

See discussions, stats, and author profiles for this publication at: http://www.researchgate.net/publication/222426889

A simulation model for projecting changes in salinity concentrations and species dominance in the coastal margin habitats of the Everglades

ARTICLE in ECOLOGICAL MODELLING · MAY 2008

Impact Factor: 2.32 · DOI: 10.1016/j.ecolmodel.2007.12.007

CITATIONS	READS
31	33

6 AUTHORS, INCLUDING:



Donald L Deangelis

United States Geological Survey 258 PUBLICATIONS 9,928 CITATIONS

SEE PROFILE



Fernando Miralles-Wilhelm University of Maryland, College Park **71** PUBLICATIONS **995** CITATIONS

SEE PROFILE



Thomas J. Smith III

United States Geological Survey

78 PUBLICATIONS 2,260 CITATIONS

SEE PROFILE



A simulation model for projecting changes in salinity concentrations and species dominance in the coastal margin habitats of the Everglades

Su Yean Teh^a, Donald L. DeAngelis^{b,c,*}, Leonel da Silveira Lobo Sternberg^b, Fernando R. Miralles-Wilhelm^d, Thomas J. Smith^c, Hock-Lye Koh^a

^a School of Mathematical Sciences, Universiti Sains Malaysia, 11800 Penang, Malaysia

^b Department of Biology, University of Miami, Coral Gables, FL 33124, USA

^c Florida Integrated Science Center, U. S. Geological Survey, USA

^d Department of Civil and Environmental Engineering, Florida International University, Miami, FL 33174, USA

ARTICLE INFO

Article history: Received 23 July 2007 Received in revised form 2 December 2007 Accepted 11 December 2007 Published on line 12 February 2008

Keywords: Storm surge Vegetation boundary shift Salinity Mangroves Hammocks Competition Regime change Everglades Coastal ecosystems Vadose zone

ABSTRACT

Sharp boundaries typically separate the salinity tolerant mangroves from the salinity intolerant hardwood hammock species, which occupy the similar geographical areas of southern Florida. Evidence of strong feedback between tree community-type and the salinity of the unsaturated (vadose) zone of the soil suggests that a severe disturbance that significantly tilts the salinity in the vadose zone might cause a shift from one vegetation type to the other. In this study, a model based upon the feedback dynamics between vegetation and salinity of the vadose zone of the soil was used to take account of storm surge events to investigate the mechanisms that by which this large-scale disturbance could affect the spatial pattern of hardwood hammocks and mangroves. Model simulation results indicated that a heavy storm surge that completely saturated the vadose zone at 30 ppt for 1 day could lead to a regime shift in which there is domination by mangroves of areas previously dominated by hardwood hammocks. Lighter storm surges that saturated the vadose zone at less than 7 ppt did not cause vegetation shifts. Investigations of model sensitivity analysis indicated that the thickness of the vadose zone, coupled with precipitation, influenced the residence time of high salinity in the vadose zone and therefore determined the rate of mangrove domination. The model was developed for a southern Florida coastal ecosystem, but its applicability may be much broader.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

In the Greater Everglades region of southern Florida, mangrove ecosystems and hardwood hammock ecosystems occupy overlapping geographical ranges (Odum et al., 1982; Odum and McIvor, 1990; Sklar and van der Valk, 2003). Areas of close proximity of mangrove vegetation and hardwood hammock vegetation have been studied in keys by Sternberg and Swart (1987); Cluett Key (Florida Bay) and Elliott Key (Biscayne Bay), on the mainland northern shore of Florida Bay; e.g., Coot Bay Hammock (Armentano et al., 2002), and on coastal strand landscape mosaics (Browder and Ogden, 1999). Previous

^{*} Corresponding author at: Department of Biology, University of Miami, 1301 Memorial Drive, Coral Gables, FL 33124, USA. Tel.: +1 305 284 1690; fax: +1 305 284 3039.

E-mail address: ddeangelis@bio.miami.edu (D.L. DeAngelis).

^{0304-3800/\$ –} see front matter © 2008 Elsevier B.V. All rights reserved. doi:10.1016/j.ecolmodel.2007.12.007

studies and field observations have shown that mangroves are able to tolerate a wide range of salinities, including above 30 ppt, while hardwood hammocks are restricted to areas with salinities below 7 ppt (Sternberg and Swart, 1987; Sternberg et al., 2007). Therefore, hardwood hammocks generally occupy areas of higher elevation, where salinities are low. However, because mangroves can grow well in low salinities, these two vegetation types are frequently in competition. Typically, mangrove and hardwood hammock trees are not interspersed, but rather there are sharp boundaries between uniform patches (sizes in the range of a hectare) of the two vegetation types, probably reinforced by interspecific competition. Hardwood hammock species appear to be competitively superior in low salinity areas, so the boundaries between patches of the two species types tend to occur at intermediate values of salinity along a gradient (roughly 7-15 ppt).

Although the boundaries between the two vegetation types are relatively stable, due to the sensitivity of the hardwood hammocks to salinity, in theory there may be circumstances where a perturbation in salinity may induce changes in the distribution of hardwood hammocks and mangroves, resulting in a shift from one vegetation type to the other. The following mechanisms underlie both the normal stability and possibility of such a shift. Both mangroves and hammock species obtain their water from the vadose zone, the unsaturated zone between the soil surface and top of the water table. In coastal areas this vadose zone is underlain by highly brackish ground water, so that evapotranspiration, by depleting water in the vadose zone during the dry season, can lead to infiltration by more saline ground water. Although hardwood hammock trees tend to decrease their evapotranspiration when vadose zone salinities begin to increase, thus limiting the salinization of the vadose zone, mangroves can continue to transpire at higher salinities, although transpiration slows at high enough values (Passioura et al., 1992). Therefore, each vegetation-type promotes local salinity conditions that favor itself in competition, which helps to explain the stability of sharp boundaries between the types. The ability of vegetation to influence the pattern of soil salinity is known in other ecosystems (e.g., Nosetto et al., 2007).

But the positive feedbacks between vegetation and soil salinity that normally stabilize boundaries could also lead to the possibility of rapid large-scale vegetation changes due to certain abiotic disturbances, if the size of the disturbance is large enough to push the system over a threshold. A sharp upward salinity perturbation of an area initially dominated by hardwood hammock, by reducing hardwood tree growth and favoring invasion by a few mangroves, may lead to a positive feedback cycle of increasing salinity and increasing mangrove invasion. This could lead to a shift in vegetation over a large spatial scale. This mechanism is analogous to others that have been proposed for rapid shifts in vegetation (e.g., Scheffer et al., 2001).

