A spatial simulation model for forest succession in the Upper Mississippi River floodplain

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ABSTRACT

A Markov-chain transition model (FORSUM) and Monte Carlo simulations were used to simulate the succession patterns and predict a long-term impact of flood on the forest structure and growth in the floodplain of the Upper Mississippi River and Illinois River. Model variables, probabilities, functions, and parameters were derived from the analysis of two comprehensive field surveys conducted in this floodplain. This modeling approach describes the establishment, growth, competition, and death of individual trees for modeled species on a 10,000-ha landscape with spatial resolution of 1 ha. The succession characteristics of each Monte Carlo simulation are summed up to describe forest development and dynamics on a landscape level. FORSUM simulated the impacts of flood intensity and frequency on species composition and dynamics in the Upper Mississippi River floodplain ecosystem. The model provides a useful tool for testing hypotheses about forest succession and enables ecologists and managers to evaluate the impacts of flood disturbances and ecosystem restoration on forest succession. The simulation results suggest that the Markov-chain Monte Carlo method is an efficient tool to help organize the existing data and knowledge of forest succession into a system of quantitative predictions for the Upper Mississippi River floodplain ecosystem.

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1. Introduction

Forest succession remains a primary interest of ecologists, especially studies of ecological processes that affect species replacement and dynamics of species composition (Wu et al., 2006a; Ménard et al., 2002). Forest succession is a major research focus for the Upper Mississippi River (UMR) Ecosystem Restoration Program, because of concerns regarding of the loss of oak-hickory forests and the impacts of altered hydrology on the floodplain ecosystem (Yin et al., 2009; Leake and Johnson, 2006; Bodaly et al., 2004; Nelson, 1997; Yin and Nelson, 1995). The current floodplain forests of the UMR have been losing hard-mast oak (*Quercus* spp.) and hickory (*Carya* spp.) species because of the altered hydrology and impacts of flooding during the past two centuries (Yin et al., 2009; Leyer, 2005; Richter and Richter, 2000; Nelson et al., 1998a,b; Brugam, 1988; Leitner and Jackson, 1981; Howell and Kucera, 1956). Küßner (2003) suggested that the observed

mortality rate of oak (*Quercus* spp.) might be mainly determined by water elevation (i.e., flooding) or topographical complexity (Marinakis, 2008), but a comprehensive understanding of the ecological processes that influence ecosystem dynamics and community succession remains incomplete (Bishir et al., 2008; Freeman et al., 2003; Bürgi and Turner, 2002). Following the 1993 flood, the US Fish and Wildlife Service and US Army Corps of Engineers became increasingly concerned that conditions of the floodplain forest might not improve without active restoration (USGS, 1999; Gomez et al., 1997; Bhowmik, 1996).

UMR floodplain forest coverage has declined from 76% in 1826 to 13% in 1972 (Bragg and Tatschl, 1977). In the UMR floodplain, the successional sequence of trees begins with a community consisting of species such as cottonwood (*Populus* spp.), willow (*Salix* spp.) and other pioneer species, transitions to a community that includes maple (*Acer* spp.), and proceeds to a mature community of maple (*Acer* spp.), elm (*Ulmus* spp.), ash (*Fraxinus* spp.), oak (*Quercus* spp.) and hickory (*Carya* spp.). Once a floodplain forest reaches maturity, factors such as age, disease, fire, flood, or other disturbance could change the forest structure and reset the pattern of succession (De Blasio and De Blasio, 2009; Latterell and Naiman, 2007; Wu et al., 2006b; Knutson and Klaas, 1998; Nelson

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and Sparks, 1998; Nelson, 1997; Yin et al., 1997; Burns and Honkala, 1990; Adams and Bhowmik, 1989).

To restore the UMR floodplain ecosystems, a comprehensive understanding of succession pattern, ecological processes, and flood impacts on the forest ecosystem is needed (Vandermeer and Lin, 2008; USACOE, 2007; Dey et al., 2000; USGS, 1999). Knowledge concerning past species composition and population dynamics in spatial and temporal dimensions also is required (Kreiling et al., 2007; Ayala-del-Río et al., 2004; Schowalter, 2000; Clebsch and Busting, 1989). It is also suggested that detailed studies of tree population dynamics as influenced by population density, basal area changes, growth, and mortality, will result in a better understanding of spatial and temporal patterns of forest succession (Proulx et al., 2009; Yin et al., 2009; Conner et al., 2002).

Ecologists and forest managers recognize the importance of detailed spatial and temporal data and knowledge on disturbance dynamics and impacts (Morozov et al., 2008). Because first-hand knowledge and baseline data to assess alternative restoration strategies are lacking for the UMR floodplain forests to guide ecosystem restoration and help understand the impacts of 1993 flood, the US Geological Survey conducted two field studies. The first field study was an annual survey of seedlings every year from 1996 to 2001. The second field survey was conducted in 1995 and 2006 to characterize the mortality and growth of woody species of the UMR floodplain in Pool 26 of the Mississippi River (Yin et al., 2009). Data analysis from two comprehensive field surveys in the UMR floodplain suggested that maples and oaks were dominant species in the ecosystem in terms of not only the total number of trees but also the total basal area in 1993 pre-flood forests of the UMR floodplain ecosystem. Unlike oaks, however, maples continued to be the dominant species during post-flood succession; it appeared that oaks suffered from the 1993 flood with continued losses in the number of trees and basal area in the post-flood 2006 surveys (Yin et al., 2009). Data analysis for understanding the mechanism of species competition and population dynamics and for reconstructing the spatial and temporal pattern via modeling efforts may provide a useful tool for studying the dynamics of forest succession and ecosystem dynamics (Wu et al., 2006b; Freeman et al., 2003; Edwards et al., 1999).

The purpose of this research was to develop a spatially explicit model using Markov-chain Monte Carlo methods to simulate forest succession in the UMR floodplain and investigate the potential of the model for spatial and temporal analysis of forest dynamics and for simulation of impacts of flood disturbance. The model—named FORSUM—was developed to achieve the followings:

(1) Test the hypotheses and understand the causes of the deterioration of oak-hickory in the Upper Mississippi River floodplain,
(2) Project the responses and life strategy of each species to flood intensity and flood frequency, and
(3) Evaluate the success and impacts of different restoration alternatives and drawdown options (flood intensity and frequency) on the woody vegetation community.

