hat{y}_1 > 0$, $\hat{x}_2 > 0$ and are found by solving (2-28) for $\hat{y}_1$. The solutions of (2-28) are

$$\hat{y}_{\pm} = \frac{\nu(1+\hat{\delta}_2)+1-\xi \pm \sqrt{(\nu(1+\hat{\delta}_2)+1-\xi)^2 - 4\nu(1+\hat{\delta}_2-\xi\kappa)}}{2\nu}. \qquad (2\text{-}34)$$

The parameters $\nu$, $\xi$, and $\kappa$ are defined in (2-29). The assumption $\theta_2 < \theta_1^{-1}\psi$ implies that $\nu$ is positive. The assumption $\delta_1 > \psi + \rho\hat{\delta}_2$ implies that $\xi > 1$ and $\kappa > 1+\hat{\delta}_2$. Therefore the radicand in (2-34) is positive, $\hat{y}_\pm$ are real, $y_- < 0$, and $y_+ > 0$. Thus $y_-$ is not feasible. Expanding the expression in the radicand of (2-34) yields that

$$(\xi-1)^2 + \nu^2(1+\hat{\delta}_2)^2 - 2\nu(1+\hat{\delta}_2) - 2\nu\xi(1+\hat{\delta}_2) + 4\nu\xi\kappa,$$

which is larger than $(\xi - 1 + \nu(1+\hat{\delta}_2))^2$ using the fact that $4\nu\xi\kappa > 4\nu\xi(1+\hat{\delta}_2)$. It follows that $y_+ > 1+\hat{\delta}_2$ so $y_+$ is not feasible since $0 < \hat{y}_1 < 1$ for coexistence. ☐

Figure 5 shows the time courses for simulations of (2-7), (2-8), (2-9) when the hypotheses of Theorem 1 are obeyed. Substituting (2-4), (2-5), and (2-6) into the assumptions in Theorem 1 yields that

$$d_A > r_A + s, \qquad r_L > \max\left\{\alpha_2 m_A, \frac{\alpha_1\alpha_2 m_A m_L}{r_A}\right\}. \qquad (2\text{-}35)$$

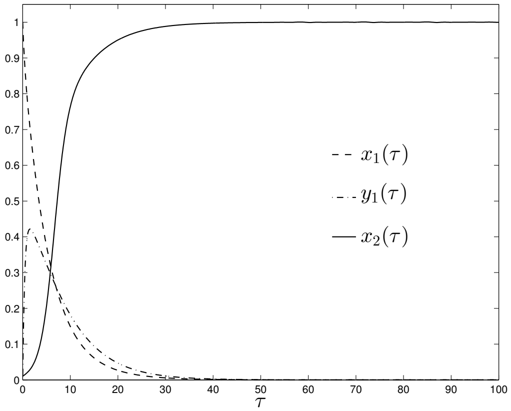

**Figure 5.** Simulation of the system (2-7), (2-8), (2-9) where the parameters are $\theta_1 = 0.1$, $\psi = 1$, $\rho = 1$, $\delta_2 = 0.1$, $\phi = 0.25$, $\delta_1 = 1.1 \cdot (\psi + \rho\hat{\delta}_2)$, and $\theta_2 = 0.9 \cdot \min\{1, \theta_1^{-1}\psi\}$. The initial conditions are $(x_1(0), y_1(0), x_2(0)) = (1, 0, 0.01)$. For these values of $\delta_1$ and $\theta_2$, the hypotheses of Theorem 1 are obeyed and $(0, 0, 1)$ is the only feasible stable equilibrium of (2-7)–(2-9).

If the growth rate of the free-floating plant $r_L$ may be enhanced by nutrient loading as described in [Scheffer et al. 2003], it may be possible that the second inequality in (2-35) is satisfied.