The possibility of such a phenomenon has led to interest in what specific perturbations might trigger such vegetation changes. Because of likely climate change, sea level rise and storm surges are potential perturbations of special interest that may cause the vegetation to shift from hardwood hammocks to mangroves. Rising global temperature might lead to more severe hurricanes as warmer temperatures heat up the ocean surface, thus providing energy for storms to intensify as they swirl through the ocean (Walsh, 2004; Webster et al., 2005; Emanuel, 1987, 2005). Along most of the US Atlantic and Gulf of Mexico coasts, sea level has been rising by about 2–3 mm year⁻¹ and is likely to rise by 55–60 cm over the next century (Titus and Richman, 2000).

An increase in salinities of the vadose zone induced by these events might eradicate the salinity-intolerant hardwood hammocks at higher elevations and promote landward migration of mangroves. Inland expansion of mangroves at the expense of freshwater vegetation has been the subject of much literature on coastal ecosystems. Stratigraphic evidence indicates that mangroves have replaced freshwater marsh along coastal southern Florida throughout the Holocene (Gleason et al., 1974; Willard et al., 1999; Williams et al., 1999). Alexander and Crook (1974) attributed the spread of mangroves into former pineland on Key Largo to sea level rise. This process occurs in other parts of the world as well. Lara et al. (2002), analyzing the impact of increasing salinity due to sea level rise, reported the progression of the black mangroves (Avicennia germinans) into the higher elevation plain dominated by grasses (Sporobulus virginicus) and herbs (Sesuvium portulacastrum) at the central part of the Bragança peninsula, Brazil, for the study period of 1972–1992. From 8.8 km² in 1972, the areas dominated by grasses and herbs have shrunk to 5.6 km² in 1997.

Rising sea level would also mean higher storm surges, even if the intensity and frequency of the storm surges do not change. A calculation made by Najjar et al. (2000) indicates that 100-year flood will occur 3-4 times more frequently by the end of 21st century in the mid-Atlantic coastal region. The mangrove and hammock forests in the low-lying Everglades are particularly vulnerable to the projected increase in hurricanes and sea level rise due to climate change. Using hurricane data from 1886 to 1990, Doyle et al. (2003) investigated the impact of hurricanes on mangrove communities in southern Florida by means of the model HURASIM-MANGRO. The study concluded that the occurrence of hurricanes is responsible for the composition of mangrove communities across southern Florida today. If the storms intensify over the next century, the structure and composition of mangrove may be altered, possibly reducing the coverage and stature of mangrove forests. The vulnerability and susceptibility of forests to hurricanes have been well documented in the field (Craighead and Gilbert, 1962; Craighead, 1971; Ellison and Stoddart, 1991; Roth, 1992; Ellison, 1993; Smith et al., 1994; Field, 1995; Paerl et al., 2001; McLeod and Salm, 2006; Gilman et al., 2006a,b).

Less attention has been given to the effects of sea level rise coupled with major storms on the boundaries between two different forest types, such as hardwood hammock and mangrove communities. But there have been some relevant studies on different vegetation types that indicate the possibility of such shifts. For example, Baldwin and Mendelssohn (1998) studied the effects of salinity and inundation coupled with clipping of aboveground vegetation on two adjoining plant communities, *Spartina patens* and *Sagittaria lancifolia*. The study concluded that the vegetation might shift to a salt-tolerant or flood-tolerant species, depending on the level of flooding and salinity at the time of disturbance. Person and Ruess (2003), using artificial flooding, studied the effects of tidal inundation on the elevational zonation of the three dominant plant communities in a subarctic saltmarsh. The woody vegetation of the 'slough levee' community at the higher elevation (ca. 25 cm above mean tidal range) subjected to the flooding declined by 83%. More generally, shifts in vegetation types in otherwise stable ecosystems due to disturbances like grazing, anthropogenic causes, fire suppression and precipitation redistribution have been widely reported (Bragg and Hulbert, 1976; Engle and Kulbeth, 1992; Weltzin and McPherson, 2000; Scholes and Archer, 2000; Briggs et al., 2002a,b; Jackson et al., 2002; Eggemeyer et al., 2006).

These examples of vegetation change suggest that rapid changes in vegetation between hardwood hammock communities and mangrove communities might be caused by large disturbances such as hurricanes. The mechanism in this case would be tilting of the feedback dynamics between the mangroves and hardwood hammocks resulting from a salinity increase due to storm surges, leading to a regime shift (e.g., see Scheffer et al., 2001). Here we use modeling to attempt to determine the size of a perturbation that might be needed to precipitate such a change. Understanding how the coastal ecosystems respond to perturbations is important for proper coastal management in order to minimize losses of coastal development, to minimize losses of valued ecosystems and to maximize available management options (Titus, 1991; Michener et al., 1997; Gilman et al., 2006b).

2. Methods

2.1. Conceptual model

Our approach is to use a spatially explicit model of two competing vegetation types, mangroves and hardwood hammocks, focusing on their competition for light and their different tolerances of salinity. The basic assumptions are similar to those in Sternberg et al. (2007), which modeled the formation of a sharp boundary between the vegetation types. Both vegetation types use water from the vadose zone, which overlies a saturated zone of brackish groundwater (Fig. 1). Hammock species are assumed to be better competitors in low salinity areas, but cannot grow well under high salinity, where they are out-competed by mangroves. If enough water is withdrawn from the vadose layer by plant water uptake or evaporation, groundwater will infiltrate by capillary action into the vadose layer and increase its salinity. On the other hand, if precipitation exceeds evaporation plus the transpiration of water, then salinity in the vadose layer is percolated towards the underlying ocean water layer and salinity decreases (Swain et al., 2003). High salinity developed during Florida's dry season is considered to be the major determinant of vegetation distribution in Florida in this model.