The principal hypotheses evaluated with the model were that (1) without flooding, oaks can be sustainable in a "climax" community, (2) oaks may be tolerant to a certain level of flood intensity but will decrease as flood intensity increases, (3) flood frequency could be an important factor affecting oak succession, (4) different species in UMR floodplain may respond to flood intensity and flood frequency differently with different life strategies, and (5) locks and dams may have

strongly altered the UMR floodplain forest community, and drawdown could be one of the effective ways to restore the floodplain ecosystems.

Stochastic and mechanistic spatially explicit and individual-based forest succession models appear particularly well suited for understanding forest dynamics and disturbance impacts (Alados et al., 2009; Ménard et al., 2002; Wu et al., 2002). The Markov-chain Monte Carlo method has been used to describe forest succession in relation to tree growth, species replacement, and species competition (Wu et al., 1997, 2006a; Benabdellah, 2003; Korotkov et al., 2001; Yang et al., 1988).

2. Methods

FORSUM was developed as a spatially explicit model using Markov-chain transition and Monte Carlo methods to simulate forest succession in the UMR floodplain. The parameters and variables of the model were derived from data analysis from two field surveys by Yin et al. (2009). The six "species" investigated with FORSUM are actually "superspecies" or species aggregates, which were defined from 24 species addressed in the data analysis (Yin et al., 2009). These species aggregates are (1) Acer (A. negundo, A. saccharinum), (2) Fraxinus (F. pennsylvanica, Fraxinus spp.), (3) Quercus (Q. bicolor, Q. palustris, Q. velutina, Quercus spp.), (4) Carya (C. cordiformis), (5) Ulmus (U. americana, U. rubra, Ulmus spp.), and (6) Others (Betula nigra, Celtis occidentalis, Cephalanthus occidentalis, Cornus spp., Diospyros virginiana, Morus rubra, Populus spp., Prunus spp., Prunus virginiana, Rhamnus cathartica, Salix spp., Zanthoxylum americanum).

The number of seedlings, density effects, seedling growth, mortality rates and patterns, DBH growth, and the basal area of trees were calculated for the above six aggregates using the data collected in the field surveys. The resulting model parameters follow (Yin et al., 2009):

(1) species composition, in the number of trees and basal area
(2) mortality rates caused by flood, in the number of trees and basal area
(3) flood-caused mortality rates $f_m(DBH)$ expressed as a function of DBH (cm) for each species, such as $f_m(DBH) = \alpha \times e^{\beta \times DBH}$
(4) pre-flood survival rates $f_s(DBH)$ and post-flood survival rates $f_d(DBH)$, expressed as a function of DBH (cm) for each species
(5) mean/maximum density of seedlings per hectare and mean/maximum annual height growth for each species
(6) correlations between seedling annual growth rates (cm/year) $f_{sg}(h)$ and seedling heights (H)
(7) correlations between seedling annual survival rates $f_{ss}(h)$ and seedling heights (H)

In this research, the Markov-chain Monte Carlo methods were used as an efficient approach to organize the existing data and understanding of forest succession into a modeling system to quantitatively predict succession in the UMR floodplain ecosystem. The Markov chain captures all the information that could influence the future evolution of the process in the forest. Future states of the forest are modeled through a probabilistic process. If the Markov chain is time-homogeneous and the process is described by a single, time-independent matrix p_{ij}, then the vector is called a stationary distribution (or equilibrium distribution or climax) for forest succession (Yang et al., 1988).

The key for using a Markov chain for prediction of forest succession is to (1) determine the present state of a forest (S_t), (2) select a set of probabilistic processes that affect forest succession, which is also called Markov-chain transition probabilities (P), and (3) establish the Markov-chain model for predicting each transition state (S_{t+1}).

For all the six species aggregates, the Markov-chain transition model could be expressed as

$$
\begin{bmatrix} Acer(AC) \\ Fraxinus(FR) \\ Quercus(QU) \\ Carya(CA) \\ Ulmus(UL) \\ Others(OT) \end{bmatrix}_{t+1} = \begin{bmatrix} f_1(x) & 0 & 0 & 0 & 0 & 0 \\ 0 & f_2(x) & 0 & 0 & 0 & 0 \\ 0 & 0 & f_3(x) & 0 & 0 & 0 \\ 0 & 0 & 0 & f_4(x) & 0 & 0 \\ 0 & 0 & 0 & 0 & f_5(x) & 0 \\ 0 & 0 & 0 & 0 & 0 & f_6(x) \end{bmatrix} \times \begin{bmatrix} AC \\ FR \\ QU \\ CA \\ UL \\ OT \end{bmatrix} = F_i(x) \times \begin{bmatrix} AC \\ FR \\ QU \\ CA \\ UL \\ OT \end{bmatrix}_t
$$

This can be written as:

$$S_{t+1} = F_i(\chi)S_t, \quad \text{or} \quad S_{t+1} = PS_t,$$

The resulting model is the spatially explicit Markov-chain transition and Monte Carlo forest succession model FORSUM. The model defines a 100×100-cell landscape with a resolution of 1 ha. With 100×100 1-ha landscape grid cells, a total of 10,000 replicates of Monte Carlo simulations were conducted. Each cell simulates the establishment, growth, and competition of each species. FORSUM is individual-based and density-dependent. The density is expressed as percent and total basal area for each species in a landscape cell. The timescale for modeled growth is 1 year. Markov-chain transition was used to simulate the succession of each species on a yearly basis for 1000 simulated years with a set of transition probabilities, coefficient, parameters, variables, and functions.

