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Patterns of forest succession and impacts of flood in the Upper Mississippi River floodplain ecosystem

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ABSTRACT

The widespread loss of oak-hickory forests and the impacts of flood have been major issues of ecological interest concerning forest succession in the Upper Mississippi River (UMR) floodplain. The data analysis from two comprehensive field surveys indicated that *Quercus* was one of the dominant genera in the UMR floodplain ecosystem prior to the 1993 flood and constituted 14% of the total number of trees and 28% of the total basal area. During the post-flood recovery period through 2006, *Quercus* demonstrated slower recovery rates in both the number of trees (4%) and basal area (17%). In the same period, *Carya* recovered greatly from the 1993 flood in terms of the number of trees (11%) and basal area (2%), compared to its minor status before the flood. Further analyses suggested that different species responded to the 1993 flood with varying tolerance and different succession strategies. In this study, the relation of flood-caused mortality rates and DBH, $f_m(d)$, can be expressed in negative exponential functions for each species. The results of this research also indicate that the growth functions are different for each species and might also be different between pre- and post-flood time periods. These functions indicate different survival strategies and emergent properties in responding to flood impacts. This research enhances our understanding of forest succession patterns in space and time in the UPR floodplain. And such understanding might be used to predict long-term impacts of floods on UMR floodplain forest dynamics in support of management and restoration.

1. Introduction

Although humans have been associated with the Upper Mississippi River (UMR) floodplain for thousands of years, the greatest anthropogenic impacts on this ecosystem have mainly occurred during the past 150 years. These impacts transformed the floodplain into one of the most altered ecosystems in North America (USACE, 2007; Dey et al., 2000; Theiling, 1999b). There have been two major issues of ecological interest concerning forest succession in the UMR floodplain: (1) the loss of oak-hickory forests and (2) the continued impacts of altered hydrology on forest structure and function (Leake and Johnson, 2006; Bodaly et al., 2004; Nelson, 1997; Yin and Nelson, 1995). The UMR floodplain forest has been losing the hard-mast oak (*Quercus* spp.) and hickory (*Carya* spp.) species during the last two centuries (Richter and Richter, 2000; Nelson et al., 1998a,b; Brugam, 1988; Leitner and Jackson, 1981; Howell and Kucera, 1956). During this period, the area of UMR floodplain occupied by forests has declined historically from 76% in 1826 to 13% in 1972 (Bragg and Tatschl, 1977).

Historical data provide some information concerning past species composition and population dynamics (Ebenhöh et al., 2009; Edwards et al., 1999). In the Upper Mississippi River floodplain, the succession sequence of trees appears as an initial community dominated by species such as cottonwood (*Populus* spp.), willow (*Salix* spp.) and other pioneer species. This early stage is replaced by a transitional community dominated by elms (*Ulmus* spp.), ash (*Fraxinus* spp.), oaks (*Quercus* spp.), hickory (*Carya* spp.), and maples (*Acer* spp.). The floodplain is eventually dominated by a mature community of maples (*Acers* spp.). Once a floodplain forest reaches maturity, biological factors such as aging, or disturbances (e.g., disease, fire, flooding) could cause the successional sequence to revert to some previous stage (Latterell and Naiman, 2007; Knutson and Klaas, 1998; Nelson and Sparks, 1998; Nelson, 1997; Yin et al., 1997; Burns and Honkala, 1990; Adams and Bhowmik, 1989; Bragg and Tatschl, 1977).

Current understanding of the relative importance of ecological processes and disturbances in determining the dynamics of floodplain forest succession remains incomplete (Freeman et al.,

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2003; Bürgi and Turner, 2002). For example, Küßner (2003) suggests that the loss of oak (*Quercus* spp.) might have resulted from changes in water elevation (i.e., flooding) and not competition (e.g., light) in the UMR floodplain forests. In contrast, the observed mortality patterns of ash (*Fraxinus* spp.) highly depend upon tree density or light availability (Küßner, 2003). The challenge remains to quantitatively describe UMR floodplain forest as a complex and dynamic integration of species life-history strategies, ecosystem processes, and disturbance regimes (e.g., Dey et al., 2000).