The main mechanism in the model is based on the feedback relationship between the two vegetation types and vadose zone salinity mentioned above. For example, consider a microsite and assume the vadose zone has a particular average salinity during the dry season, which is not sufficiently high to decrease the complete domination of hammock species in an area. During the dry season, as freshwater hammock species continue to transpire water from the vadose



Fig. 1 – Coastal hardwood hammock species transpiration and water uptake (T) as a function of salinity of the vadose layer compared with mangrove species. The vadose layer, often having lower salinity water, overlays a body of saline ocean water. P, E and I are precipitation, evaporation and infiltration, respectively. The dashed lines show negative asymmetric effects of canopy shading, which is included only in the model.

layer, ocean water tends to infiltrate and increase the salinity of the vadose layer of the microsite. Because freshwater plants are sensitive to salinity (Munns, 2002), they decrease their transpiration rates, reducing further infiltration of ocean water. In this way the salinity of the vadose layer may be stabilized at low concentrations that are not lethal to freshwater plants. Conversely, consider the alternate equilibrium state where mangroves dominate an area. As mangroves transpire the water from the vadose layer, ocean water infiltrates; but unlike the hammock species, mangroves will continue to transpire and continue to increase the salinity of the vadose layer to levels which would not be tolerated by freshwater hammock species. Thus there is a tendency of one or the other vegetation-type to stabilize itself in a given area, by reinforcing salinity conditions favorable to its persistence.

This mechanism may explain observations at the landscape level, as described in <u>Sternberg et al. (2007)</u>. Our model conceptualizes the landscape as a grid of microsites, or spatial cells, and assumes each grid cell to be occupied by a closed canopy of a small number of plants, which can include both mangrove and hammock individuals. Each cell, whether currently dominated by mangrove or hammock species, is assumed to always contain at least some small fraction of the other type, which can act as 'seeds' for growth under more favorable conditions, or at least to be rapidly colonized. Each cell is exposed to precipitation, evaporation, tidal deposition of saline water (depending on the cell's elevation in the landscape) and transpiration, which produce vertical fluxes of water in a cell and either increase or decrease the salinity of the vadose zone of that cell. The evapotranspiration depends on the fractions of each of the vegetation types in the cell. The vadose layer of the cell is also assumed to be linked with neighboring cells through lateral movement of salinity. The strongest mechanism for this transport may be water uptake by the roots of plants in the neighboring cells, which redistributes water and salinity between cells. Thus there is some tendency for adjacent cells to approach over time the same vadose zone salinity, allowing the possibility for each vegetation-type to spread horizontally from one cell to dominate adjacent cells.

We hypothesize that a model landscape of mangrove and hardwood hammock trees, initially randomly mixed and then subjected to these abiotic factors, will self-organize into a pattern similar to those observed in nature, having strong aggregation into areas of either solid hammock or mangrove vegetation (vegetation clumping), such that there can be rapid spatial changes from one vegetation type to the other along gradual clines in microtopography. In addition, we hypothesize that a large enough disturbance can change this pattern. For example, a storm surge that deposits a large amount of saline water across the landscape may cause hammock trees to slow their growth sufficiently to be outcompeted by mangroves over a sufficiently long time period to allow mangroves to take over. Thus a large area may undergo a 'regime shift' in vegetation-type.

2.2. Quantitative model

This conceptual model was implemented quantitatively as a 2D grid of square spatial cells, where the sides of each cell were assumed to be 1 m, but the model could also be applied, with some parameter changes, to somewhat larger cells.

2.2.1. Hydrology and salinity

The salinity in a given spatial cell is determined first of all by the difference between the precipitation, P, which brings in fresh water to the top of the vadose zone, and the evaporation, E, and plant uptake of water, R_{TOTAL} . This difference is called the infiltration rate, I_{NF} ;

$$I_{\rm NF} = E + R_{\rm TOTAL} - P \,\rm mm \, day^{-1}. \tag{1}$$

and the dynamics of salinity in the vadose zone are given by the equations

$$nz\frac{dS_v}{dt} = I_{NF}S_{wt} \quad \text{for } I_{NF} > 0 \tag{2}$$

$$nz\frac{dS_v}{dt} = I_{NF}S_v \quad \text{for } I_{NF} < 0 \tag{3}$$

where z (mm) is the depth of the vadose zone of a given cell, n is the porosity, and S_v and S_{wt} are the salinities of the pore water in the vadose zone and of the underlying saline groundwater, respectively. Positive values of infiltration (2) occur when precipitation is less than the water demanded by evaporation and transpiration; then water from the underlying saline groundwater infiltrates upward into the vadose zone. Note that when $I_{NF} > 0$, salt is deposited in the vadose zone by evapotranspiring water, so concentrations can build up to high levels. Nega-



Fig. 2 – Transpiration (mm d^{-1}) of mangrove vegetation and by freshwater hammocks as a function of vadose pore water salinity.

tive values occur when precipitation exceeds evaporation and transpiration demands; then water percolates downward into the underlying groundwater table.

The assumption of a groundwater table with fixed salinity is a useful first approximation, but it is also possible that the salinity dynamics of at least the surface layer of groundwater is more complex. The effect of an upper layer, or lens, of groundwater that is affected both by precipitation and flow of groundwater from higher elevations is examined in an appendix (see on-line Appendix 1). Here, for brevity and because we are simply demonstrating a mechanism, we restrict ourselves to examining the model with the simpler hydrologic assumption.

Evaporation was assumed to be small compared with evapotranspiration and was neglected, since we are assuming a dense canopy in each cell, which inhibits evaporation. Moreira et al. (1997) and Harwood et al. (1999) both observed that in forests transpiration dominates as the vapor generator compared to evaporation. R_{TOTAL} depends on the transpiration and gross productivity of each vegetation type in the spatial cell (see (13) below). The maximum possible water uptake rate by freshwater hammocks is assumed to be 2.6 mm d⁻¹. This value is based on previous studies indicating that transpiration in tropical forests lies within this range (Cabral et al., 1996). Uptake of water as a function of salinity by the hardwood hammock $R_1(S_v)$ and mangrove species $R_2(S_v)$ is estimated by the respective empirical relations (Fig. 2):

$$R_1(S_v) = 2.6 \left(1 - \frac{S_v}{3.14 + S_v}\right) \text{ mm day}^{-1}$$
(4a)

$$R_2(S_v) = 4.4 \ \left(\frac{100-S_v}{15+100-S_v}\right) \ mm \ day^{-1}, \eqno(4b)$$

in which hammocks reduce their transpiration by half when the salinity of the pore water is 3.14 ppt, while mangrove transpiration is not reduced by half until the salinity of the pore water is 85 ppt. These estimates are very similar to those described in detail in <u>Sternberg et al. (2007)</u>, which are based on greenhouse studies (e.g., Lin and Sternberg, 1992). Relevant studies in the field are difficult, and we do not know of any.