The detailed mechanism of FORSUM is based on field-survey data of seedling density, germination probability, height growth, seedling survival probability, spatial distribution and density of individual trees, basal area growth, and survival probability of each tree. First, to initiate a simulation, the model assigns a random (R) number of trees (T_i) based on the maximum density (M_D) for each species i in each 1-ha cell ($T_i = R \times M_D$) with different DBH ($DBH_i = R \times F_i(DBH)$) for each tree ($j$) based on DBH distribution ($F_i(DBH)$) for a species i. The model then simulates each individual tree's (j) establishment, growth and mortality of each species in each 1-ha cell.

The model was used to simulate the damage caused by the 1993 flood and forest succession after the flood. The tree mortality caused by the 1993 flood was simulated as $S(T)_{t+1} = R \times F_i(DBH) \times S(T)_t$ and the DBH loss as $S(DBH)_{t+1} = R \times F_i(DBH) \times S(DBH)_t$. Post-flood succession was simulated by the recruiting of seedlings for each species ($T_i = R \times C_i \times D/M_D$) based on the recruiting coefficient (C_i) forest density (D) at the time t. Seedlings of different species were growing into canopy to be simulated as individual trees based on the height growth ($HG_i = R \times F_{sg}(H)$) and survival rates ($SR_i = R \times F_{ss}(H)$).

With the comparison to the 1993 flood, we were able to create different intensity coefficients (ϖ_i) of flooding such as 12.5%, 25%, ... or 125%, 150%, ... of 1993 food severity and their impacts on forest succession. To understand the flood impact, we simulated not just with a range of flood intensity but also with a range of flood frequency (ϕ_i) from 1 to 10 floods within each 100-year period by random distribution. We also simulated flood impacts on flood-plain forests based on the simulations of (1) a water-level drawdown of 2 ft, (2) less flooding in upper pool areas, and (3) more flooding in lower pool areas of Pool 5 on Upper Mississippi River (Wu et al., 2006a) to evaluate how locks and dams may alter water level and affect forest dynamics and species composition.

Monte Carlo methods are computational algorithms based on repeated random simulations to sample their results. Monte Carlo simulation methods are especially useful in studying systems with significant uncertainty in inputs, parameters, and variables such as forest succession and dynamics (Ulanowicz et al., 2009; Yin et al., 2009; Benabdellah, 2003; Korotkov et al., 2001; Brannan et al., 1984). In this research, model sensitivity was evaluated in relation to initial conditions, model parameters, and variables, as well as the model's utility in assessing the impact of introduced flood disturbances on species densities, composition, and dynamics. In the meantime, the model simulation results were compared to the results of the Upper Mississippi River pre-flood 1993, post-flood 1995, and post-flood 2006 field-survey data for model verification, model sensitivity analysis and model calibration. Scenario simulations were conducted by changing flood intensity and frequency as well as water levels in the lower, middle, and upper section of UMR Navigation Pool 5 to examine forest succession, predict the possible results of different management or restoration alternatives and project impacts of flooding.

3. Results

Model verification was conducted by comparing simulations to the field-survey observations of total density and total basal area (Fig. 1) for 1993 (before the flood), 1995 (right after the flood), and 2006 (more than 13 years of growth after the flood) (Fig. 1a). For all the species combined, the simulated number of trees was 3325, and the observed number was 3238 in 1993 before the flood. In 1993, the simulated basal area was 116 m²/h and measured basal area was 123 m²/h. The model predicted 1460 trees compared to 1395 observed in 1995, 2 years after the flood. A simulated basal area of 65 m²/h compared favorably with the observed 83 m²/h in 1995. Thirteen years after the 1993 flood, the model simulated 4194 trees and 90 m²/h of basal area, compared to the measured 5177 trees and 100 m²/h of basal area (Fig. 1a).

To verify the model, the comparisons of simulations and observations were also studied for each species in the pre-flood year 1993 (Fig. 1b) and the post-flood years 1995 (Fig. 1c) and 2006 (Fig. 1d). Simulated results were very close to the observations for all the six species aggregates in number of trees and basal area. For Quercus, the simulation of 412 trees/ha can be compared to the observation of 449 for 1993, 150 to 230 for 1995, and 265 to 193 for 2006. The basal area simulation of 24 m²/h can be compared to the observation of 34 for 1993; 10–22 for 1995; and 12–17 for 2006. As supported by the field data, the simulations also suggest damage and recovery as reflected in density and basal for each species in 1995 and 2006, respectively. The comparisons of the simulation results to the observations for other species aggregates also suggest that the model was able to match the simulations to observations not only in the forest succession patterns but also in impacts of 1993 flood (Fig. 1).