## 3. Conclusion

We have presented a modified Lotka–Volterra competition model (2-1)–(2-3) for two competing aquatic plants where one species is a submersed plant while the other is a free-floating plant. We investigated how herbivory by grass carp affects the competitive abilities of the submersed and free-floating plants. In Section 2.1 we analyzed a reduced model (2-10) by phase-plane methods and computed equilibria and stability of these equilibria. We derived conditions in (2-35) on the grass carp stocking rate $d_A$ so that the free-floating plant extinction equilibrium is unstable and free-floating plants may dominate the ecosystem. In addition, we showed that grass carp stocking may exhibit a hysteresis effect whereby grass carp may be decreased below the critical level at which the free-floating plant extinction equilibrium loses stability and suppression of the submersed plant biomass may still be achieved. This is depicted in the bifurcation diagram in Figure 3. In Section 2.2 we included the belowground biomass dynamics of the submersed plant. We proved Theorem 1 which provides sufficient conditions (2-35) on the grass carp stocking rate $d_A$ and free-floating plant growth rate $r_L$ that guarantee the free-floating plant carrying capacity equilibrium is the only feasible equilibrium and is locally stable.

Although the model (2-1)–(2-3) is qualitative and not intended to give a detailed quantitative description of the biology, it may be analyzed without extensive numerical computations and the results are amenable to biological interpretation and experimentation. For example, (2-35) shows that the minimal stocking rate is the sum of the growth rate of the aboveground biomass for the submersed plant ($r_A$) and the rate at which the aboveground biomass supplies energy for growth of the belowground biomass ($s$). Both of these quantities depend on the particular species of submersed and floating plant being considered, but they may be measured experimentally and an experimentally determined stocking rate may then be compared with the minimal stocking rate predicted here. Similarly, the predicted hysteresis effect may be experimentally verified just as in [Scheffer et al. 2003].

Finally, we discuss some model weaknesses and future work. Grass carp were assumed to graze on aboveground biomass at a rate proportional to the amount of aboveground biomass, with $d_A$ the proportionality constant, resulting in the term $d_A A$ in (2-2). This is a linear functional response [Turchin 2003] in grass carp herbivory. The hyperbolic or Holling's type II functional response [Turchin 2003] is $kNA(D+A)^{-1}$. Here $A$ is the aboveground biomass of the submersed plant, $k$ is the maximum killing rate, $N$ is the number of grass carp, and $D$ is the prey (submersed plant) density at which the killing rate is half of the maximum. This functional response models a saturation of the grass carp feeding rate so that grass carp have a maximum rate of consumption ($kN$) of submersed plant biomass. Future work will include analysis of a model with hyperbolic functional response for the grass carp. We have also assumed spatial heterogeneity in our formulation of the model using ordinary differential equations. Future investigations will be to include modeling spatial heterogeneities in the ecosystem with partial differential equations.

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jalford@shsu.edu
*Mathematics and Statistics, Sam Houston State University,*
*P.O. Box 2206, Hunstville, TX 77341-2206, United States*

cab035@shsu.edu
*Mathematics and Statistics, Sam Houston State University,*
*P. O. Box 2206, Huntsville, TX 77341-2206, United States*

kxp004@shsu.edu
*Department of Chemistry, Sam Houston State University,*
*P. O. Box 2117, Huntsville, TX 77341-2117, United States*

cxh016@shsu.edu
*Mathematics and Statistics, Sam Houston State University,*
*P.O. Box 2206, Huntsville, TX 77341-2206, United States*

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| Józeph H. Przytycki | George Washington University, USA<br>przytyck@gwu.edu |
| Richard Rebarber | University of Nebraska, USA<br>rrebarbe@math.unl.edu |
| Robert W. Robinson | University of Georgia, USA<br>rwr@cs.uga.edu |
| Filip Saidak | U of North Carolina, Greensboro, USA<br>f_saidak@uncg.edu |
| James A. Sellers | Penn State University, USA<br>sellersj@math.psu.edu |
| Andrew J. Sterge | Honorary Editor<br>andy@ajsterge.com |
| Ann Trenk | Wellesley College, USA<br>atrenk@wellesley.edu |
| Ravi Vakil | Stanford University, USA<br>vakil@math.stanford.edu |
| Antonia Vecchio | Consiglio Nazionale delle Ricerche, Italy<br>antonia.vecchio@cnr.it |
| Ram U. Verma | University of Toledo, USA<br>verma99@msn.com |
| John C. Wierman | Johns Hopkins University, USA<br>wierman@jhu.edu |
| Michael E. Zieve | University of Michigan, USA<br>zieve@umich.edu |

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