In addition to the above hydrologic processes, tidal effects were imposed on all spatial cells at elevations low enough to be affected. The effect of tides on the salinity of spatial cells was calculated as follows. On each day a single high tide was assumed (subsequent sensitivity analysis showed that simulation of two daily high tides made no significant difference in results). The height of the tide above the surface of each spatial cell was generated as a function of the mean and random variation within the observed limits of tidal flux of the empirical data, so that the number of spatial cells covered by the tide on a given day varied in number. The amount of salt contained in the volume of water above the cell, assumed to have a salinity of 30 ppt, was allowed to mix homogeneously with the vadose zone below. In all model simulations precipitation and effects of tides were prescribed on a daily basis. Means and standard deviations of daily precipitation (NOAA, National Weather Services Forecast Office, Florida) and daily tidal height (NOAA, Tide & Current Historic data base, Key West Station) for each month were derived from 162 and 5 years of empirical data, respectively. Daily values were determined using a normal random number generator, with values truncated at zero.

We assumed there is also horizontal diffusion of salinity between cells. We used a diffusion constant of D = 0.0003. This is about two times the theoretical value used by Passioura et al. (1992) and three times the laboratory values of Hollins et al. (2000). However, we assume that the extension of roots across cell boundaries can substantially increase the mixing of solute among cells, so we believe our value is reasonable. Sensitivity analysis on D showed little difference in the results over that range of diffusion coefficients.

2.2.2. Vegetation dynamics

A given cell could be occupied by the two types of vegetation simultaneously, and, in fact, even in cells dominated by one type, small amounts of the other type tended to persist. The biomasses of each species in a given spatial cell were explicitly modeled, as well as the mechanism of competitive dominance of the hammock vegetation over mangrove vegetation under very low soil salinity conditions. We used an approach similar to that of Herbert et al. (2004) for competition between species of different functional types, with a slight difference. Herbert et al. assumed that the plant types differed in their abilities to compete for light and nutrients. Here we assumed that the plants differed only in their ability to compete for light, with the additional assumption that the hardwood species were superior in low salinity. Following Herbert et al., we assumed that in any particular microsite the equations for the different vegetation types (hardwood hammock and mangrove in this case) were

$$\frac{dB_{Ci}}{dt} = U_{Cvi} - M_{Cvi} - L_{Cvi}, \quad i = 1, 2.$$
(5)

where B_{Ci} is carbon in plant biomass (g C m⁻²), U_{Cvi} is gross productivity (g C m⁻² d⁻¹),

$$U_{Cvi} = \frac{Q(S_v)g_{Ci}w_{Ci}I(1 - e^{-k_i S_{CT}})}{w_{C1} + w_{C2}}, \quad i = 1, 2,$$
(6)

where w_{C1} and w_{C2} incorporate competition for light, depending on how much of the canopy of a spatial cell each occupies

(see Herbert et al. for details);

$$w_{\rm Ci} = \frac{(1 - e^{-k_{\rm I}S_{\rm Ci}})(1 + e^{-k_{\rm I}S_{\rm Cj}})}{2}, \quad i = 1, 2,$$
 (7)

which takes into account the amount of canopy of each competing tree-type, but makes the assumption that there is no canopy dominance of either tree-type (e.g., the relative degree to which trees of one species shade another due to height differentials). S_{Ci} (m² m⁻²) is the leaf area index of species *i* in a spatial cell,

$$S_{Ci} = b_{Ci}B_{Ai}, \quad i = 1, 2.$$
 (8)

where b_{Ci} is the leaf area index per unit active tissue carbon, B_{Ai} (g C m⁻²), of tree types,

$$B_{Ai} = \frac{c_{ij}B_{A\max,i}B_{Ci}}{B_{A\max,i} + c_{1i}B_{C1} + c_{2i}B_{C2}}.$$
(9)

where the parameters c_{ij} are allometric parameters governing the amount of energy allocated to active tissue (leaves). Note that the biomass of species *j* can affect the allocation of biomass of species i. We assumed the effect of salinity on productivity of species *i*, $Q_i(S_v)$, occurs through its effect on the water uptake rate (which also affects uptake of nutrients), normalized by the maximum possible rate;

$$Q_i(S_v) = \frac{R_i(S_v)}{R_i(0)}, \quad i = 1, 2.$$
 (10)

 M_{Cvi} (g C m⁻² d⁻¹) is the respiration of each plant;

$$M_{Cvi} = m_{Ai}B_{Ai} + m_{wi}(B_{Ci} - B_{Ai}), \quad i = 1, 2,$$
 (11)

where the rates differ between dead and living matter. L_{Cvi} (g C m⁻² d⁻¹) is litterfall,

$$L_{Cvi} = l_{Ai}B_{Ai} + l_{wi}(B_{Ci} - B_{Ai}), \quad i = 1, 2.$$
 (12)

Total evapotranspiration from a cell was linearly related to the evapotranspiration of each species, multiplied by its fraction of the primary production in that spatial cell;

$$R_{\text{TOTAL}} = \frac{U_{\text{Cv1}}}{U_{\text{Cv1}} + U_{\text{Cv2}}} R_1 + \frac{U_{\text{Cv2}}}{U_{\text{Cv1}} + U_{\text{Cv2}}} R_2.$$
(13)

We do not have parameter values related to light competition in the above equations for these vegetation types. Instead, we used parameter values of temperate forest that were used by Herbert et al. (2004) for both tree community types, except that we gave the hardwood hammock trees a 24% advantage in light use efficiency that allowed hardwood hammock vegetation to dominate for salinities below 7 ppt. Therefore, despite our not deriving light use parameters specific to these tree types, we believe the model reasonably simulates the mechanisms of competition. All parameters not defined above are defined in Table 1.

Table 1 – Parameter values used for simulations				
Parameter	Value	Unit	Comments	
Diffusion, D Simulation time Domain size Grid size Time step Porosity, n Evaporation, E Sea water salinity Initial vadose zone salinity, S _v Groundwater salinity, S _{wt}	0.0003 20,000 100×100 1.0 0.5 0.0 30.0 0.0 19.5	$m^2 d^{-1}$ d m^2 m day - $mm d^{-1}$ ppt ppt ppt		
Initial biomass, B _C Light-use efficiency, g _{Ci} Hammock Mangrove	20,000 420.0 340.0	g C GJ ⁻¹ g C GJ ⁻¹		
Solar irradiance, I Light extinction factor, k_I Leaf area per unit carbon, b_{Ci} Maximum value attainable by B_{Ai} , $B_{Amax,i}$ Active tissue respiration rate, r_{Ai} Woody tissue respiration rate, r_{Wi} Active tissue litter loss rate, m_{Ai} Woody tissue litter loss rate, m_{Ai}	0.01 0.5 0.0455 350 4.0 0.0296 1.700 0.0148	GJ m ⁻² d ⁻¹ - m ² /g C g C m ⁻² year ⁻¹ year ⁻¹ year ⁻¹	Ham & Man. Ham & Man. Ham & Man. Ham & Man. Ham & Man. Ham & Man.	
c ₁₁ , c ₂₁ c ₁₂ , c ₂₂ Precipitation Tidal height Maximum hammock water uptake	0.1, 0.1 0.5, 0.5 NOAA rec. NOAA rec. 2.6	- mm d ⁻¹ mm d ⁻¹		
Maximum mangrove water uptake	4.4	$\rm mmd^{-1}$		