The results of model sensitivity analysis suggest that forest succession patterns of each species in FORSUM are highly sensitive to the flood-intensity coefficient, ϖ_i, which is proportional to the 1993 flood intensity. For example, a ϖ_i of 0.125 is 87.5% less severe than the 1993 flood, and a value of 1.50 is 50% more severe. Density (Fig. 2a) and basal area (Fig. 2b) of the six aggregates responded differently to ϖ_i as it was varied from 0.125 to 2.00 (Fig. 2). It appears that the Quercus aggregate can be sustained at a high level of density and basal area if ϖ_i is less than 0.25. As ϖ_i increases, Quercus decreases in both simulated density and basal area. Interestingly, the simulated density and basal area for Quercus
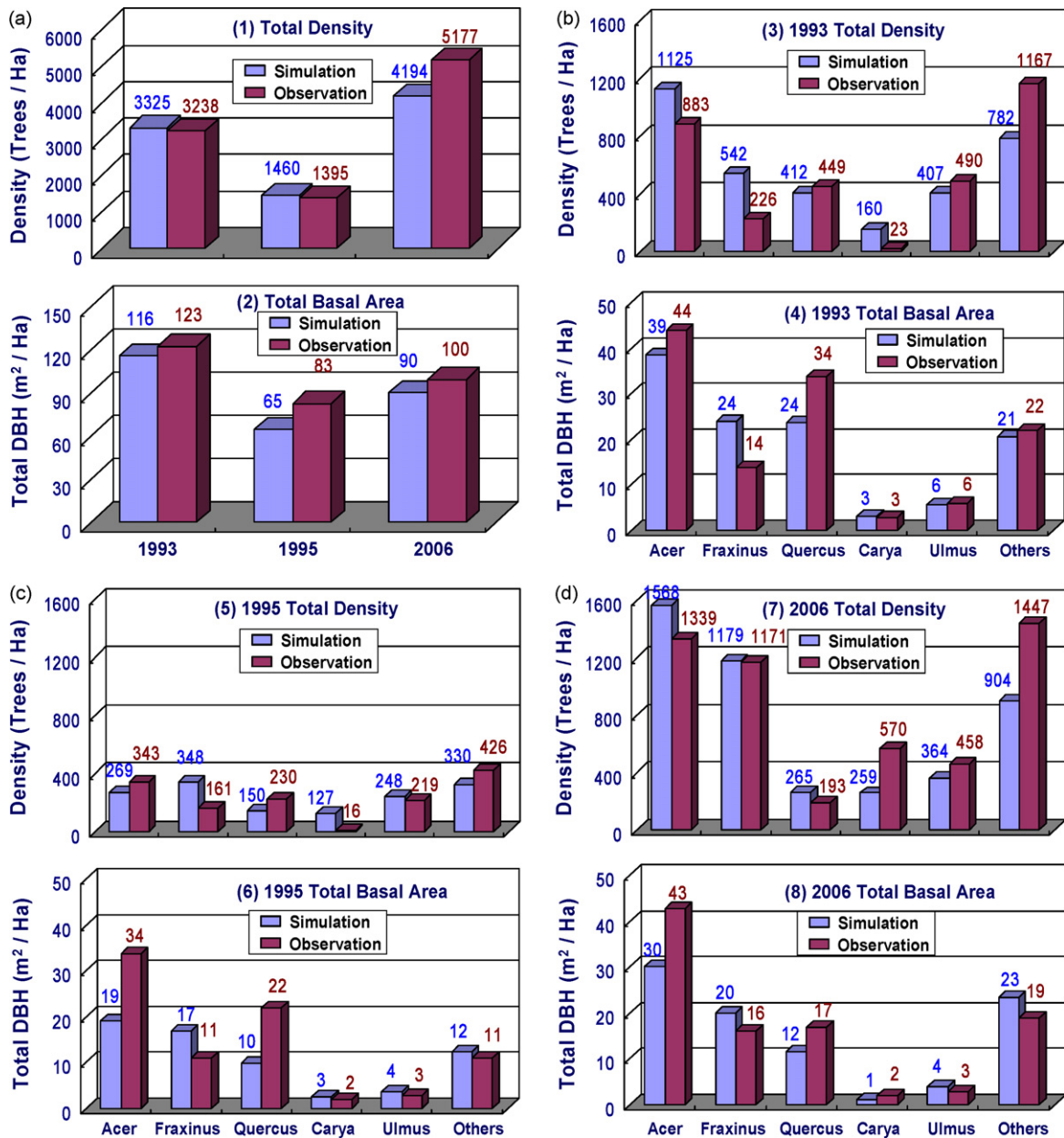
Fig. 1. Model verification for the comparison between simulations and field-survey observations for the total density and total basal area for all the species combined (a) and for each species in the pre-flood year 1993 (b) and the post-flood years 1995 (c) and 2006 (d).

increase from their lowest point, at a (ϖ_i) of 1.75, to a ϖ_i of 2.00 (Fig. 2). Based on the density, the model simulations also suggest that the aggregates Acer, Fraxinus, and Others may be tolerant to floods, whereas Quercus, Carya, and Ulmus may not be.

As different aggregates responded to the flood-intensity coefficient (ϖ_i) differently, the aggregates also responded to flood-frequency coefficient, ϕ_i, differently in the model simulations (Fig. 3). The coefficient ϕ_i is the number of floods in each 100 years, such that a coefficient of 1 represents 1 flood per 100 years with a flood probability of 1%, 2 represents 2 floods in 100 years with flood probability of 2%, and so on. In this case, all the simulations of varied flood frequency have the same flood intensity, 1.0 (the same as 1993 flood intensity). The simulation results suggested that Quercus could further decrease in density and basal area if a flood of the 1993 intensity happens more than once in 100 years (Fig. 3). Another interesting result from the simulation is that all the species respond to an increase in ϕ_i from 1 to 2, but not much from 2 to 10 (Fig. 3).

The first scenario simulation was to assume no flood for 1000 years from the first year as the model initiated the "seedling establishment and growth". The simulation suggests that all the species in the community reach the climax, with stable density and basal area for each species, after 500 simulated years. This further suggests that the Markov-chain is a stationary distribution (or equilibrium distribution) that defines a climax forest (Fig. 4). The simulation also suggests that Quercus should be the dominant aggregate based on the basal area composition if there is no flooding in the floodplain forest; specifically, the mean basal area for Quercus is 60 m²/h, compared to less than 30 m²/h for all other species (Fig. 4b).

