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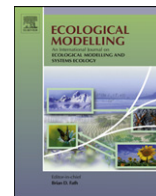
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Modeling ecosystem responses to prescribed fires in a phosphorus-enriched Everglades wetland: II. Phosphorus dynamics and community shift in response to hydrological and seasonal scenarios

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ABSTRACT

Fires have been proposed as one of the important options to manage and restore degraded wetlands through changing nutrient regimes; however, their effects on nutrient dynamics and community shift have not been studied sufficiently. In this study, wetland ecosystem model (WEM) was enhanced by incorporating plant competition, and applied to a moderately phosphorus-enriched area in the Everglades with a mixed cattail (*Typha domingensis*) and sawgrass (*Cladium jamaicense*) community. The WEM model was first validated by comparing simulated results against field observations, and applied to evaluate the effects of multiple surface fires on phosphorus (P) dynamics and the structure of a mixed cattail and sawgrass community. The simulation results indicated that a single fire could substantially alter the P dynamics in surface water for nearly two months, while multiple fires within a two-year interval, regardless of season, could cause a shift of plant community structure, expressed as a desirable increase in sawgrass and a decrease in cattail. After the successive fires, the biomass and composition of recovering plant community did not reach the pre-fire level within six years. Regardless of season, the fires conducted under the low-water-depth condition, compared with the high-water-depth condition, yielded stronger effects on P dynamics in soil, surface water, porewater, and on the plant community composition. Regardless of water depths, February fires, compared to July fires, caused a stronger shift in plant community structure expressed as a decrease in cattail biomass and an increase in sawgrass biomass. Regardless of seasons and water depths, fires caused a short-term increase and long-term decline in total phosphorus (TP) concentration in soil, surface water, and porewater. These results might suggest that the winter fires, under low-water-depth appear to be the best fire management option for accelerating recovery of a cattail-dominated wetland to a sawgrass-dominated wetland. In the proposed fire and hydrological regimes, four fires at two-year intervals generated the maximum suppressing effect on cattail, and the maximum stimulating effect on sawgrass. The results of this study support the concept that fire could be used as an option to manage plant composition and dominance. However, further process-based studies are necessary to explore additional fire regimes and hydrological scenarios to maintain sawgrass over cattail.

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1. Introduction

Wetlands have been recognized as one of the most valuable ecosystems in providing goods and services to human society, and wetland sustainability has become an important issue for

human society (Costanza et al., 1997; Wetzel, 2001; Mitsch and Gosselink, 2007). Therefore, a better understanding of wetland degradation mechanisms and exploration of potential solutions to slow or reverse this process have become an important issue facing human society (Zedler, 2000; Finlayson and Rea, 1999). Nutrient loading, especially phosphorus (P) and nitrogen (N) (Reddy et al., 1999; Reddy and DeLaune, 2008), and associated eutrophication (Wright et al., 2009), as well as the shift in community structure (Zedler and Kercher, 2004), have been recognized as a major cause and feature of wetland degradation and have drawn increasing attention from the public, government, and scientific

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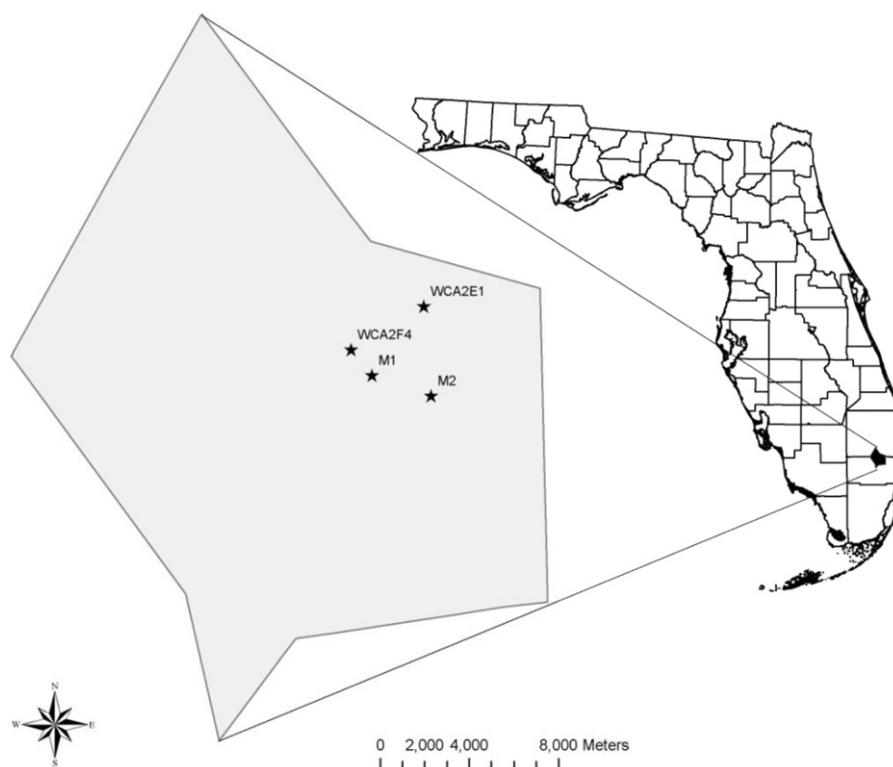


Fig. 1. A schematic diagram showing locations of study sites and monitoring stations for climate and other data (WCA2E1 and F4 are routine sites for water monitoring, water table, water temperature and nutrient concentration were measured in these sites; M1 and M2 are two sites chosen in the Fire Project; vegetation properties, including biomass and dead mass, TP in water and soil, and water and soil temperature were measured in these sites).

community (Zedler, 2000; Finlayson and Rea, 1999; NRC, 2007, 2008).

Regions of the Florida Everglades, in particular, have experienced a serious degradation during the past half century, characterized by P enrichment and the expansion of cattail (*Typha domingensis*) into the historical sawgrass (*Cladium jamaicense*) community (Miao and Sklar, 1998; NRC, 2007, 2008). A P gradient resulting from high P loading to the Everglades (DeBusk et al., 2001; Smith and McCormick, 2001) is associated with a parallel gradient of plant species (Reddy et al., 1999; Reddy and DeLaune, 2008; Miao and Sklar, 1998; Miao and DeBusk, 1999). For example, upstream highly P-enriched areas feature a cattail-dominated landscape; downstream moderately P-enriched areas feature cattail–sawgrass mixed vegetation coverage; while downstream reference areas feature a sawgrass-dominated landscape (DeBusk et al., 2001; Rutchey et al., 2008).

Many options have been proposed for Everglades' wetland restoration; however, most of them are still under debate (NRC, 2007, 2008). For example, natural recovery will be very slow and will likely take an undesirably long period of time to return to the pre-disturbance state (Burns and McDonnell, 2003). Additional human perturbation may result in pollutants reaching the undisturbed downstream area (Miao and Carstenn, 2005). Fire management, one potential restoration option, has been proposed but has not yet been well-documented in wetlands (Ponzio et al., 2004; Miao and Carstenn, 2005). Compared to other restoration methods, surface fires impact the plant community through direct combustion while not directly disturbing the enriched soil P storage. For this reason, primary surface fires will not greatly affect the P concentration downstream (Miao et al., 2009).

The moderately P-enriched area in the Everglades appears to be an ideal place for the evaluation of fire effects on P dynamics and community structure, because this area is the transition point along both the degradation and recovery trajectories (Miao and

Carstenn, 2005). A large-scale experiment, the Fire Project (Miao et al., 2009, 2010), was conducted, in part, within the moderately P-enriched wetland, to evaluate the effects of multiple surface fires on P dynamics and plant community shift (Fig. 1). However, it was not feasible for the Fire Project researchers to implement more than two burns for several reasons, such as difficulty in controlling water depths in field and the slow buildup of fuel biomass following a burn and the cost and labor necessary for field sampling. Therefore, the Fire Project researchers were unable to directly assess the effects of several successive surface fires on plant community composition and P dynamics.

Models aid us in resolving the time limitations of field experiments. In this case, a modeling effort allowed us to extend the study period beyond the two fires implemented by the Fire Project researchers. During the past decades, a few models have been developed to simulate P dynamics and/or plant growth in wetlands (Fitz and Tribble, 2006; Zhang et al., 2002; Wang and Mitsch, 2000; Chen and Twilley, 1999; Richardson et al., 1996; Wynn and Liehr, 2001; Wang et al., 2007); however, most of them lack the capacity for simulating one or more major components: plant growth, wetland hydrology, fire, or soil biogeochemistry. Because of this limitation, these models could not be used for the Fire Project (Tian et al., 2010). In a previous study, the wetland ecosystem model (WEM) was developed to evaluate the effects of a prescribed fire on P dynamics and plant growth in a highly P-enriched area of the Everglades (Tian et al., 2010). The model was also used to evaluate the effects of fire on P dynamics and cattail regrowth in highly and moderately P-enriched areas. In this study, the extant model was enhanced to incorporate two plant species (sawgrass and cattail) and their competition for light, nutrients, and space. The model was calibrated, validated, and then applied to a moderately P-enriched Everglades wetland to evaluate the multiple-fire effects on P dynamics and plant community structure.

The objectives of this study were: (1) to enhance the extant WEM in simulating a mixed cattail–sawgrass community; (2) to verify the WEM's ability to simulate P dynamics and growth of cattail and sawgrass in a moderately enriched area; (3) to further apply the WEM to evaluate fire effects on P dynamics and post-fire dynamics of cattail and sawgrass biomass and dead mass; and (4) to estimate the fire effects on the shift of the cattail–sawgrass community. The present study, in combination with the results obtained from field experiments, should provide important information for managers deciding whether fire could be used as a tool to alter the P dynamics and plant community with the result of accelerating restoration in nutrient-enriched areas of the Everglades.