3. Model simulations

Simulations were performed in a 100×100 cell landscape with a topography that increased along one horizontal dimension an average of 10 mm per cell length (the vadose zone thickness also increased by 10mm per cell along the elevation gradient). The first objective of the simulations was to determine if the landscape, subjected to realistic daily hydrologic conditions, would self-organize into a typical distribution of mangrove and hammock zones. Therefore, spatially random initial conditions were prescribed for the distribution of vegetation. Initially, 85% of the 100 \times 100 cells were assumed to be dominated by hardwood hammocks and 15% by mangroves. The mangrove-dominated cells were randomly distributed over the study domain. The dominant vegetation in a cell was initiated as having 80% of the total biomass in the cell. The landscape was allowed to self-organize into two sharply spatially divided types after 10,000 days (27.4 years). The 10,000 days provided enough time for a stable zonation pattern to develop under pre-surge conditions, starting from a random distribution of sites.

To investigate the effects of the increased salinity in the vadose zone due to storm surge on mangroves and hardwood hammocks, a storm surge was assumed to take place after 10,000 days (27.4 years), flooding the entire study domain for 1 day. Several intensities of the storm surge were employed in the simulations, ranging from a light surge that saturated the vadose zone at 7.5 ppt to a heavy surge event that saturated the

vadose zone at 30 ppt. After the inundation, processes of precipitation, tides, and evapotranspiration acted on each cell and vegetation was allowed to undergo succession. The simulation was continued for an additional 23 years.

4. Results and discussion

Under stable environmental conditions, in which there were no major disturbances, such as storm surges, that would cause a catastrophic shift of vegetation, hardwood hammocks occupied the higher elevation cells, while mangroves occupied the lower elevation cells (which were frequently inundated by tides), except for some patches of mangroves at higher elevations (Fig. 3(a)). However, small amounts of biomass of the subdominant species remained in every spatial cell, which could act like seeds in the event of an environmental change, such as a storm surge.

In the event of a light surge, hardwood hammocks were able to restore the salinity to low levels in a short time period. After 50 years, hardwood hammocks still dominated the cells at higher elevation but the patches of mangrove-dominated cells were larger (Fig. 3(b)) compared to the case without a storm surge event (Fig. 3(a)). A medium surge event that saturated the vadose zone at 15 ppt caused the mangroves to invade the cells at higher elevation that were initially dominated by hardwood hammocks (Fig. 3(c)). A heavy surge caused the mangroves to take over the entire study domain after 50 years (Fig. 3(d)). Snapshots of salinity in the vadose zone at inter-



Fig. 3 – Distribution of mangroves and hammocks at the end of a 50-year simulation (a) without a storm surge, and subject to storm surges that saturate the vadose zone homogeneously to the following levels of salinity for 1 day during year 27: (b) 7.5 ppt, (c) 15 ppt and (d) 30 ppt. Magenta represents mangroves and yellow represents hardwood hammock. Tops of frames are higher elevation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

vals of 1000 days (~2.74 years) are shown in Fig. 4. These show that a heavy salinity input on day 10,000 (27.4 years) tended to wash out over the next few years, but ultimately began to increase steadily again. Fig. 5 shows the distribution of mangrove-dominated spatial cells for the same time intervals. The increase in mangroves explains the steady increase in salinity (in Fig. 4 some of the variations in the salinity pattern from one time interval picture frame to the next occur because the intervals fall in different seasons within the year. The effects of tides and precipitation on vadose zone salinity vary at different seasons of the year). At exactly 10,000 days (\sim 27.4 years), the vadose zone was saturated at 30.0 ppt due to storm surge flooding. After that, much of the salinity washed out in response to daily hydrology processes, though it would take close to a year to return salinity to its pre-surge levels. But that time period was sufficient for the gross primary production rate of hammock trees to decline enough that respiration and litterfall combined to cause a net loss of hammock biomass.

The small fractions of mangroves in those cells were able to compete for sunlight and start increasing in biomass. This growth was slow at first, but it was enough to tilt the balance. As the mangroves increased in each cell, they increased the evapotranspiration, which increased vadose zone salinity. This resulted in positive feedback in those cells. There was also slow lateral mixing of salinity among cells. The mixing was slow, with an equilibration time of 5–10 years between adjacent cells, but this was enough to facilitate the expansion of clusters of mangroves across the landscape (Fig. 5). It is quite clear that these dynamics were a result of the storm surge. As the salinity saturation level by storm surge increases, the percentage of cells dominated by hardwood hammocks in the higher elevation regions decreased (Fig. 6).

To understand how the feedback of vegetation affects the salinity regime in the vadose zone, we removed that feedback by artificially 'fixing' the composition of the vegetation right after the heavy storm surge, preventing it from changing fur-



Fig. 4 – Snapshots of salinity (ppt) across the 100 × 100 cell landscape at time intervals of 2.74 years during the heavy storm surge simulation (left to right and down), shown starting at 19.18 years. Darker colors indicate higher salinity. Frame 4 shows the day on which the entire area was inundated by the storm surge. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)



Fig. 5 – Distribution of mangroves across the 100 × 100 cell landscape at intervals of 2.74 years during the heavy storm surge (left to right then down), shown starting at 19.18 years. Note that after an initial random distribution at high biomass, the mangroves are virtually eliminated from the high elevations. After the storm surge at year 27, mangroves started to invade and took over by 50 years.



Fig. 6 – Fraction of cells occupied by hammocks vs. salinity saturation level by storm surge after about 50 years as a function of the severity of the storm surge in terms of ppt saturation of the vadose zone.

ther. Under those conditions, the changes in average salinity of cells in each height class that range from 1 (lowest elevation) to 30 (highest elevation) is plotted at 1 day, 0.25 year, 0.5 year, 1 year, 5 years, 10 years, 15 years and 20 years after the storm surge (Fig. 7). One day after the heavy surge, the salinity in the vadose zone remained at about 30 ppt throughout the entire study domain. After 0.25 year, the relatively reduced evapotranspiration associated with the high fraction of hardwood hammocks biomass in the cells coupled with precipitation significantly reduced the salinity. Because the biomasses of hardwood hammocks and mangroves in the cells were artificially not allowed to change, the salinity in the vadose zone was maintained at low levels (below 5 ppt) after 5 years following the storm surge. On the other hand, in the parallel case in which the vegetation was allowed to change, after an initial period of decrease, the salinity started to creep back up around



Fig. 7 – Average salinity (ppt) profiles along the elevation gradient at eight times starting from 1 day following the inundation, for the scenario in which vegetation was artificially not allowed to change.