In comparing the proportion of density and basal area for each aggregate in the "no-flood" simulation, the proportion of density and basal area for each species was "proportionally similar" except for Quercus. Without flood disturbance, Quercus grows much well in terms of basal area and takes about 55% of the total basal area in a stand (Fig. 5a). As "no-flood" favors Quercus growth in basal area,
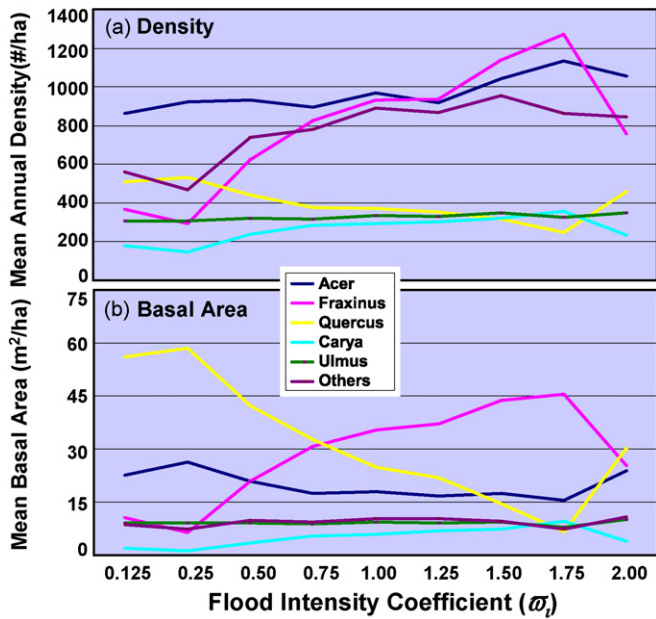
Fig. 2. Model sensitivity analysis by simulations of different flood intensity coefficients (ϖ_i) for responses of each species on tree density (a) and basal area (b) in forest succession.
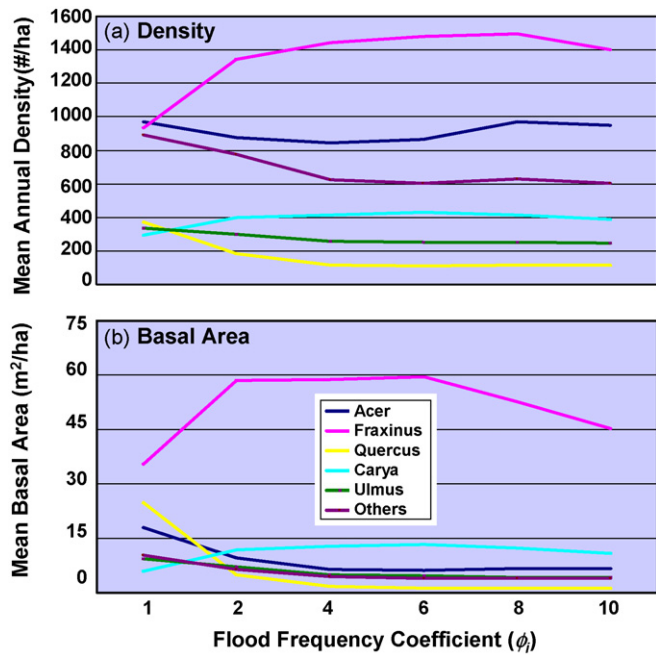

Fig. 3. Model simulations of different flood-frequency coefficients (ϕ_i) for responses of each species on tree density (a) and basal area (b) in forest succession.

Fig. 4. Scenario simulations without flood for 1000 years for the study of species composition in both density (a) and basal area (b) in a climax community.

Fig. 5. Comparison of the proportion of density and basal area for each species with "no-flood" simulation (a), and the difference between "no-flood" simulation and 1993 field observation for density (b) and basal area (c).

it may have limited all other species in basal area growth (Fig. 5a). When we compared the "no-flood" stand to 1993 (pre-flood) stand in both the density (Fig. 5b) and basal area (Fig. 5c), it appeared that "no-flood" conditions favor the growth in density of Acer and Quercus but not the density of Ulmus and the other species aggregates. Also, without flood, the category of "Others" as successional species may be significantly reduced in both density and basal area, comparing 17% for "no-flood" to 36% for 1993 with density (Fig. 5b) and 6% for "no-flood" to 26% for 1993 with basal area (Fig. 5c).

As mentioned previously, FORSUM was used to simulate the response of the community and each aggregate's response to locks and dams in UMR floodplain with three scenarios: (1) drawdown of
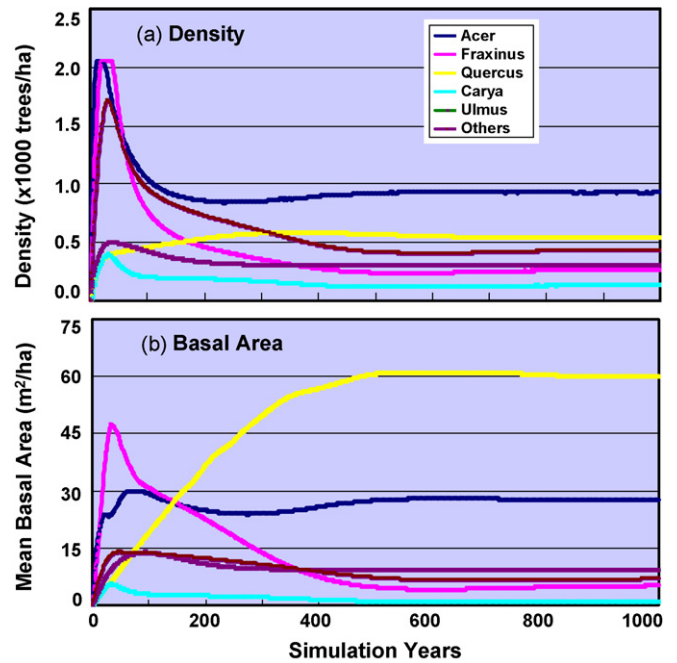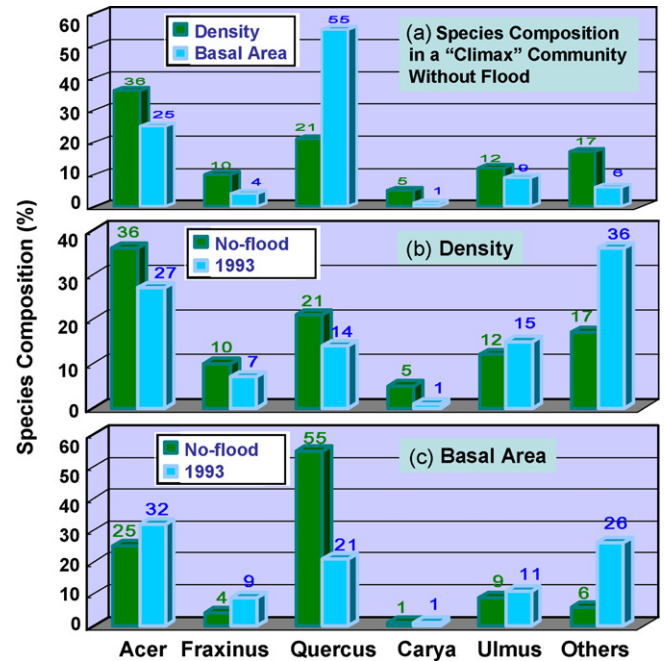
2 ft (Fig. 6a), (2) less flooding in the upper pool areas (Fig. 6b) and (3) more flooding in the lower pool areas (Fig. 6c), for which the flood-intensity coefficient, ϖ_i and flood-frequency coefficient, ϕ_i were generated from historical data. The model simulated the landscape for 500 years to reach the climax status without flood and then incorporated the above three flood scenarios for another 500 years of simulations.