2. Materials and methods

2.1. Model description

The WEM was developed to evaluate the effects of fires on plant growth and P dynamics in natural wetland ecosystems (Tian et al., 2010). Detailed information could be found in the [supplementary online material](#). Four major modules (fire, water chemistry, soil, and vegetation) were included. The conceptual diagram of the WEM could be referred to in Tian et al. (2010). The WEM used a daily time step with some physiological and hydrological processes being updated every 30 min; for instance, heat transfer between different water and soil layers and nutrient ion diffusion in the water matrix were simulated in a time step of half an hour. The daily time step was chosen because the dynamics of the ecosystem and cycling of P in the system can be easily captured and described computationally at this scale. The WEM was developed using the C++ programming language.

The vegetation module simulated plant growth, carbon (C) cycling, and nutrient uptake and accumulation in plants. The soil module simulated the dynamics of C, N, and P in soil as well as other physical and chemical properties (e.g. soil thermal dynamics). The water chemistry module was used for simulating the water budget, consisting of input from rainfall and upstream inflow, water losses from evapo-transpiration (ET) and downstream outflow, and the associated nutrients. The fire module considered biomass burning and nutrient deposition (mainly as ash) into the ecosystem as the key nutrient recycling process, and the diffusion and downwind transport of ash as the main nutrient export process from the experimental plot. Compared to previous studies (Tian et al., 2010), the model's inclusion of plant competition allowed this study to focus on a plant community shift between cattail and sawgrass. The detailed information and equations could be found in [supplementary online material](#).

2.2. Model implementation, calibration and validation

The initial conditions for the WEM are defined in Table 1. The WEM test simulation was prepared with the input data, and then the major parameters were tuned to conduct the calibration process (Table 2).

The WEM was calibrated against the field data from an unburned control plot, and then validated against the field data from a burned plot monitored by the Fire Project (Miao et al., 2010) (Table 3). Continuous inflow and outflow prevented a hydrological equilibrium from existing in this system. Therefore, multi-year average daily climatic data and inflow data for 1998–2008 were used to reiterate the model for 50 years, and then the simulation was extended to cover the time period of 1998–2030. The three-year average of 2006–2008 climate data was used as the driving force for the post-2008 simulation since the climate condition for these three years are close to the multiple-year average. The 50-year period

for model reiteration was selected because P loading to the Everglades occurred over the past half century (Miao and DeBusk, 1999; NRC, 2007, 2008). The cell size for the simulation was set at 300 m × 300 m to be consistent with the Fire Project field experiment (Miao et al., 2009, 2010).

2.3. Data sources

Data for the model simulation in this study included routine climatic datasets, such as air temperature, rainfall, solar radiation, Photosynthetically Active Radiation (PAR), and inflow water and associated nutrient dynamics. These data were retrieved from the DBHYDRO database at <http://my.sfwmd.gov>. All climate data were measured at the site WCA2F4, which was the only weather station located in WCA-2A (DBHYDRO database) (Fig. 1). Water level data were measured at site WCA2AE1. Because no water outflow data were available for the specific study area, reference water level data were used as the control for the water depth fluctuation in the simulations. Both N and P atmospheric deposition rates were assumed to occur evenly throughout the time period. Based on a synthesis of field observations (Brezonik and Pollman, 1999), the N deposition was set as 0.002 g N/day, and the P deposition was set as 0.00015 g P/day. All other data, including vegetation, water chemistry and soil data were from the Fire Project and/or the literature (Table 3).

2.4. Statistical methods used to compare the model and data fit

As same as our previous study (Tian et al., 2010), a total of five criteria were used to evaluate the modeled results against the observations. The first criterion was the coefficient of determination (R^2) which was calculated as the correlation between observations and predictions; a higher R^2 value means better model performance. The second criterion was the Theil's inequality coefficient U (Theil, 1966; Blanco et al., 2007). Parameter U could be 0 or greater than 1. A resulting $U=0$ meant a perfect fit between the model results and observations; a larger U value meant poorer model performance (Blanco et al., 2007). The third criterion used was modeling efficiency (ME) (Vanclay and Skovsgaard, 1997). A resulting ME = 1 indicated a perfect fit, ME = 0 reveals that the model was no better than a simple average, and negative values indicated poor performance. The fourth criterion was the average absolute bias (AAB), expressed as a percentage (Tian et al., 2010). A resulting AAB = 0 meant a perfect fit, a lower negative AAB or a higher positive AAB indicated worse model performance. The fifth criterion, equivalence testing, is a powerful method to evaluate the comparison between observations and predictions (Fujisaki et al., 2009). Contrasted with the traditional t -tests, the equivalence test evaluates the null hypothesis of dissimilarity. Two criteria (ε) were expressed relative to the sample standard deviation (25% and 50%) to represent a "strict" and "liberal" criterion, respectively, according to the guidelines in Wellek (2003). The t -value was calculated as follows:

$$td = \frac{\bar{D}_i}{s_{Di}}$$

D_i = observed _{i} – predicted _{i} The calculated t value was then compared with the cutoff value of C , which is the α -quantile (0.05 in this study) of the non-central F distribution with degrees of freedom $\nu_1 = 1$ and $\nu_2 = n - 1$ and non-centrality parameter $\lambda = n\varepsilon^2$. If the t value was lower than the cutoff value, the null hypothesis of dissimilarity was rejected (Robinson and Froese, 2004). In essence, the test was used to check whether the critical value of a two-tailed F distribution (the C parameter) was contained within the rejection region defined by the selected criteria ($-\varepsilon, +\varepsilon$) (Blanco et al., 2007).

Table 1

Initial Conditions for the WEM in simulation of a moderately P-enriched area in the Everglades (POC, particulate organic carbon; PON, particulate organic nitrogen; POP, particulate organic phosphorus; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; DOP, dissolved organic phosphorus).

Parameters	Values	References
<i>Soil conditions (top 0.3 m)</i>		
Bulk density (g/cm ³)	0.069	Fire Project; Reddy and DeLaune (2008)
Soil C (μg C/cm ²)	11430.88	Fire Project
Soil N (μg N/cm ²)	734.05	Fire Project
Soil P (μg P/cm ²)	7.33	Fire Project
<i>Nutrients in surface water</i>		
NH ₄ (mg N/L)	0.0120	Qualls and Richardson (2003)
NO ₃ (mg N/L)	0.0145	Qualls and Richardson (2003)
PO ₄ (μg P/L)	17.22	Qualls and Richardson (2003)
POC (mg C/L)	3.5406	Qualls and Richardson (2003); Fire Project
PON (mg N/L)	0.1186	Qualls and Richardson (2003); Fire Project
POP (μg P/L)	0.304	Qualls and Richardson (2003); Fire Project
DOC (mg C/L)	30.9084	Qualls and Richardson (2003); Fire Project
DON (mg N/L)	1.1356	Qualls and Richardson (2003); Fire Project
DOP (μg P/L)	2.916	Qualls and Richardson (2003); Fire Project
<i>Nutrients in pore water</i>		
NH ₄ (mg N/L)	0.0230	Fire Project
NO ₃ (mg N/L)	0.02778	Fire Project
PO ₄ (μg P/L)	13.31	Fire Project
POC (mg C/L)	3.5406	Calculated based on surface water concentration and Fire Project observations
PON (mg N/L)	0.2278	Calculated based on surface water concentration and Fire Project observations
POP (μg P/L)	0.235	Calculated based on surface water concentration and Fire Project observations
DOC (mg C/L)	33.908	Fire Project
DON (mg N/L)	2.1815	Calculated based on surface water concentration and Fire Project observations
DOP (μg P/L)	2.253	Calculated based on surface water concentration and Fire Project observations
<i>Cattail biomass</i>		
Leaf (C, N, P) (g/m ²)	237, 4.0169, 0.147	Fire Project
Shoot base (C, N, P) (g/m ²)	222.5, 3.7712, 0.069	Fire Project
Rhizome (C, N, P) (g/m ²)	123, 1.7083, 0.020	Fire Project
Root (C, N, P) (g/m ²)	134, 1.86, 0.022	Fire Project
<i>Sawgrass biomass</i>		
Leaf (C, N, P) (g/m ²)	79, 1.13, 0.079	Fire Project
Shoot Base (C, N, P) (g/m ²)	74.2, 1.37, 0.212	Fire Project
Rhizome (C, N, P) (g/m ²)	41, 0.68, 0.055	Fire Project
Root (C, N, P) (g/m ²)	44.7, 1.28, 0.045	Fire Project

The power of this test was calculated using the following equation (Wellek, 2003):

$$\beta_{\alpha; n-1}(\varepsilon) = 2Ft(C_{\alpha; n-1}(\varepsilon)) - 1$$

where Ft is the cumulative distribution function for the non-central t -distribution (Robinson and Froese, 2004).

2.5. Simulation designs

A total of eight simulations were set up (Table 4). The first one (Sc) was used for comparison purpose; the second one (S0) was used for model validation. Six additional simulations were run to evaluate the effects of fires under different hydrological and seasonal scenarios on TP concentrations in surface water, porewater, and plant community. The two hydrologic scenarios consisted of a high-water-depth (0.5 m) and a low-water-depth (0.1 m) condition. The water depth was manipulated for 10 days pre-fire and 90 days post-fire, for each fire. The two seasonal burn scenarios included February and July burns. All the simulated fires occurred at two-year intervals and were run for ten successive burns.

Specifically, the Sc run simulated ecosystem dynamics without burns; the S0 run simulated two fires, a February fire in 2006 and an July fire in 2008, and was used for model validation. The third simulation (S1) consisted of a fire under low-water-depth conditions in 2006 and multiple fires under high-water-depth conditions during 2008–2024 occurring at two-year intervals. The fourth simulation (S2) included fires occurring at two-year intervals during 2006–2024 under low-water-depth conditions. Simulations S4 and S5 included the fires under identical conditions to S1 and S2, respectively, except that the fires occurred in February. The remaining two

simulations were run under field hydrological conditions for 2006 and 2008, then the low-water-depth scenario was used for the fires during 2010–2024; these two simulations were S3 (July fires) and S6 (February fires).