Fig. 8 – Average salinity (ppt) profiles along the elevation gradient at eight times starting from 1 day following the storm inundation, for the scenario in which vegetation was allowed to undergo successional changes.



Fig. 9 – Elevational profiles showing the fractions of cells occupied predominately by hammocks vegetation at eight times following the storm surge inundation.

5 years after the storm surge (Fig. 8). Initially, hardwood hammocks dominated the cells at higher elevation (higher height class). After the storm surge, mangroves started to invade the higher elevation regions, resulting in a lower percentage of cells dominated by hardwood hammocks in higher height class (Fig. 9).

An odd phenomenon in the model results is that higher elevation cells were dominated by mangroves at a faster rate than cells at mid-elevations (see the 15- and 20-year lines in Fig. 9), with the exception of the low elevation cells that were frequently inundated by tide. This is mainly due to the thickness (or depth) of the vadose zones, which increased by 10 mm per cell with elevation. The higher volume of salinity at higher elevation cells required a longer period of time to be flushed out, causing the mangroves to have an advantage over the hardwood hammocks for a longer duration. If the height of the vadose zone were constant throughout the cells, all of the cells above the influence of tides would be taken over by mangroves at approximately the same pace (Fig. 10). To illustrate the effects of vadose zone thickness, salinity changes over time in a single cell with vadose zone height of 1.0 m and 0.2 m were simulated (Fig. 11). After a heavy surge at the 10 000th day, salinity in the cell with vadose zone height of 0.2 m recovers to pre-storm level (Fig. 11(a)). On the other hand, salinity never recovers to pre-storm level in the cell with vadose zone height of 1.0 m after the storm surge (Fig. 11(b)). The simulation results discussed are typical results with no significant variations between the presented results and the results of replicates.

A key question is how well the model results reflect reality. We have performed extensive sensitivity analyses on the



Fig. 10 – Elevation profile showing the fraction of cells occupied by hammocks under a scenario in which each vadose zone was assumed to have the same thickness, rather than increasing thickness with elevation.

model. We will only report on the general results here. In particular, our assumption of mangrove evapotranspiration (Eq. (4b)) might be considered high. Sternberg et al. (2007) used a maximum of 2.6 for the maximum transpiration rate of mangroves in water of zero salinity, rather than our 3.8. When we used a value of 3.0, the heavy storm surge was not able to cause a regime shift from hammock to mangrove trees. However, with a somewhat higher value of groundwater salinity (25 ppt rather than 19.5), we obtained essentially the same results of a regime shift as shown in our figures. What is important for mangroves to gain dominance following the surge is that they can draw enough salt from the groundwater to more than compensate for the effects of precipitation, so higher groundwater salinity is a factor that can promote that mechanism. In addition, Appendix 1 shows the results of modeling groundwater hydrology in greater detail, including a flowing freshwater lens. While this lens decreased the likelihood of a regime shift, if the lens was thin and often dominated by freshwater flow, it did not change our results if the lens was thick and relatively stable in salinity. Therefore, sensitivity analysis of our model shows that a regime shift in vegetation from hammock trees to mangroves due to a heavy storm surge is a possibility, but whether it can occur may depend on detailed conditions of groundwater hydrology and evapotranspiration. Because future changes in climate will probably increase the likelihood of severe storm surges, and changes in atmospheric CO₂ levels may affect transpiration rates (e.g., Snedaker and Araújo, 1998), more detailed modeling and experimental studies on such coastal systems is warranted.



Fig. 11 - Salinity (ppt) changes over time (day) in about (a) 0.2 m and (b) 1.0 m thick vadose zone (SS = storm surge).

5. Conclusions

Our model is designed to explore the possibility of regime shifts between mangrove and hardwood hammock types that might be triggered by a large storm surge. It is not a rigorous model, as many of the model relationships are only rough estimates of what may occur in the field. Nonetheless, it is important to recognize the possibility that changes in vegetation may occur not only through gradual changes in the environment, but also by a sudden disturbance event. Simulations by the model indicate that a significant 1-day storm surge event could feasibly initiate a vegetation shift to mangroves from hardwood hammocks in areas initially dominated by the latter. In the model mangroves take over more than half of the higher elevation cells if the storm surge saturates the vadose zone at more than 15 ppt. It is observed that the shift occurs decades after the storm surge. A light storm surge that saturates the vadose zone by less than 7 ppt will not cause a vegetation shift (Fig. 6). The rate of domination by mangroves in the high elevation cells after a storm surge was found to depend on the thickness or depth of the vadose zone. A thicker vadose zone will have a larger volume of high salinity which takes longer to be flushed out by precipitation. Thus, for an extended period of time, the growth of hardwood hammocks will be suppressed while mangroves will continue to grow. This will promote a faster rate of mangroves takeover. On the other hand, a smaller volume of high salinity will be washed out quickly by precipitation and therefore, allowing the hardwood hammocks to recover.

It is documented that mangroves have migrated approximately 3.3 km inland in the southern Everglades during the past half-century, largely at the expense of freshwater marshes and swamp forest (Gaiser et al., 2006). This is certainly in part due to effects of both sea level rise and upstream hydrological manipulation, which has reduced the amount of freshwater flowing down the coastal estuaries. Whether the effects of storm surges could accelerate such spread is not known, but the fact that a hypothetical mechanism exists (at least for hardwood hammock vegetation, as shown here) makes this possibility worth investigating. We know of no available before and after data from which our hypothesis of a vegetation shift can be tested. However, Hurricane Wilma (2005) produced a large storm surge of 4.6 m at the coast, causing a 1.0-m pulse 19.5 km upstream in Shark River (Smith et al., 2007). The area impacted by Wilma's sediment deposition was 285 km². It would be useful to follow the fates of some of the hardwood hammocks, as well as other freshwater vegetation, which have been impacted by the surge from Hurricane Wilma.