The simulation results suggest that the density and basal area growth responses of each aggregate are different among the different flood scenarios (Table 1). For example, it appeared that
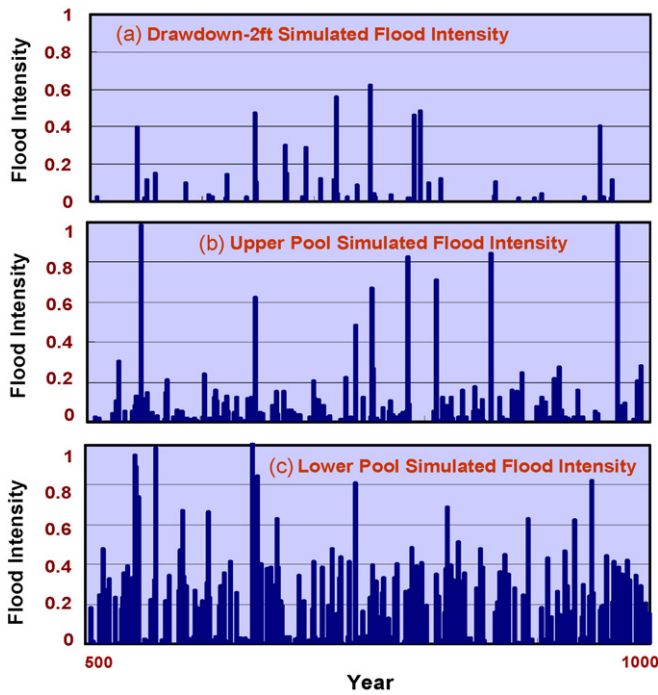
Fig. 6. Simulated flood intensity and flood frequency created from historical data in three scenarios:(a) water-level drawdown of 2 ft, (b) less flooding in upper pool areas, and (c) more flooding in lower pool areas.

Fig. 7. Species composition in terms of density (a) and basal area (b) before the 1993 flood (rectangles) and their correlations to the flood intensity coefficient (ϖ_i).

locks and dams altered the species composition in favor of Fraxinus, which had a 7% pre-1993 density and about a 40% density in upper and lower pool simulations; this compares with Acer, Quercus, Ulmus, and Others densities of 27%, 14%, 15% and 36% pre-1993 and 19%, 3%, 7% and 16% in the upper pool simulation, respectively (Table 1). Based on the simulations, floods in the upper and lower pool areas might cause the loss of Quercus in the floodplain, as evidenced by the 26 m²/h (20%) of basal area in pre-1993 forests compared to 2 m²/h (1%) in the upper pool simulation and 1 m²/h (<1%) in the lower pool simulation (Table 1). In contrast, the model suggests that Fraxinus competes well in the community under flood conditions for both density and basal area growth, with 226 trees/ha (7%) for density growth and 12 m²/h (10%) for basal growth in pre-1993 forests; 1300 trees/ha (41%) for density and 77 m²/h (70.6%) for basal area in the upper pool simulation; and 1417 trees/ha (40%) for density and 56 m²/h (66%) for basal area in the lower pool simulation (Table 1).

Consistent with UMR ecosystem restoration objectives, FOR-SUM was used to simulate the effects of a water-level drawdown of 2 ft. The simulation results suggest that the Quercus, Ulmus, and
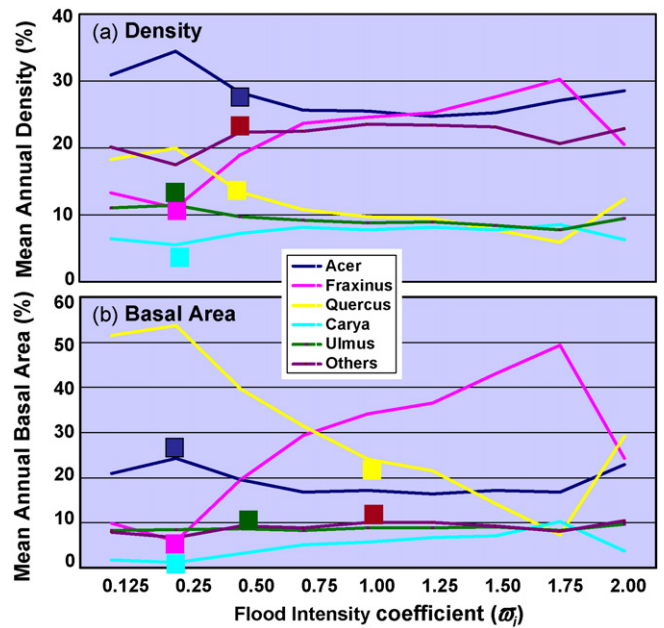
Others aggregates responded positively to drawdown with higher density (188, 274, and 756 trees/ha, respectively) and more basal area growth (9, 7 and 8 m²/h, respectively). In contrast, Acer, Fraxinus, and Carya did not respond to drawdown significantly (Table 1).

As shown in Table 1, the density and basal area of each species before the 1993 flood are in the range between the no-flood and drawdown simulations, which means that the species composition of pre-1993 flood forests should reflect some flood intensity and frequency (Table 1). When we compared the percent density and percent basal area of each species to different flood-intensity coefficients, ϖ_i from 0.125 to 2.00, we found that the species composition or the percent density and percent basal area from the pre-flood field survey are mainly between ϖ_i of 0.25 and 1.00 (Fig. 7). As we compare a set of scenario simulations of different flood intensities to the 1993 flood ($\varpi_i = 1.0$), we see indications that Quercus might persist if the flood intensity is less than that of the 1993 flood (ϖ_i between 0.25 and 1.0). The species composition, in terms of both density and basal area, before the 1993 flood seems to be the result of Quercus growing in a habitat where flood intensity was less severe than that of the 1993 flood (Fig. 7).