All scenarios were used for the analysis of the effects of fire on P dynamics and plant growth. A comparison of the S1 and S2 simulations was used to reveal the hydrological effects on the July fire impacts; a comparison of the S4 and S5 simulations was used to reveal the hydrological effects on the February fire impacts; and a comparison of the S3 and S6 simulations was used to reveal the fire impacts in different seasons. The effects of fire on P concentration in surface water and porewater, and the biomass and dead mass of cattail and sawgrass were evaluated.

3. Results

3.1. Model performance evaluation

The WEM was verified by comparing simulated results against field data collected by the Fire Project in the burned plot (Figs. 2–5). Simulated surface water and soil temperatures were consistent, both seasonally and quantitatively, with field measurements (Fig. 3). Approximately 84% of the variability in observed surface water temperature, 82% in soil temperature, 26% in surface water TP, and 15% of the variability in observed porewater TP were captured by the simulations (Fig. 4). These goodness-of-fits indicated the robustness of WEM in simulating hydrological processes and soil physical processes in this ecosystem. It should be noted that the simulated P in surface and pore water were not matched very well with observations; this implies the complexity of P dynamic and needs for improvements on P simulations. The simulated biomass

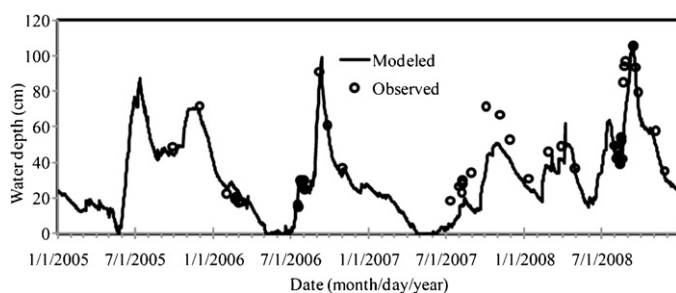
Table 2

Major parameters for the WEM in simulation of a moderately P-enriched area in the Everglades (LAI, leaf area index; PON, particulate organic nutrient (C, N, and P)).

Parameters	Values	References
<i>Plant (cattail)</i>		
Maximum biomass carbon (g C/m ²)	750	Fire Project; Reddy et al., 1999
Maximum Height (m)	2.5	Fire Project; Reddy et al., 1999
Maximum LAI (m ² /m ²)	4.0	Fire Project; Reddy et al., 1999
Mortality (g C/g C)	0.0055	Fire Project; calibrated ^a
Respiration (leaf, rhizome, shoot-base, root) (g C/g C)	0.0000025–0.00005	Fire Project; Reddy et al., 1999; calibrated ^a
Leaf C:N ratio (g C/g N)	70	Fire Project; Reddy et al., 1999; calibrated ^a
Leaf C:P ratio (g C/g N)	1000	Fire Project; Reddy et al., 1999; calibrated ^a
Rhizome C:N ratio (g C/g N)	60	Fire Project; Reddy et al., 1999; calibrated ^a
Rhizome C:P ratio (g C/g N)	750	Fire Project; Reddy et al., 1999; calibrated ^a
Shoot-base C:N ratio (g C/g N)	54	Fire Project; Reddy et al., 1999; calibrated ^a
Shoot-base C:P ratio (g C/g N)	350	Fire Project; Reddy et al., 1999; calibrated ^a
Root C:N ratio (g C/g N)	35	Fire Project; Reddy et al., 1999; calibrated ^a
Root C:P ratio (g C/g N)	1000	Fire Project; Reddy et al., 1999; calibrated ^a
Nitrogen resorption (g N/g N)	0.45	Fire Project; Reddy et al., 1999; calibrated ^a
Phosphorus resorption (g P/g P)	0.75	Fire Project; Reddy et al., 1999; calibrated ^a
<i>Plant (sawgrass)</i>		
Maximum biomass carbon (g C/m ²)	650	Fire Project; Reddy et al., 1999
Maximum height (m)	2.0	Fire Project; Reddy et al., 1999
Maximum LAI (m ² /m ²)	4.0	Fire Project; Reddy et al., 1999
Mortality (g C/g C)	0.0065	Fire Project; calibrated ^a
Res (leaf, rhizome, shoot-base, root) (g C/g C)	0.000065–0.00035	Fire Project; Reddy et al., 1999; calibrated ^a
Leaf C:N ratio (g C/g N)	70	Fire Project; Reddy et al., 1999; calibrated ^a
Leaf C:P ratio (g C/g N)	1000	Fire Project; Reddy et al., 1999; calibrated ^a
Rhizome C:N ratio (g C/g N)	60	Fire Project; Reddy et al., 1999; calibrated ^a
Rhizome C:P ratio (g C/g N)	750	Fire Project; Reddy et al., 1999; calibrated ^a
Shoot-base C:N ratio (g C/g N)	54	Fire Project; Reddy et al., 1999; calibrated ^a
Shoot-base C:P ratio (g C/g N)	350	Fire Project; Reddy et al., 1999; calibrated ^a
Root C:N ratio (g C/g N)	35	Fire Project; Reddy et al., 1999; calibrated ^a
Root C:P ratio (g C/g N)	1000	Fire Project; Reddy et al., 1999; calibrated ^a
Nitrogen resorption (g N/g N)	0.45	Fire Project; Reddy et al., 1999; calibrated ^a
Phosphorus resorption (g P/g P)	0.75	Fire Project; Reddy et al., 1999; calibrated ^a
<i>Hydrological</i>		
PON sedimentation (g Nutrient/g Nutrient)	0.05	Calibrated ^a
Diffusion (g Nutrient/g Nutrient/h)	0.03–0.055	Reddy et al., 1999; calibrated ^a
<i>Soil</i>		
Bottom temperature (°C)	5	Fire Project; calibrated ^a
Maximum absorbed NH ₄ (g N/m ³)	25	Calibrated ^a ; Reddy et al., 1999
Half-saturation coefficient of adsorbed NH ₄ (g N/m ³)	5	Calibrated ^a ; Reddy et al., 1999
Maximum absorbed NO ₃ (g N/m ³)	25	Calibrated ^a ; Reddy et al., 1999
Half-saturation coefficient of adsorbed NO ₃ (g N/m ³)	5	Calibrated ^a ; Reddy et al., 1999
Maximum absorbed PO ₄ (g N/m ³)	2.5	Calibrated ^a ; Reddy et al., 1999
Half-saturation coefficient of adsorbed PO ₄ (g N/m ³)	0.5	Calibrated ^a ; Reddy et al., 1999
<i>Fire</i>		
Fire intensity (fraction of litter burned out)	0.9	Fire Project; calibrated ^a
Leaf carbon fire efficiency (gCO ₂ /g C)	0.7	Fire Project; calibrated ^a
Leaf nitrogen fire efficiency (gNO ₃ /g C)	0.55	Fire Project; calibrated ^a
Litter carbon fire efficiency (gCO ₂ /g C)	0.95	Fire Project; calibrated ^a
Litter nitrogen fire efficiency (gNO ₃ /g C)	0.9	Fire Project; calibrated ^a

^a Parameters were adjusted to make the output comparable against the observed data.

and dead mass of cattail and sawgrass around first fire match the observations (Table 5). Given the hardness of soil sampling processes in natural wetlands, there are large uncertainties in field data. The WEM simulation results show obvious seasonal variations in plant biomass and dead mass, yet the observations did not.

**Fig. 2.** Comparison of WEM-derived water depth against field observations.

The model performance was also evaluated by four other common criteria applied in the model literature (Tian et al., 2010) including: the Theil's index (U), modeling efficiency (ME), average absolute bias, and equivalence test (Table 6). Low U index for the comparisons of modeled and observed variables indicated good performance in simulating most variables. The calculated modeling efficiencies showed that the WEM performed well in simulating water depth, water and soil temperatures, aboveground biomass, and dead mass of cattail, and sawgrass aboveground biomass, but it did not perform well in simulating cattail and sawgrass belowground biomass and dead mass. The average absolute bias showed that the WEM performed well for simulating all variables except porewater TP, and sawgrass aboveground dead mass and belowground biomass. The equivalence test showed that the WEM performed well in simulating soil temperature and sawgrass aboveground dead mass, but it did not do so well in simulating all other variables. Although different criteria showed slightly different results, the WEM is argued to be reliable in simulating water depth, water, soil temperature, aboveground biomass, and did fairly well simulating surface water and porewater TP, and belowground

Table 3

Site descriptions including major parameters and observational data used to calibrate and test the WEM model (most of the input data and portions of data for calibration are from DBHYDRO, the online dataset in South Florida Water Management District).

Site name	Location	Variables	Data sources
Major input data			
WCA2F4	N26.32, W80.38	Rainfall, solar radiation, air temperature, PAR	DBHYDRO
WCA2E1	N26.35, W80.35	Reference water depth	DBHYDRO
Gainesville, Cedar Key, Apopka, Belle Glade	Four sites average	N and P deposition	Brezonik and Pollman (1999)
Site and major parameters for model calibration			
M1 (unburned area)	N26.32, W80.37–N26.53, W80.63	Cattail aboveground biomass Cattail belowground biomass Cattail aboveground dead mass Cattail belowground dead mass Water depth Surface water TP Soil TP	Fire Project Fire Project Fire Project Fire Project Fire Project Fire Project Fire Project
Site and major parameters for model validation			
M2 area	N26.31, W80.35–N26.53, W80.59	Cattail aboveground biomass Cattail belowground biomass Cattail aboveground dead mass Cattail belowground dead mass Water depth Surface water TP Soil TP Soil and surface water temperature	Fire Project Fire Project Fire Project Fire Project Fire Project Fire Project Fire Project Fire Project

Table 4

Detailed information of simulation design for July and February fires under two hydrological scenarios (the hydrology was shown as 10 days pre-fire water depth and 90 days post-fire water depth).