Acknowledgments

We thank David Sumner (USGS) for his helpful comments on an earlier version of this paper. We thank two anonymous reviewers whose comments have substantially improved our manuscript. Financial support provided to the first author by the Government of Japan, UNESCO and the UNESCO/Keizo Obuchi Fellowship is gratefully acknowledged. DLD and TJS were supported by the Florida Integrated Science Center.The useful comments of D. Sumner and W. Nuttle, as well as of two anonymous reviewers, are greatly appreciated.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2007.12.007.

REFERENCES

- Alexander, T.J., Crook, A.G., 1974. Recent vegetational changes in southern Florida. In: Gleason, P.J. (Ed.), Environments of Southern Florida: Present and Past. Memoir 2: Miami Geological Society, Miami, Florida, pp. 61–72.
- Armentano, T.V., Jones, D.T., Ross, M.S., Gamble, B.W., 2002. Vegetation pattern and process in tree islands of the Southern Everglades and adjacent areas. In: Sklar, F.H., van der Valk, A. (Eds.), Tree Islands of the Everglades. Kluwer Academic Press, The Netherlands.
- Baldwin, A.H., Mendelssohn, I.A., 1998. Effects of salinity and water level on coastal marshes; an experimental test of disturbance as a catalyst for vegetation change. Aquat. Bot. 61, 255–268.
- Bragg, T.B., Hulbert, L.C., 1976. Woody plant invasion of unburned Kansas bluestem prairie. J. Range Manage. 29, 19–23.
- Briggs, J.M., Knapp, A.K., Brock, B.L., 2002a. Expansion of woody plants in Tallgrass Prairie: a fifteen year study of fire and fire-grazing interactions. Am. Midl. Nat. 147, 287–294.
- Briggs, J.M., Hoch, G.A., Johnson, L.C., 2002b. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to Juniper virginiana forest. Ecosystems 5, 578–586.
- Browder, J.A., Ogden, J.C., 1999. The natural South Florida system II: predrainage ecology. Urban Ecosyst. 3, 245–277.
- Cabral, O.M.R., McWilliam, A.-L.C., Roberts, J.M., 1996. In-canopy microclimate of Amazonian forest and estimates of transpiration. In: Gash, J.H.C., Nobre, C.A., Roberts, J.M., Victoria, R.L. (Eds.), Amazonian Deforestation and Climate. Wiley Press, Chichester, UK, pp. 207–220.
- Craighead, F.C., 1971. The trees of South Florida. The Natural Environments and Their Succession, vol. 1. University of Miami Press, Coral Gables, Florida.
- Craighead, F.C., Gilbert, V.C., 1962. The effects of Hurricane Donna on the vegetation of southern Florida. Quart. J. Florida Acad. Sci. 25, 1–28.
- Doyle, T.W., Girod, G.F., Books, M.A., 2003. Chapter 12: Modeling mangrove forest mitigation along the southwest coast of Florida under climate change. In: Integrated Assessment of the Climate Change Impacts on the Gulf Coast. Ning, Z.H., Turner, R.E., Doyle, T., Abdollahi, K.K. (lead authors). Region. Gulf Coast Climate Change Assessment Council (GCRCC) and Louisiana State University (LSU) Graphic Services, pp. 211–221.
- Eggemeyer, K.D., Awada, T., Wedin, D.A., Harvey, F.E., Zhou, X., 2006. Ecophysiology of two native invasive woody species and two dominant warm season grasses in the semiarid grasslands of the Nebraska sandhills. Int. J. Plant Sci. 167 (5), 991–999.
- Ellison, J.C., 1993. Mangrove retreat with rising sea level, Bermuda. Estuar. Coast. Shelf Sci. 37, 75–87.
- Ellison, J.C., Stoddart, D.R., 1991. Mangrove ecosystem collapse during predicted sea-level rise: Holocene analogues and implications. J. Coast. Res. 7, 151–165.
- Emanuel, K., 1987. The dependence of hurricane intensity on climate. Nature 326, 483–485.
- Emanuel, K., 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436, 686–688.

Engle, D.M., Kulbeth, J.D., 1992. Growth dynamics of crowns of eastern red cedar at 3 locations in Oklahoma. J. Range Manage. 45, 301–305.

Field, C.D., 1995. Impact of expected climate change on mangroves. Hydrobiologia 295, 75–81.

Gaiser, E.E., Zafiris, A., Ruiz, P.L., Tobias, F.A.C., Ross, M.S., 2006. Tracking rates of ecotone migration due to salt-water encroachment using fossil mollusks in coastal South Florida. Hydrobiologia 569, 237–257.

Gilman, E.L., Ellison, J., Jungblut, V., Van Lavieren, H., Wilson, L., Areki, F., Brighouse, G., Bungitak, J., Dus, E., Henry, M., Kilman, M., Matthews, E., Sauni Jr., I., Teariki-Ruatu, N., Tukia, S., Yuknavage, K., 2006a. Adapting to Pacific Island mangrove responses to sea level rise and climate change. Clim. Res. 32, 161–176.

Gilman, E.L., Ellison, J., Coleman, R., 2006b. Assessment of mangrove response to projected relative sea-level rise and recent historical reconstruction of shoreline position. Environ. Monit. Assess. 124, 105–130.

Gleason, P.J., Cohen, A.D., Brooks, H.K., Stone, P., Smith, W.G., Spackman Jr., W., 1974. The environmental significance of Holocene sediments from the Everglades and saline tidal plain. In: Gleason, P.J. (Ed.), Environments of Southern Florida: Present and Past. Memoir 2: Miami Geological Society, Miami, Florida, pp. 61–72.

 Harwood, K.G., Gillon, J.S., Roberts, A., Griffiths, H., 1999.
 Determinants of isotopic coupling of CO₂ and water vapor within a Quercus petraea forest canopy. Oecologia 119, 109–119.

Herbert, D.A., Rastetter, E.B., Gough, L., Shaver, G.R., 2004. Species diversity across nutrient gradients: an analysis of resource competition in model ecosystems. Ecosystems 7, 296–310.

Hollins, S.E., Ridd, P.V., Read, W.W., 2000. Measurement of the diffusion coefficient for salt in salt flat and mangrove soils. Wetlands Ecol. Manage. 8, 257–262.

Jackson, R.B., Banner, J.L., Jobbágy, E.G., Pockman, W.T., Wall, D.H., 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418, 623–626.

Lara, R., Szlafsztein, C., Cohen, M., Berger, U., Glaser, M., 2002. Implications of mangrove dynamics for private land use in Bragança, North Brazil: a case study. J. Coast. Conserv. 8, 97–102.