Table 1
The comparisons of different flood scenario simulations of (1) drawdown-2 ft, (2) upper pool, (3) lower pool, (4) no-flood, and (5) pre-1993 flood for their responses on the density (trees/ha) and basal area (BA, m²/h) for each species category.

| Flood	Growth	Acer (%)	Fraxinus (%)	Quercus (%)	Carya (%)	Ulmus (%)	Others (%)	Total
Drawdown	Density (#/h)	626 (18)	1139 (33)	188 (6)	434 (13)	274 (8)	756 (22)	3417
	BA (m²/h)	8 (7)	67 (58)	9 (8)	16 (14)	7 (6)	8 (7)	115
Upper pool	Density (#/h)	595 (19)	1300 (41)	94 (3)	464 (15)	221 (7)	522 (16)	3198
	BA (m²/h)	5 (4)	77 (71)	2 (1)	17 (16)	5 (4)	4 (4)	110
Lower pool	Density (#/h)	862 (24)	1417 (40)	99 (3)	394 (11)	229 (7)	546 (15)	3547
	BA (m²/h)	7 (8)	56 (66)	1 (1)	13 (15)	4 (5)	4 (5)	85
No-flood	Density (#/h)	932 (36)	254 (10)	547 (21)	130 (5)	304 (12)	422 (16)	2590
	BA (m²/h)	30 (26)	5 (4)	67 (55)	1 (1)	10 (8)	7 (6)	120
Pre-1993	Density (#/h)	883 (27)	226 (7)	449 (14)	23 (1)	490 (15)	1167 (36)	3238
	BA (m²/h)	40 (32)	12 (10)	26 (20)	2 (1)	14 (11)	33 (26)	127
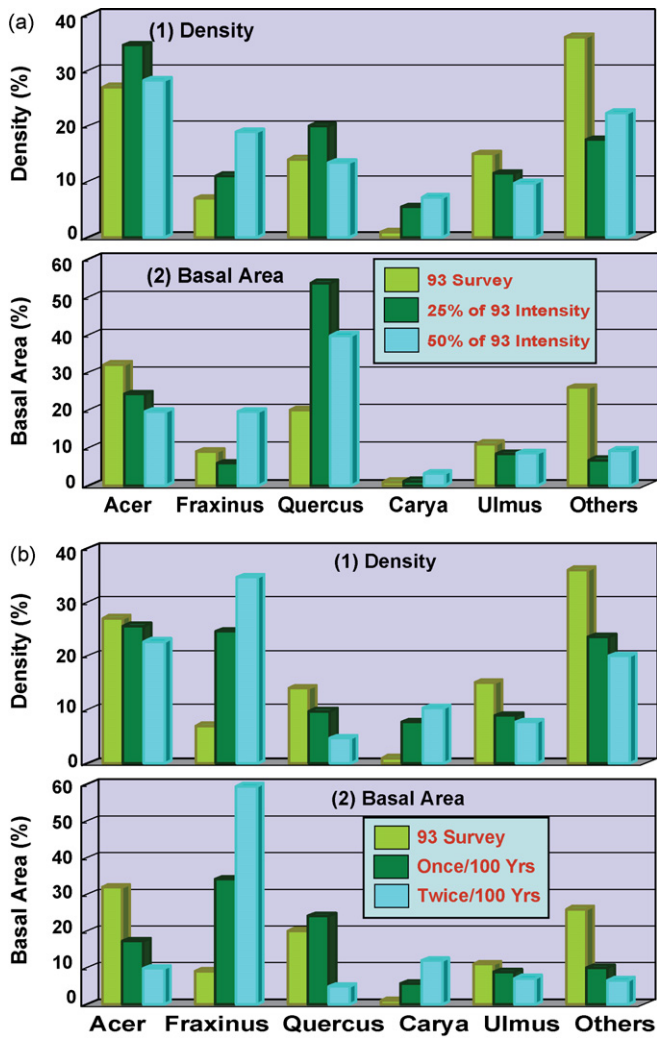
Fig. 8. Comparisons of density (a) and basal area (b) for each species responding to three simulations for the same 1000 years with flood intensity coefficient (ϖ_i) equal to 0.25 and 0.50 (25% and 50% of the 1993 flood intensity) and equal to 1.0 (1993 flood intensity).

Three simulations were conducted for the same 1000 years with ϖ_i equal to 0.25, 0.50 (25% and 50% of the 1993 flood intensity) and 1.0 (1993 flood intensity). The simulated densities of the aggregates Acer, Quercus, and Ulmus appeared to be similar to those before the 1993 flood (Fig. 8a). As simulated flooding becomes less intense (ϖ_i = 0.25 or 0.50), Quercus increases in basal area, although the density may not vary (Fig. 8a). When the simulated flood frequency is increased from once every 100 years to twice in 100 years, the model results suggest that the Fraxinus, Quercus, Cayra, Ulmus, and Others aggregates respond to flood frequency differently; and, given the pattern of the change from the 1993 survey, it appears that these species all grew in an environment where flood frequency was less than or equivalent to 1 flood in 100 years with an intensity less severe or equivalent to that of the 1993 flood (Fig. 8b). More frequent flooding produced changes in species composition and basal area that were different from pre-1993 (Fig. 8).