Fire season		Hydrology in different years (water depth as m)		
		2006	2008	2010–2024
Sc	No burns			
S0	1st fire on February 20, 2006; 2nd fire on August 13, July 2008	Real condition (0.27 and 0.27)	Real condition (0.39 and 0.39)	
S1	July, 25, 2006–2024	0.1 and 0.1	0.5 and 0.5	0.5 and 0.5
S2	July, 25, 2006–2024	0.1 and 0.1	0.1 and 0.1	0.1 and 0.1
S3	July, 25, 2010–2024	Real condition (0.27 and 0.27)	Real condition (0.39 and 0.39)	0.1 and 0.1
S4	February, 25, 2006–2024	0.1 and 0.1	0.5 and 0.5	0.5 and 0.5
S5	February, 25, 2006–2024	0.1 and 0.1	0.1 and 0.1	0.1 and 0.1
S6	February, 25, 2010–2024	Real condition (0.27 and 0.27)	Real condition (0.39 and 0.39)	0.1 and 0.1

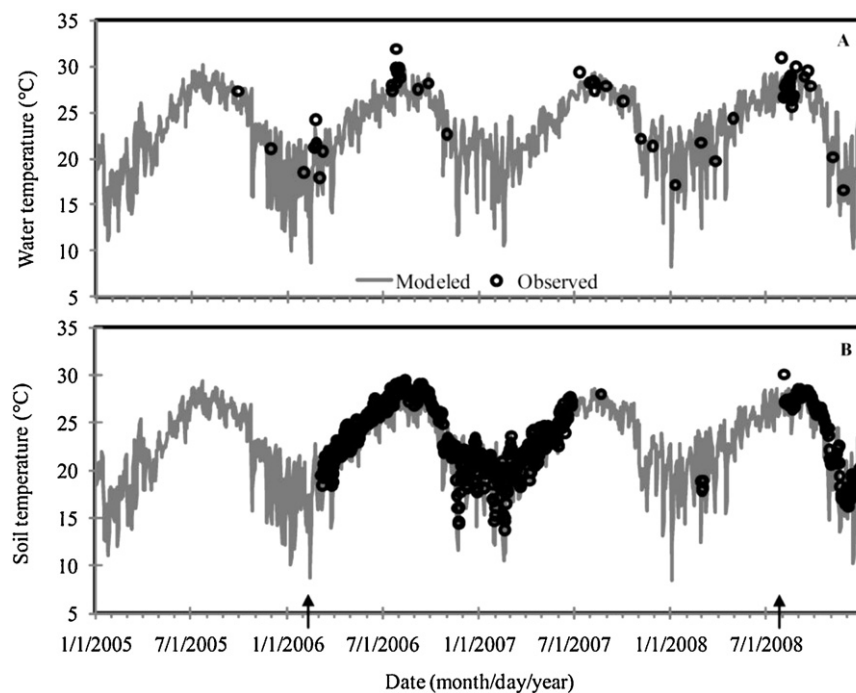


Fig. 3. Comparison of WEM-derived (A) water temperature and (B) soil temperature against observations (arrows indicate the occurrence of fires).

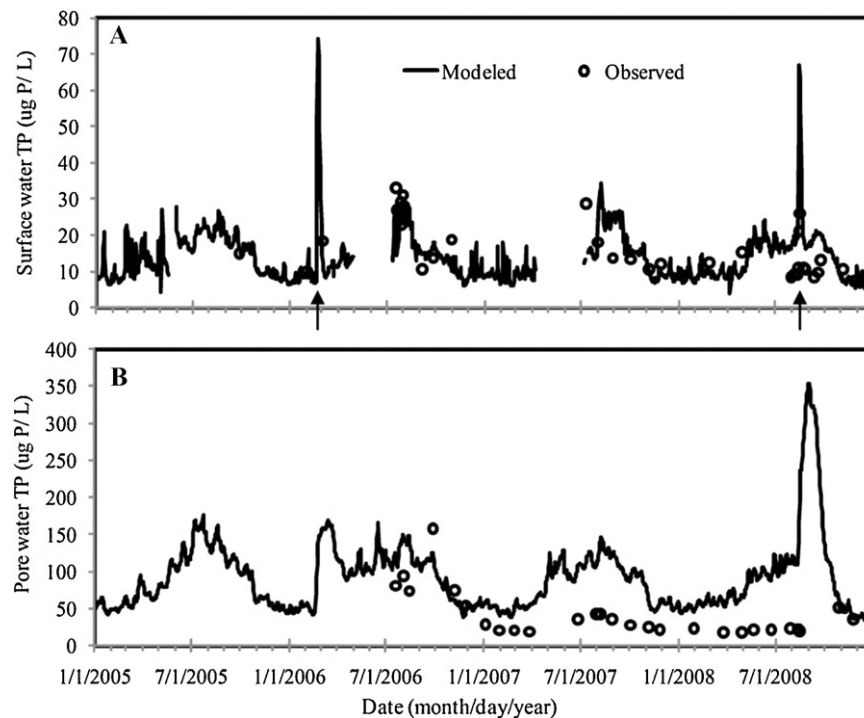


Fig. 4. Comparison of WEM-derived surface water TP (A) and porewater TP (B) against observations (arrows indicate the occurrence of fires).

biomass and dead mass. Due to the small number of sampling data points, one date before a fire was selected to show the model's ability in simulating pre-fire plant biomass and dead mass for mixed cattail and sawgrass community (Table 5).

3.2. Fire effects on TP in water and soil under different hydrological scenarios

Fires usually generate strong effects on nutrient dynamics in water and soil (Wan et al., 2001). Fire-induced ash return will increase water nutrient concentration in short term. The simulation results show that the first July fire induced a pulse of TP in the surface water as high as 76 $\mu\text{g P/L}$ (Fig. 6A); while the first February fire caused a pulse of TP in the surface water as high as 66 $\mu\text{g P/L}$, compared to a background TP concentration in the surface water of 5–15 $\mu\text{g P/L}$ (Fig. 6B). The fire-induced pulses in surface water TP were similar for each fire, with smaller and smaller TP pulse magnitudes caused by successive fires. Compared to the background

TP concentrations in porewater at 20–100 $\mu\text{g P/L}$ (Fig. 7B), induced a pulse of TP concentration was as high as 418 $\mu\text{g P/L}$ in July fire and 259 $\mu\text{g P/L}$ in the first February fire (Fig. 7A). The fire-induced pulses in porewater TP concentration were similar for each fire, with a reduction in magnitude of the TP pulse caused by the successive fires. Porewater TP concentrations were similarly affected by fires as surface water TP, yet in higher concentrations.

The fires under low-water-depth conditions during 2008–2024 generated higher short-term TP pulses than those under high-water depth; however, soon after the TP pulses, the surface water TP concentration following the high-water-depth-fires became higher than that following low-water-depth-fires (Fig. 6). It is same for porewater TP (Fig. 7). Overall, the concentrations of TP in surface water and porewater declined over time with successive fires. After the fires were terminated, the TP concentration increased, but did not reach pre-fire levels within the following six years (Fig. 8).

There was an obvious seasonality in TP concentrations in surface- and porewater pre-fire (Figs. 6 and 7), indicating the seasonal variations in sources or sinks of TP, or both. Comparisons between Figs. 6 and 7(A and B), reveal that the July fires caused a larger pulse of TP than the February fires. This is probably because the July fire consumed more plant biomass and dead mass and provided more ash to the surface water (Fig. 9). This resulted in the deposition of more particulate organic P, the major source of TP in surface waters (Salas et al., 2003). The porewater TP concentration was directly controlled by surface water TP in the short-term, so it had a similar response to July and February fires (Figs. 6 and 7). In summary, regardless of the hydrological condition, the July fires generated similar effects on the increases of TP in surface- and porewater, but in larger magnitude, than February fires.

Soil TP concentrations changed in response to July and February fires under low-water-depth and high-water-depth conditions, and the results were summarized in Fig. 8. The first July fire induced an increase of soil TP concentration as high as 0.52 g P/m³ two months post-fire compared to the unburned simulation (Fig. 8A); while the first February fire caused an increase of soil TP concentration as high as 0.23 g P/m³ two months post-fire compared to the

Table 5
Comparison of simulated ecosystem properties to observed data on the peak date of the year previous to first fire (August 4, 2005) for biomass and dead mass.

Variables	Simulated	Observed
Cattail aboveground biomass (g/m ²)	580.67	531.0
Cattail aboveground dead mass (g/m ²)	1108.3	1033.0
Cattail belowground biomass (g/m ²)	1302.0	955.4
Cattail belowground dead mass (g/m ²)	1508.1	1396.0
Sawgrass aboveground biomass (g/m ²)	32.4	50.0
Sawgrass aboveground dead mass (g/m ²)	73.0	§
Sawgrass belowground biomass (g/m ²)	33.3	6.8
Sawgrass belowground dead mass (g/m ²)	528.8	606.0
Surface water TP ($\mu\text{g P/L}$) [*]	23.75	22.0
Porewater TP ($\mu\text{g P/L}$) ^{**}	80.0	80.7
Soil TP (g P/m ³)	52.6	47.4

^{*} Simulated and observed surface water TP concentrations are 5-day post-fire average.

^{**} Simulated and observed porewater TP concentrations are 150-day post-fire average.

§ No observations.