Lin, G., Sternberg, L., da, S.L., 1992. Effect of growth form, salinity, nutient, and sulfide on photosynthesis, carbon isotope discrimination and growth of Red Mangrove (Rhizophora mangle L.). Aust. J. Plant Physiol. 19, 509–517.

McLeod, E., Salm, R.V., 2006. Managing Mangroves for Resilience to Climate Change. The World Conservation Union (IUCN), Gland, Switzerland, 64 pp.

Michener, W.K., Blood, E.R., Bildstein, K.L., Brinson, M.M., Gardner, L.R., 1997. Climate Change, hurricanes and tropical storms, and rising sea level in coastal wetlands. Ecol. Appl. 7 (3), 770–801.

Moreira, M.Z., Sternberg, L., Martinelli, L.A., Victoria, R.L., Barbosa, E.M., Bonates, C.M., Nepstad, D.C., 1997. Contribution of transpiration to forest ambient vapor based on isotopic measurements. Global Change Biol. 3, 439–450.

Munns, R., 2002. Comparative physiology of salt and water stress. Plant Cell Environ. 25, 239–250.

Najjar, R.G., Walker, H.A., Anderson, P.J., Barron, E.J., Bord, R.J., Gibson, J.R., Kennedy, V.S., Knight, C.G., Megonigal, J.P., O'Connor, R.E., Polsky, C.D., Psuty, N.P., Richards, B.A., Sorenson, L.G., Steele, E.M., Swanson, R.S., 2000. The potential impacts of climate change on the mid-Atlantic coastal region. Climate Res. 14, 219–233.

Nosetto, M.D., Jobbágy, E.G., Tóth, T., Di Bella, C.M., 2007. The effects of tree establishment in naturally salt-affected grasslands. Oecologia 152, 695–705.

Odum, W.E., McIvor, C.C., 1990. Mangroves. In: Myers, R.L., Ewel, J.J. (Eds.), Ecosystems of Florida. The University of Central Florida Press, Orlando, FL, USA, pp. 517–546.

Odum, W.E., McIvor, C.C., Smith, T.J., 1982. The ecology of the mangroves of South Florida: a community profile. US Fish and Wildlife Service. FWS/OBS-81/24.

Paerl, H.W., Bales, J., Ausley, L., Buzzelli, C., Crowder, L., Eby, L., Fear, J., Go, M., Peirls, B., Richardson, T., Ramus, J., 2001. Ecosystem impacts of three sequential hurricanes (Dennis, Floyd, and Irene) on the United States's largest lagoonal estuary, Pamlico Sound, NC. PNAS 98 (10), 5655–5660.

Passioura, J.B., Ball, M.C., Knight, J.H., 1992. Mangrove may salinize the soil and in so doing limit their transpiration rate. Funct. Biol. 6, 476–481.

Person, B.T., Ruess, R.W., 2003. Stability of a subartic saltmarsh: plant community resistance to tidal inundation. Ecoscience 10 (3), 351–360.

Roth, L.C., 1992. Hurricanes and mangrove regeneration: effects of Hurricane Joan, October 1988, on the vegetation of Isla del Venado, Bluefields, Nicaragua. Biotropica 24, 375–384.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596.

Scholes, R.J., Archer, S.R., 2000. Tree-grass interactions in savannas. Annu. Rev. Ecol. Syst. 28, 517–544.

- Sklar, F.H., van der Valk, A. (Eds.), 2003. Tree Islands of the Everglades. Kluwer Academic Publishers, Boston.
- Smith, T.J., Robblee, M., Wanless, H., Doyle, T., 1994. Mangroves, hurricanes, and lightning strikes. BioScience 44 (4), 256–262.
- Smith, T.J., Anderson, G.H., Tiling, G., 2007. A tale of two storms: surges and sediment deposition from Hurricanes Andrew and Wilma in Florida's southwest coast mangrove forests. In: Farris, G.S., Smith, G.J., Crane, M.P., Demas, C.R., Robbins, L.L., Lavoie, D.L. (Eds.), Science and Storms: The USGS Response to the Hurricanes of 2005. USGS Circular 1306. U. S. Geological Survey, Reston, Virginia, pp. 169–174.

Snedaker, S.C., Araújo, R.J., 1998. Stomatal conductance and gas exchange in four species of Caribbean mangroves exposed to ambient and increased CO₂. Mar. Fresh Res. 49, 325–327.

Sternberg, L., Swart, P.K., 1987. Utilization of freshwater and ocean water by coastal plants of Southern Florida. Ecology 68, 1898–1905.

Sternberg, L., Teh, S.Y., Ewe, S., Miralles-Wilhelm, F., DeAngelis, D.L., 2007. Competition between hardwood hammocks and mangroves. Ecosystems 10, 648–660.

Swain, E.D., Wolfert, M.A., Bales, J.D., Goodwin, C.R., 2003. Two-dimensional hydrodynamic simulation of surface-water flow and transport to Florida Bay through the Southern Inland and Coastal Systems (SICS). U.S. Geological Survey Water-Resources Investigations Report 03-4287.

Titus, J.G., 1991. Greenhouse effect and coastal wetland policy: how Americans could abandon an area the size of Massachusetts at minimum cost. Environ. Manage. 15 (1), 39–58.

Titus, J., Richman, C., 2000. Maps of lands vulnerable to sea level rise: Modeled elevations along the U.S. Atlantic and Gulf Coasts. Clim. Res. 18, 205–228.

Walsh, K., 2004. Tropical cyclones and climate change: unresolved issues. Clim. Res. 27, 77–83.

Webster, P.J., Holland, G.J., Curry, J.A., Chang, H.-R., 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. Science 309, 1844–1846.

Weltzin, J.F., McPherson, G.R., 2000. Implications of precipitation redistribution for shifts in temperate savanna ecotones. Ecology 81 (7), 1902–1913.

Willard, D.A., Holmes, C.W., Orem, W.H., Weimer, L.M., 1999. Plant communities of the Everglades: a history of the last two millenia. In: Gerould, S., Higer, A. (compilers). U. S. Geological Survey Program on the South Florida Ecosystem—Proceedings of South Florida Restoration Science Forum, May 17–19, 1999, Boca Raton, Florida. U. S. Geological Survey Open-File Report 99-181, Tallahassee, Florida, pp. 118–119. Williams, K., Pinzon, Z. S., Stumpf, R. P., Raabe, E. A., 1999. Sea level rise and coastal forests on the Gulf of Mexico. Open-File Report 99-441. U.S. Geological Survey, Center for Coastal Geology, St. Petersburg, Florida.