4. Discussion and conclusions

Markov-chain transition and Monte Carlo simulation were used to develop the spatially explicit model FORSUM with variables, probabilities, functions, and parameters derived from the data analysis. The intent of model verification in this research was to make sure that the model results/outputs were what modelers expected (Wu et al., 2006a; Sargent, 2004). The model used a set of parameters and variables for the analysis of the field data. If all the parameters, variables, and functions in the model are correct, FORSUM should be able to generate similar results to the field-survey data. The simulation results suggest that the total tree density and total basal area compare favorably to observations in 1993, 1995, and 2006 (Fig. 1a). With a simulation beginning in 1900, the simulated tree density and basal area growth for each species aggregate in 1993 were similar to the data (Fig. 1b). The model also simulated the 1993 flood damage and the survival of trees and basal area growth in 1995, in which the patterns between the simulations and observation were similar (Fig. 1c). For the post-flood period to 2006, the model again was able to simulate the post-flood succession patterns in both tree density and total basal area for each species aggregate that matched the observed patterns (Fig. 1d). Model verification also suggests that the species-aggregate composition in terms of density and basal area for both field-survey data and simulation results were not significantly different.

Model sensitivity analyses provided important information on how each parameter contributes to the model results and how sensitive a parameter is in FORSUM simulations. The result suggested that the flood-intensity coefficient ϖ_i and the flood-frequency coefficient ϕ_i are sensitive factors, affecting forest succession patterns of each species. Compared to 1993 flood severity, it appears that the Quercus species aggregate might decrease in both density and basal area as ϖ_i increases. It also appears that Quercus could be sustained at a high level of both density and basal area with a ϖ_i of less than 0.25 (Fig. 2). Based on the density, the model simulation also suggested that the Acer, Fraxinus, and Others aggregates may be more tolerant to flood. In contrast, the Quercus, Carya, and Ulmus aggregates may not be sustainable as flood intensity increases (Fig. 2). It seems, therefore, that Quercus growth and population density are limited by flood intensity (Fig. 2); Quercus may be tolerant to a certain low level of flood intensity but will decrease in density and nasal area as the flood intensity increases.

Based on the simulation results, Quercus could decrease in density and basal area if the flood frequency (ϕ_i) exceeds once in 100 years (Fig. 3). Flood frequency could be an important factor affecting Quercus during succession. Interestingly, the model results showed that all the species aggregates respond substantially to the ϕ_i increases from 1 to 2 but less so for increases from 2 to 10 (Fig. 3). As a result, different species in UMR floodplain may respond markedly to flood intensity and flood frequency differently with different life strategies. This was observed in riparian plant species richness by Lite et al. (2005).

To further understand the floodplain forest succession patterns within the Upper Mississippi River ecosystem and to predict long-term impacts of flood on the forest succession, FORSUM scenario simulations were used to predict spatial-temporal patterns in species composition that define succession patterns. These scenario simulations were conducted to understand the mechanism of an ecosystem, predict the possible results of different management or restoration alternatives, or project impacts of different disturbances—specifically, with or without flood, with or without locks and dams, and with ecosystem restoration alternatives such as river-level drawdown. Simulation results from the first scenario indicated that Acer and Quercus could be the dominant species in the community if there was no flood impact on the ecosystem (Fig. 4). It appeared that "no-flood" conditions favor increased density of Acer, Fraxinus, and Quercus but not the density of Ulmus and Others aggregates. Also, without flood, Quercus can be sustainable in a climax community, and the Others category as successional species may be significantly reduced in density, 36% to 17% and 26% in basal area to 6% with and without

flooding, respectively (Fig. 5b and c). This scenario confirms that the UMR floodplain has supported the community of oaks for centuries (Richter and Richter, 2000; Nelson et al., 1998a,b; Brugam, 1988; Leitner and Jackson, 1981; Howell and Kucera, 1956) and the altered flood intensity and frequency might be the major reason caused the loss of oaks in the UMR (Yin et al., 2009; Leake and Johnson, 2006; Bodaly et al., 2004; Küßner, 2003).

Results from scenario simulations also suggested that each category of species has a different life strategy in responding to the locks and dams on the Upper Mississippi River, which changed the flood intensity and flood frequency. It appeared that locks and dams altered the species composition, with more Fraxinus in the upper and lower pool areas and less Acer, Quercus, Ulmus, and Others (Table 1). The simulations also confirmed that floods in the upper and lower pool areas might have caused the loss of oaks in the floodplain (Table 1).

The simulation results for water-level drawdown suggested that the Quercus, Ulmus, and Others aggregates responded positively to drawdown with increases in density and basal area. In contrast, Acer, Fraxinus, and Carya did not respond to drawdown significantly (Table 1). It appeared that locks and dams may have strongly altered UMR floodplain forest community and that drawdown could be an effective way to restore the floodplain ecosystems.

As suggested by Küßner (2003), the observed mortality rate of oak might be mainly determined by water elevation (i.e., flooding). In contrast, the mortality patterns of ash highly depend upon tree density (Küßner, 2003). This is consistent with our model simulations, in which the Fraxinus species grow better under a flooded environment whereas Quercus is affected by flood with low density and basal area in growth. What remains challenging is to understand to what extent that these floodplain forest communities are artifacts of various combinations of succession patterns, species life strategy, flood regime, and geomorphology (Alados et al., 2009; Marinakis, 2008; Prato, 2008; Dey et al., 2000).

This modeling study suggests that increased water flooding caused by the construction of locks and dams led to substantial changes in the spatial distribution of floodplain forest species composition. The study provides information about the overall impact of flooding on plant species composition and specific species' response patterns to different flood intensities and flood frequencies. The methodology reported here allows accurate prediction of shifts in floodplain vegetation in response to human-induced alterations in floodplain landscapes. FORSUM can be used as a tool for assessing river regulation measures and for floodplain restoration purposes, such as drawdown.

This study also demonstrates that the combined Markov-chain transition and Monte Carlo modeling, applied in the form of the FORSUM, provides an efficient approach to integrate variables, probabilities, functions, and parameters derived from field data analysis. This model integration was used to characterize and predict forest succession, spatial and temporal patterns, and species composition and competition. The simulation results further suggest that the model was able to reconstruct the succession pattern in the UMR floodplain on the basis of model inputs. The model further helps in understanding the succession patterns and appears to be useful predicting a long-term impact of flooding and water-level management on forest succession. This modeling approach also provides a useful tool for testing hypotheses about forest succession and enables users to evaluate the impacts of flood disturbances, river impoundment, and ecosystem restoration alternatives on forest succession.

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