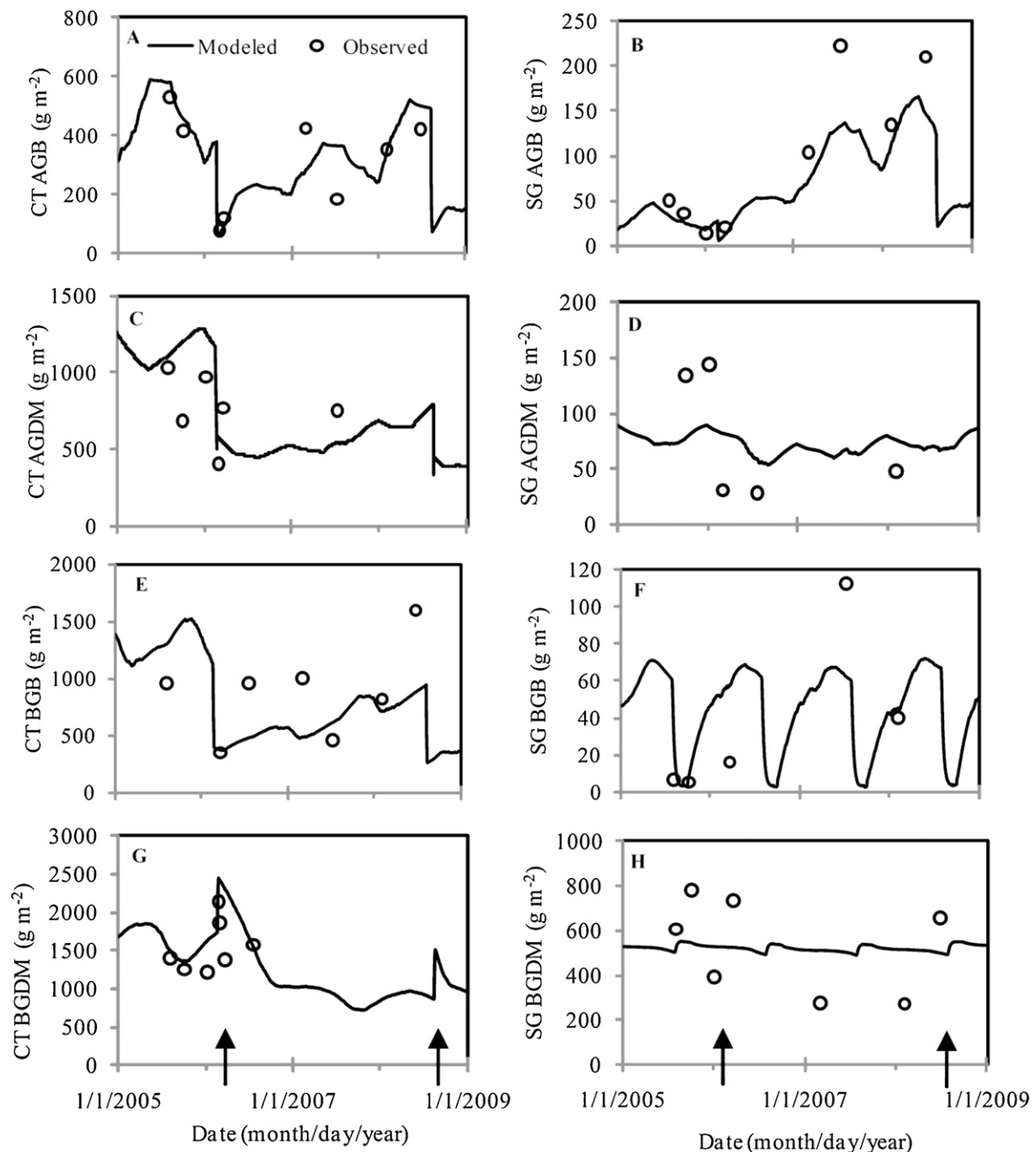


Fig. 5. Comparison of WEM-derived aboveground biomass (AGB), aboveground dead mass (AGDB), belowground biomass (BGB), and belowground dead mass (BDM) against data collected by the Fire Project for cattail (CT) and sawgrass (SG) (arrows indicate the occurrence of fires).

unburned simulation (Fig. 8B). Three months post-fire, a decrease in soil TP was observed for all simulation scenarios. For both July and February fires, lower water depth enhanced the fire effects on the soil TP concentration decline (Fig. 8).

3.3. Fire effects on biomass and dead mass of cattail and sawgrass under different hydrological scenarios

Fires could change vegetation community by generating different effects on various plant species (Flores et al., 2011). Fig. 9 shows the dynamics of cattail and sawgrass above- and below-ground biomass and dead mass in response to July fires under high-water-depth and low-water-depth conditions. As anticipated,

fire was predicted to reduce the cattail and sawgrass biomass and dead mass immediately. In 2008 the low-water-depth fire directly consumed the cattail aboveground biomass, reducing it from 462 g/m² to 81 g/m², and to as low as 29 g/m² one week later; while the high-water-depth fire decreased the cattail aboveground biomass from 462 g/m² to 101 g/m², and to as low as 80 g/m² a few days later. Throughout the simulation period, fires caused decreases in cattail biomass and dead mass, and increases in sawgrass biomass and dead mass (Fig. 9A–D). Fire-induced increases in sawgrass aboveground biomass were as high as 151 g/m² for fires under low-water-depth, and as high as 131 g/m² for fires under high-water-depths (Fig. 9). In summary, fires under low-water-depths caused slightly stronger

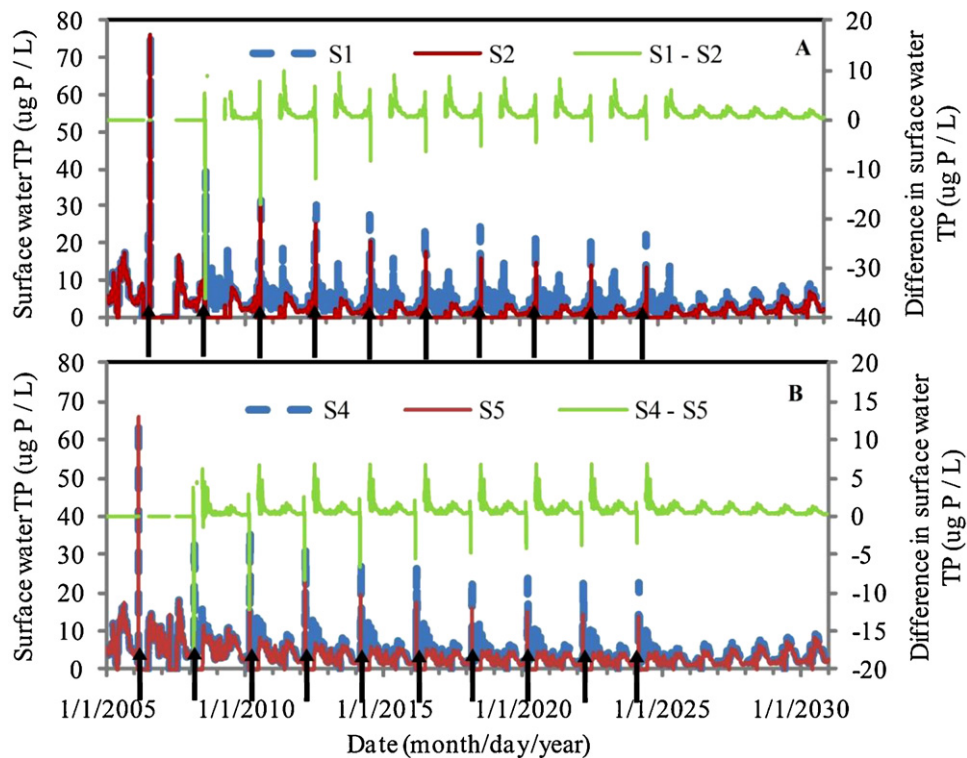


Fig. 6. TP concentrations in surface water in response to fires in (A) July and (B) February under different hydrological scenarios. While S1 and S4 refer to: high-water-depth, S2 and S5 to low-water-depth; and S1–S2 and S4–S5 to the differences of TP concentrations in surface water between fires under high and low water depths (arrows indicate the occurrence of fires).

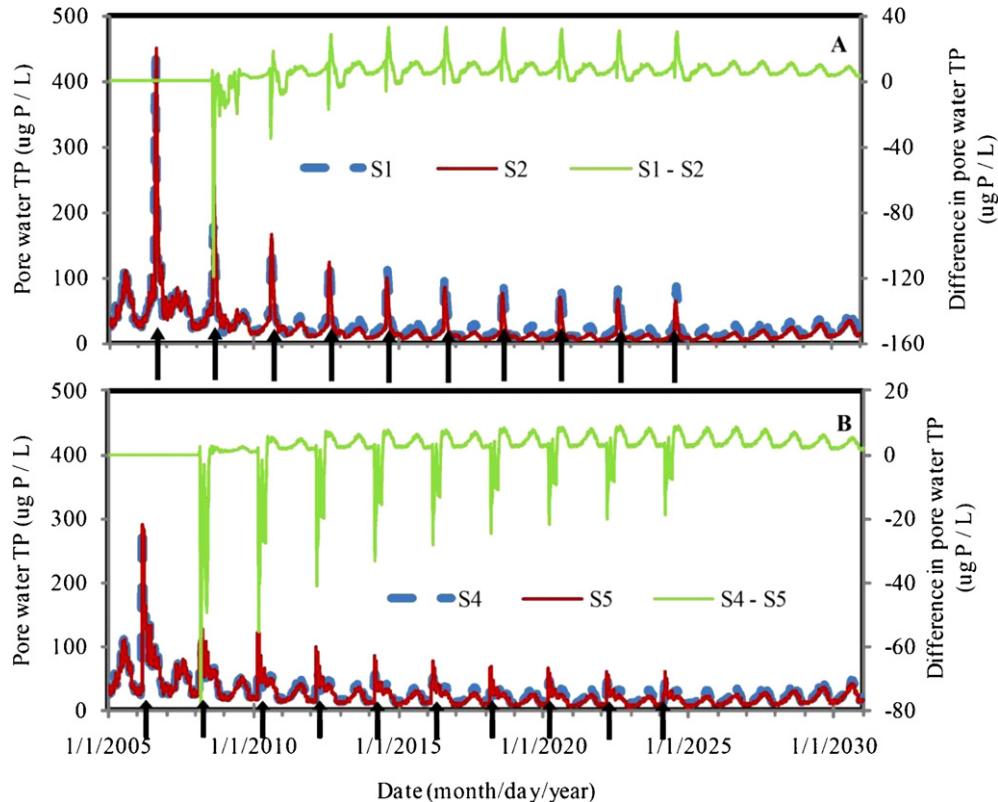


Fig. 7. TP concentration in porewater in response to fires in (A) July and (B) February under different hydrological scenarios (S1: high-water-depth; S2: low-water-depth; S4: high-water-depth; S5: low-water-depth; the differences in TP concentration in surface water (S1–S2 and S4–S5) show the hydrological effects on fire impacts on surface water TP; arrows indicate the occurrence of fires).

Table 6
Statistical comparison of the overall fit of model outputs against field data (see footnotes).

Statistic	Water depth	Water temperature	Soil temperature	Surface water TP	Porewater TP	CTAGB	CTAGDM	CTBGB	CTBGDM	SWAGB	SWAGDM	SWBGB	SWBGDM
R^2	0.84	0.84	0.82	0.26	0.15	0.74	0.33	0.19	0.48	0.97	0.34	0.42	0.18
U	0.23	0.06	0.08	0.42	1.34	0.26	0.36	0.43	0.29	0.34	0.50	0.59	0.34
ME	0.69	0.81	0.77	-0.15	-1.00	0.72	0.22	-0.95	-0.11	0.31	-21.41	-1.58	-240.56
Average absolute bias (%)	-11.51	-1.18	-3.60	27.38	180.95	7.01	16.50	-11.29	22.36	-24.85	52.07	133.76	16.60
$ t_d $	4.99	1.97	13.20	2.01	5.83	0.57	0.89	1.23	2.63	2.74	0.002	0.34	0.11
$C (\varepsilon = 25\%)$	0.12	0.14	21.46	0.06	0.03	0.007	0.006	0.007	0.007	0.007	0.006	0.006	0.007
$C (\varepsilon = 50\%)$	4.30	4.72	118.03	2.74	1.28	0.031	0.019	0.024	0.024	0.031	0.015	0.015	0.024
Diss ($\varepsilon = 25\%$)	NR	NR	R	R	NR	NR	NR	NR	NR	NR	R	NR	NR
Diss ($\varepsilon = 50\%$)	NR	R	R	R	NR	NR	NR	NR	NR	NR	R	NR	NR
$\beta (\varepsilon = 25\%)$	0.9996	0.9996	1	0.99	0.94	0.38	0.29	0.33	0.33	0.38	0.24	0.24	0.33
$\beta (\varepsilon = 50\%)$	1	1	1	1	1	0.95	0.86	0.92	0.92	0.95	0.78	0.78	0.92
N	56	59	633	44	31	8	6	7	7	8	5	5	7

Notes: R^2 , coefficient of determination; U, Theil's coefficient; ME, modeling efficiency; t_d , equivalent t value; C, criteria of 25% and 50%; Diss, hypothesis of dissimilarity (NR, not rejected; R, rejected); β , power of the equivalence test (see text for details); CT, cattail; SW, sawgrass; AGB, aboveground biomass; ADM, aboveground dead mass; BGB, belowground biomass; BGD, belowground dead mass).

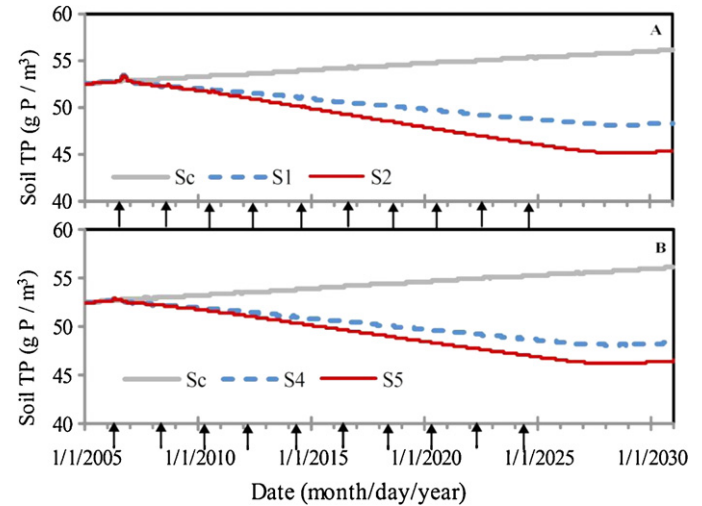


Fig. 8. Soil TP concentration in response to fires in (A) July and (B) February under different hydrological scenarios (Sc; control simulation; S1: high-water-depth; S2: low-water-depth; S4: high-water-depth; S5: low-water-depth; arrows indicate the occurrence of fires).

effects on biomass and dead mass than fires under high-water-depths.

Fig. 10 shows the dynamics of cattail and sawgrass above- and belowground biomass and dead mass in response to February fires under high-water-depth and low-water-depth conditions. Fires immediately reduced cattail and sawgrass biomass and dead mass. In 2008, the low-water-depth fires directly consumed the cattail aboveground biomass, and reduced it from 372 g/m² to 64 g/m², and to as low as 25 g/m² one week later; while the high-water-depth fires decreased cattail aboveground biomass from 372 g/m² to 147 g/m², and to as low as 55 g/m² a few days later. At the annual time scale, fires caused decreases in cattail biomass and dead mass, and increases in sawgrass biomass and dead mass (Fig. 10A–D). Fire-induced increases in sawgrass aboveground biomass were as high as 137 g/m² for fires under low-water-depths, and 119 g/m² for fires under high-water-depths (Fig. 10). In summary, fires under low-water-depths caused a slightly stronger effect on biomass and dead mass than those under high-water-depths.

3.4. Fire effects on the structure of cattail–sawgrass community

To further assess the fire effects on the structure of mixed cattail and sawgrass community, above- and belowground biomass of both species were compared. The fires reduced the growth of cattail above- and belowground biomass, while stimulating sawgrass above- and belowground biomass (Fig. 11). Thus, the fires changed the community structure relative to the biomass of cattail and sawgrass, in less than two years. After the first fire, the following fires continued exerting suppressing effects on cattail, indirectly stimulating effects on sawgrass, until the fourth fire. After four fires, the fraction of cattail and sawgrass biomass remained relatively stable. When the fires were terminated, the cattail recovered and outcompeted sawgrass to dominate the community again.

To further quantitatively estimate the fire effects on the structure of the mixed cattail–sawgrass community, the fractional changes of the two species in response to fires were examined (Fig. 12). The fraction of cattail aboveground was shown as its percentage of the summed aboveground biomass of the entire mixed community (cattail aboveground + sawgrass aboveground), and the fraction of cattail belowground was shown as its percentage of the summed belowground biomass. Prior to any fires, the cattail aboveground biomass accounted for more than 90% of

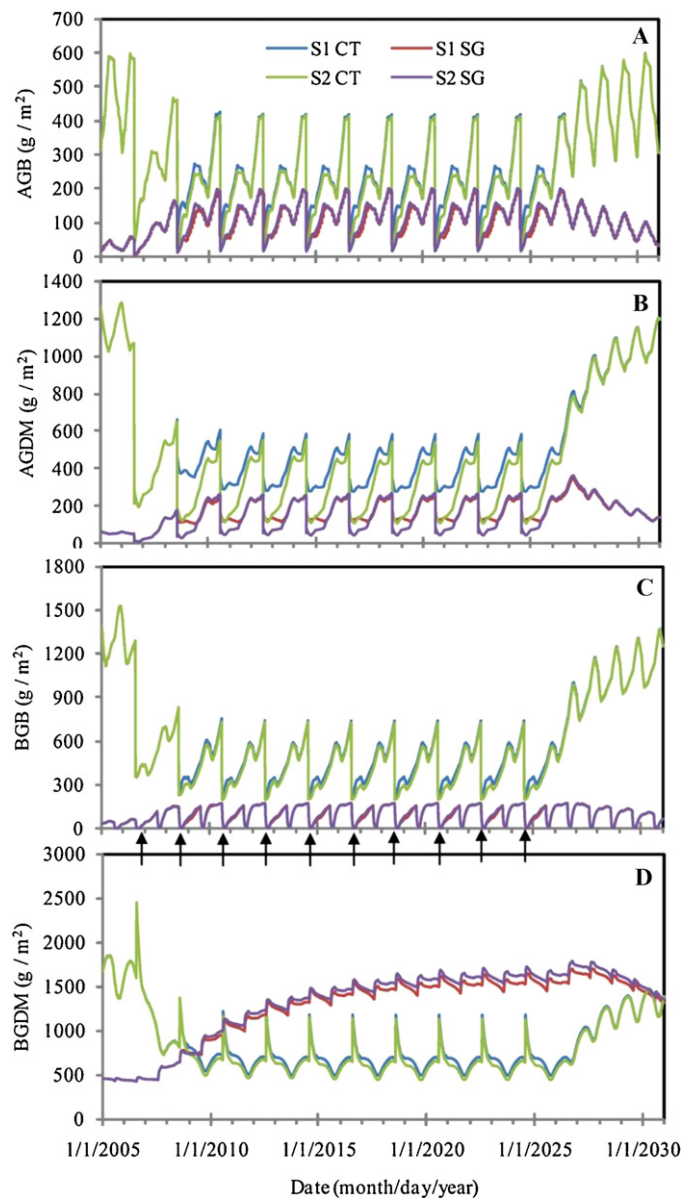


Fig. 9. Variations of cattail (CT) and sawgrass (SG) above- and belowground biomass and dead mass in response to July fires under different hydrological scenarios (AGDM: aboveground dead mass; BGB: belowground biomass; BGDM: belowground dead mass; S1: high-water-depth; S2: low-water-depth; CT: cattail; SG: sawgrass).

the total aboveground biomass. However, after the first July fire, the cattail aboveground biomass reduced to 70%, with a further decrease to 60% after continuous multiple July fires at two-year intervals (Fig. 12). After the first February fire, the cattail aboveground biomass reduced to 65%, with a further decrease to 50% after continuous multiple February fires at two-year intervals (Fig. 13).

4. Discussion

4.1. Number of fires needed to slow down cattail growth

The results presented here indicate that multiple fires could lead to a decline of cattail and an increase of sawgrass. The next important questions are how many continuous fires are needed to reach the maximum effect on slowing cattail growth, and how long will it take for cattail and sawgrass to recover after a fire event. To this end, the seasonal effects of fire on the cattail and sawgrass

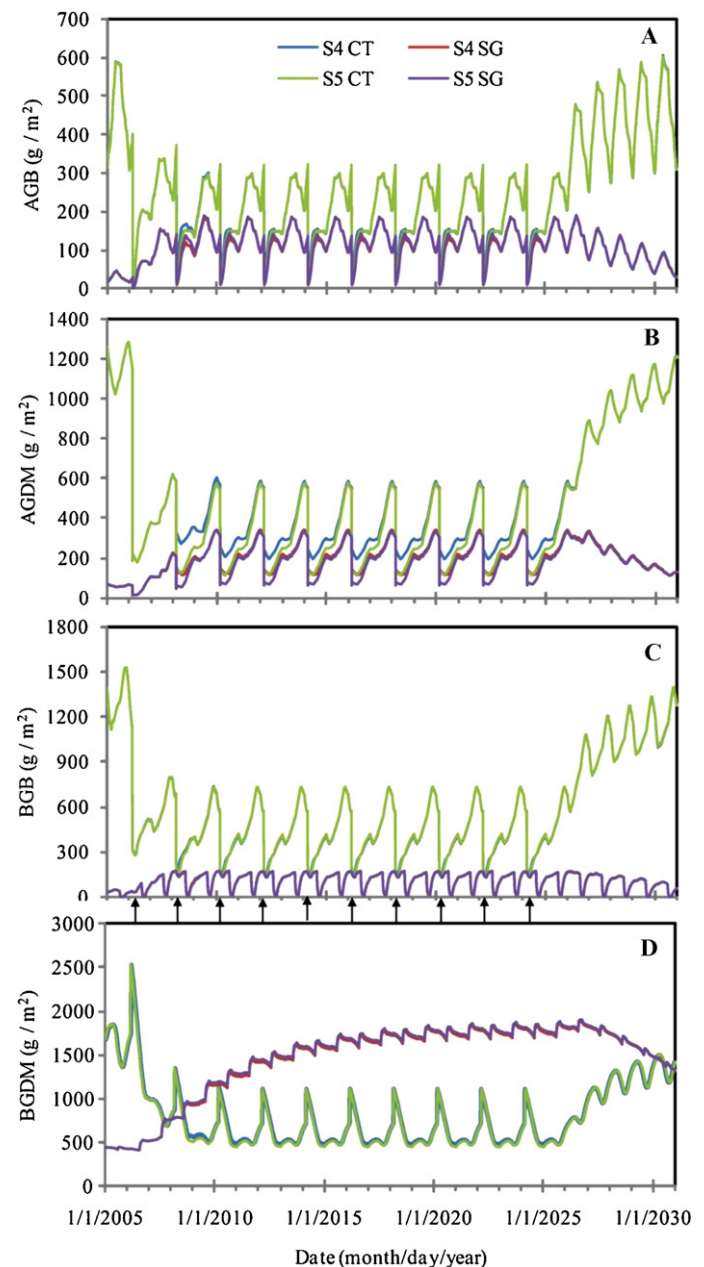


Fig. 10. Variations of cattail and sawgrass above- and belowground biomass and dead mass in response to February fires under different hydrological scenarios (A, aboveground biomass; B, aboveground dead mass; C, belowground biomass; D, belowground dead mass; AGB, aboveground biomass; AGDM, aboveground dead mass; BGB, belowground biomass; BGDM, belowground dead mass; S4, high-water-depth; S5, low-water-depth; CT, cattail; SG, sawgrass).

communities were further compared. To eliminate the potential influence from climate or other factors, two scenarios (S3 and S6) were considered, where all the parameters were the same except for the fire date (Table 4). The fires for these two scenarios were set starting in 2010. The low-water-depth hydrological scenario for these simulations was used because of the stronger negative effects of fires under low-water-depth scenario on plant growth, compared to the fires under a high-water-depth scenario (Figs. 9 and 10). The above- and belowground biomass for cattail and sawgrass were selected as indicators because both of them represent plant growth.

The application of four fires was predicted to provide the maximum suppressing effect on cattail. Beyond four fires, plant

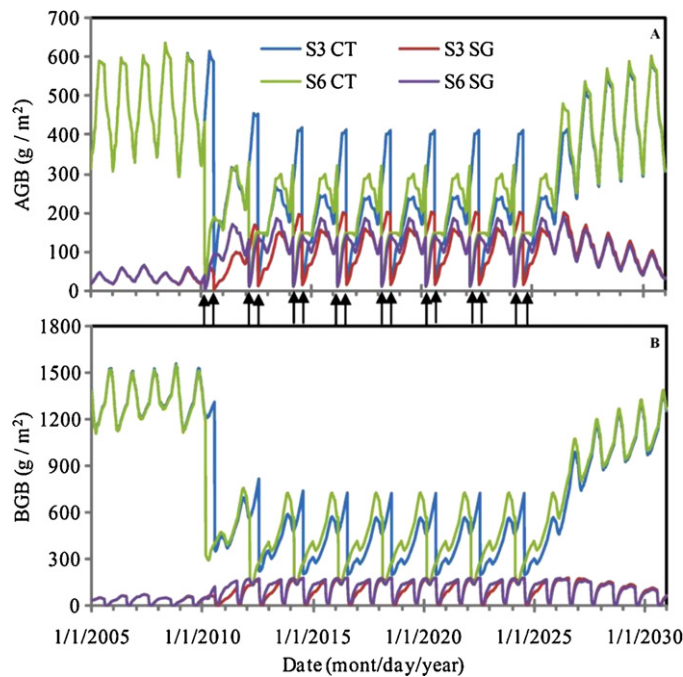


Fig. 11. Variations of (A) aboveground and (B) belowground biomass of cattail and sawgrass in responses to multiple-fire in July and February (CT, cattail; SG, sawgrass; AGB, Aboveground biomass; BGB, Belowground biomass; arrows indicate the occurrence of fires).

regrowth reached a steady state. This may reflect the length of time needed to deplete excess plant nutrient storage, and the plant's nutrient allocation reaches a new lower steady state. This may explain the increased suppression of cattail with February fires as nutrient reserves are low preceding the growing season, and the plants have fewer reserves to draw on for regrowth. Once the application of fire was stopped, some components of cattail returned to

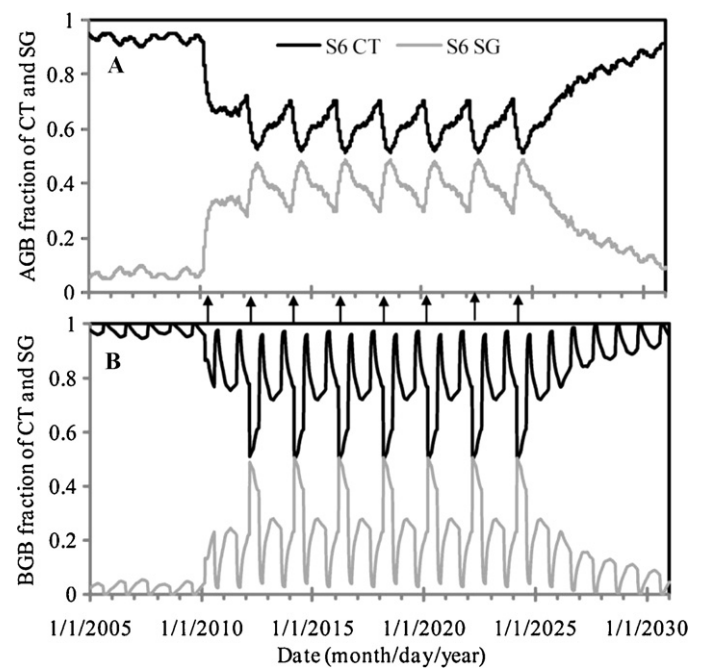


Fig. 13. Changes in cattail-sawgrass community showing as fraction of (A) aboveground and (B) belowground biomass in responses to multiple-fire in February under low-water-depth scenario (CT, cattail; SG, sawgrass; arrows indicate the occurrence of fires).

pre-fire levels within six years. Although P concentrations in the water and soil were reduced by fire over time and did not return to pre-fire levels (Figs. 6–8), there was still sufficient P availability to support pre-fire level biomass production. Therefore, mostly likely more fires rather than four fires may be necessary to create a permanent shift in the vegetation community.

4.2. Fire effects on community shift

The model simulation results showed that the ratio of cattail biomass to sawgrass biomass changed in response to fires, so the community structure shifted. The decreases in cattail biomass caused by fires created a large canopy window which allowed more incoming light and space and thereby stimulated the growth of sawgrass. This is consistent with the field observation that more ramets of sawgrass emerged following fire than with the pre-fire condition in the moderately P-enriched area. However, six months later, the recovery of cattail has closed the canopy window and slowed the growth of sawgrass. Before the cattail fully recovered, an additional fire suppressed the cattail and stimulated the regrowth of sawgrass. The subsequent fires at two-year intervals shifted the community, but not to the point where sawgrass growth outcompeted cattail. The fire effects on community structure are supported by experiments, which concludes that the fires could benefit non-dominate plant species (Flores et al., 2011) while depressing dominate plant species (Ford and Grace, 1998).

Comparisons of the effects of July fires and February fires indicate that July fires yielded a stronger suppression of cattail and stimulation of sawgrass than February fires in absolute magnitude (Fig. 11A and B); however, February fires had relatively stronger effects on community shift than July fires (Figs. 12 and 13). Community composition under both July and February fires returned to near pre-fire levels within six years, indicating that altering the timing of fire will not affect the success of producing a long-term plant community shift after the cessation of fire application.

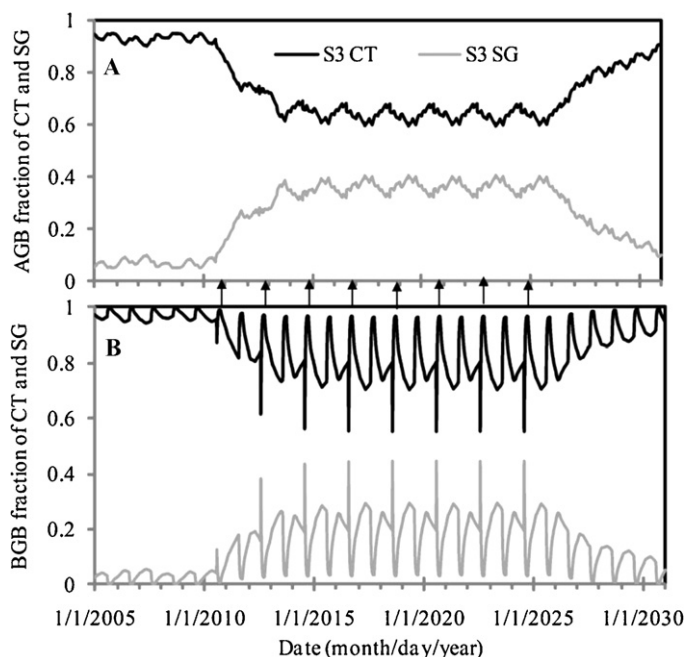


Fig. 12. Changes in cattail-sawgrass community showing as fraction of (A) aboveground and (B) belowground biomass in responses to multiple-fire in July under low-water-depth scenario (CT, cattail; SG, sawgrass; arrows indicate the occurrence of fires).

4.3. Importance of hydrological regimes in fire effects

A comparison of the simulated effects of fires under two hydrological conditions revealed that fires occurring under low-water-depths generated a higher pulse in TP in surface- and porewater than the fires under high-water-depths. This was true for both July and February fires. However, one and a half months post-fire, the TP concentrations under high-water-depths were higher than that under low-water-depths. This may be a dilution effect, as when the higher water levels return, the TP concentration had stronger decreases in water affected by fire under low-water-depth conditions.

Water TP may influence soil TP through adsorption and desorption (Tian et al., 2010), so the changes in surface water and porewater TP changed soil TP concentration. The short-term increase in soil TP might be caused by precipitation of particulate P and adsorption of TP in porewater by soil particles, while the long-term decrease in soil TP may be caused by plant uptake, which in part supports the hypothesis of the Fire Project (Miao and Carstenn, 2005). Regardless of seasons, lower water depth enhanced the decrease in soil TP concentration with fires; and July fires, compared to February fires, caused slightly stronger effects on soil TP concentration decline (Fig. 8). The hydrological and seasonal effects on fire impacts of soil TP indicate the vegetative dominance in soil TP dynamics.

The varied hydrological conditions yielded substantially different fire effects on cattail and sawgrass biomass and dead mass because the biomass and dead mass under water is not consumed. The fires under low-water-depths consumed more aboveground biomass and dead mass, and yielded stronger negative effects on cattail but stimulated sawgrass, than the fires under high-water-depths (Figs. 9 and 10). This has important implications for producing the desired plant community shift from cattail toward sawgrass. Low-water-depth fires are a greater stressor on cattail than high-water-depth fires although more nutrients are released. Cattail is less fire tolerant than sawgrass as sawgrass has inflammable spongy tissue protecting its meristem (Gunderson, 1994). Sawgrass can recover quickly from fire with the removal of the cattail canopy and can increase in biomass relative to cattail. Though not considered in this model, increased sawgrass biomass with low-water-depth fires may increase the sawgrass seed bank resulting in a greater probability of a plant community shift with continued cattail stress (Miao and Zhou, 2009).

4.4. Seasonal impacts of fire

The seasonality of plant growth explains the different amounts of mass available for fires in July and February (Urban et al., 1993; Tian et al., 2010), so it is expected that there will be different fire effects during different seasons. In general, July fires caused larger decreases in biomass and dead mass for both cattail and sawgrass (Figs. 9 and 10, Section 4.3) due to the fact the July is within the growing season for both cattail and sawgrass and the pre-fire biomass and dead mass were higher than in February. Therefore, the July fires consumed more biomass and dead mass than February fires. Meanwhile, post-February-fire cattail and sawgrass biomass were lower than those of post-July fire. This is due to the fact that February is the start of the growing season when plant storage (shoot base) is used for plant growth; February fires' suppression effects on plant aboveground mass yielded strong effects on storage pool, while July fires did not substantially reduce the plant storage pool. In summary, regardless of the hydrological condition, the July fires, compared to February fires, generated similar effects, but with a larger magnitude, on cattail and sawgrass biomass and dead mass.

4.5. Ecological evaluation of model performance

Besides standard statistical testing, the evaluation of behavior of WEM in capturing ecological significance is also important to show its capability to simulate the key ecological processes in Everglades' wetland (Blanco et al., 2007). The WEM was reasonably good at simulating water depth, water and soil temperature, TP in surface water and porewater, growth of cattail and sawgrass, and their responses to fires (Table 6). The simulated pulses of TP in surface water and porewater fell within the ranges of field observations; and the patterns matched closely. This indicated that the WEM was reliable in its prediction of the multiple-fire effects on TP concentration in surface water and porewater. The simulated cattail and sawgrass biomass and dead mass agreed well with the observational data relative to the absolute value, yet did not agree well with regard to the seasonal variations. This discrepancy might be due to either uncertainties in the model, the observational data, international variability, or all.

As Blanco et al. (2007) stated, when validating complex models with multiple output variables, it is necessary to carefully consider the level of confidence in field-measured variables and associated interpretations or summaries. The challenges in sampling plants in wetlands have long been treated as one of the major uncertainty sources in wetland studies due to both the difficulty of sampling plant organs and the high spatial heterogeneity of plant and soil properties in wetlands (Mitsch and Gosselink, 2007; Reddy and DeLaune, 2008).

4.6. Uncertainties

This study enhanced an extant wetland ecosystem model to incorporate plant competition between cattail and sawgrass for light and nutrients. In addition to addressing the data limitations, several improvements to the model are needed in future work for creating better simulations and estimates for fire management in the Everglades. First, environmental factors influencing ash diffusion and fire severity, such as wind velocity and direction, and humidity, might improve the model's ability in simulating fire effects. Second, the competition between cattail and sawgrass might also involve other environmental factors, for example, soil redox potential (Lorenzen et al., 2001; Li et al., 2010). The model improvement of cattail–sawgrass competition on other environmental factors may be an option to enhance the model's ability in predicting sawgrass expansion and cattail decline. Third, fires in months other than July and February might provide information for further fire management options. Fourth, the seasonal variations of cattail and sawgrass are probably a result of their different life cycles (Miao et al., 2008); incorporation of their life cycles might enhance the model performance. Fifth, it would be a large improvement to estimate the seasonal effects of other parameters, like wind, temperature, and solar radiation etc. Sixth, the composition of the seed bank and its interaction with nutrient enrichment in the Everglades wetland might also influence the post-fire recovery of cattail and sawgrass as suggest by an experiment (Miao et al., 2009). Final, it would also be important to investigate the effects of varied fire intensities and frequencies on the recovery of cattail and sawgrass.

5. Conclusions

The following conclusions were drawn from this modeling study:

- (1) Regardless of hydrologic scenario and season, multiple surface fires were predicted to cause a shift of a mixed community of

- cattail and sawgrass from cattail-dominated community to a cattail-sawgrass mixed one.
- (2) Compared to July fires, multiple February fires under low-water-depths were predicted to result in larger shifts of the cattail-sawgrass community, expressed as the increase in sawgrass biomass and decrease in cattail biomass. The fire impacts on plant storage pool might explain this seasonal effect.
 - (3) Four fires under low-water-depths were predicted to reach the maximum suppressing effects on cattail growth, thus the community shift. When successive fires terminated, the biomass and composition of recovering plant community did not reach the pre-fire level within six years.

Based on the above model predictions, it is concluded that multiple fires exert negative effects on cattail and could cause a shift in the plant community from cattail-dominated to cattail-sawgrass mixed, which in part supports the hypothesis that multiple fires could alter the P dynamics and plant community, and may trigger a faster restoration process in moderately P-enriched areas of the Everglades. More research is needed to explore various fire regimes and different hydrologic scenarios to support the expectation of using fires to restore the moderately P-enriched Everglades' wetlands.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2011.09.003.

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