The "Great Flood of 1993" on the Upper Mississippi River provided an opportunity to assess the impact of this significant disturbance on UMR floodplain forest dynamics. The 1993 flood was among the most devastating ever to occur in the UMR floodplain (Theiling, 1999a; Lott, 1993). The flooded area was approximately 1200 km long and 700 km wide, or a total of 380,000 km^2 (NOAA, 1994; Braatz, 1994). In terms of duration, area inundated, displaced people, damage to crops and property, and the number of record river levels, the 1993 flood event is second only to the Great Mississippi Flood of 1927, the largest flood ever recorded for this river (Jacobson and Oberg, 1997; Gomez et al., 1997; Bhowmik, 1996; NOAA, 1994; Lott, 1993). Following the 1993 flood, U.S. federal and state natural resource management agencies were concerned that impacts to the floodplain forests would require active restoration (Flinn et al., 2008; Yin, 1999; Theiling, 1999b). As a result, efforts to restore the UMR floodplain should derive from a more complete understanding of the succession pattern, ecological processes and flood impacts on this ecosystem (Kenow et al., 2007; USACE, 2007; Barko et al., 2006; Wu et al., 2006a; Klimas et al., 2005). Thus, in addition to this opportunity to further understand floodplain forest dynamics, there is an urgent need to apply this understanding to intelligent management and restoration of UMR floodplain forests in the aftermath of the 1993 flood (Damgaard and Ejrnæs, 2009; Lubinsky and Theiling, 1999).

The study reported here presents the analysis of two field studies conducted to (1) assess the impacts of the 1993 flood on current succession patterns (e.g., continued loss of oak and hickory species), (2) characterize the health and emergent properties of the floodplain ecosystem after the 1993 flood; and (3) provide data that can be used to reconstruct and forecast succession patterns in space and time in the UMR floodplain. These studies permitted the analysis of the pre- and post-flood population densities, growth, and mortality of individual tree species in terms of their contribution to spatial and temporal patterns of forest succession. Previous investigations have demonstrated the importance of population-level data and species descriptions in describing and understanding forest succession dynamics (Laperrière et al., 2009; Kreiling et al., 2007; Ayala-del-Río et al., 2004; Conner et al., 2002; Schowalter, 2000; Wu et al., 1997; Clebsch and Busting, 1989). The results of the data analysis described here permit reconstruction of floodplain forest structure in space and time. Such reconstruction might provide insight concerning future patterns of succession and help define effective actions to restore and manage these valued resources (Prager and Reiners, 2009; Souza et al., 2009; Bennett et al., 2009; Wu et al., 2006b; Freeman et al., 2003; Edwards et al., 1999).

2. Methods

2.1. Study sites and field surveys

To guide ecosystem restoration and help understand the impacts of the 1993 flood, the U.S. Geological Survey conducted two field studies starting in 1995. The study sites were located in the areas of Navigation Pools 4, 8, 13, and 26 on the Upper Mississippi River and the LaGrange Pool on the Illinois River (Fig. 1). In each pool floodplain forests, two study sites were chosen with each site consisting of a 30-m radius sampling plot. Surveys performed at these locations produced data to assess the severity of flood impacts, evaluate post-flood forest regeneration, and identify potential challenges to the successful restoration of these UMR floodplain forests.

The first field study included annual surveys of tree seedlings from 1996 to 2001. Within each 30-m radius plot, 15 1-m^2 subplots were randomly located. At each subplot, each seedling was identified to species and marked with a unique tag number. The height (cm) of each seedling was also recorded. These subplots were revisited once each month to measure the growth or record the mortality of each tagged seedling. New seedlings observed in these subplots were also identified, measured, and tagged.

The second field survey was conducted in both 1995 and 2006 to characterize the growth and mortality of mature trees in Pool 26. Within each of two 30-m radius sampling plots, each mature (living or dead) tree was identified and its diameter at breast height (DBH) was measured. During the 1995 survey, all dead trees within the plots were identified if it was caused by the 1993 flood and they were alive before the 1993 flood.

2.2. Species composition

There were 24 species of woody plants identified in the field survey. For purposes of analysis, these 24 species were grouped into six categories or "super-species" which were defined as (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 eleven species that define the category "Others" were grouped largely because they were rarely encountered in the sampling subplots, but with the recognition that they include representative species from different stages of succession within the UMR floodplain forests.

2.3. Data analysis

Data describing the number of seedlings, density, and seedling growth in height, mortality rates and patterns, DBH growth, basal area and DBH for each species were summarized for each of the six broad categories of species. DBH data were categorized into 10-cm intervals for each species. Maximum and mean values of heights, DBH growth and density were determined. Yearly seedling survival and mortality rates were estimated. Probabilities of mortality, survival, growth, and density effects were also calculated. In this study, the species composition was represented by basal area and density. In subsequent analysis, different functions used to estimate correlations between (1) growth and density, (2) survival rates and DBH, and flood mortality rates and DBH for each species. All the correlations were tested using *t*-tests. The data were analyzed to address the following questions:

(1) How did each species respond to the 1993 flood? (e.g., was oak more or less tolerant to the flood?)
(2) Did tree size affect its flood tolerance?
(3) How did each species regenerate after the flood? (e.g., did oak regenerate after the flood?)
(4) How successful were different species in recovering from the flood (e.g., number of trees and basal area?)
(5) What is the apparent successional strategy of each species?
(6) What were the major changes between pre- and post-flood forest structure?

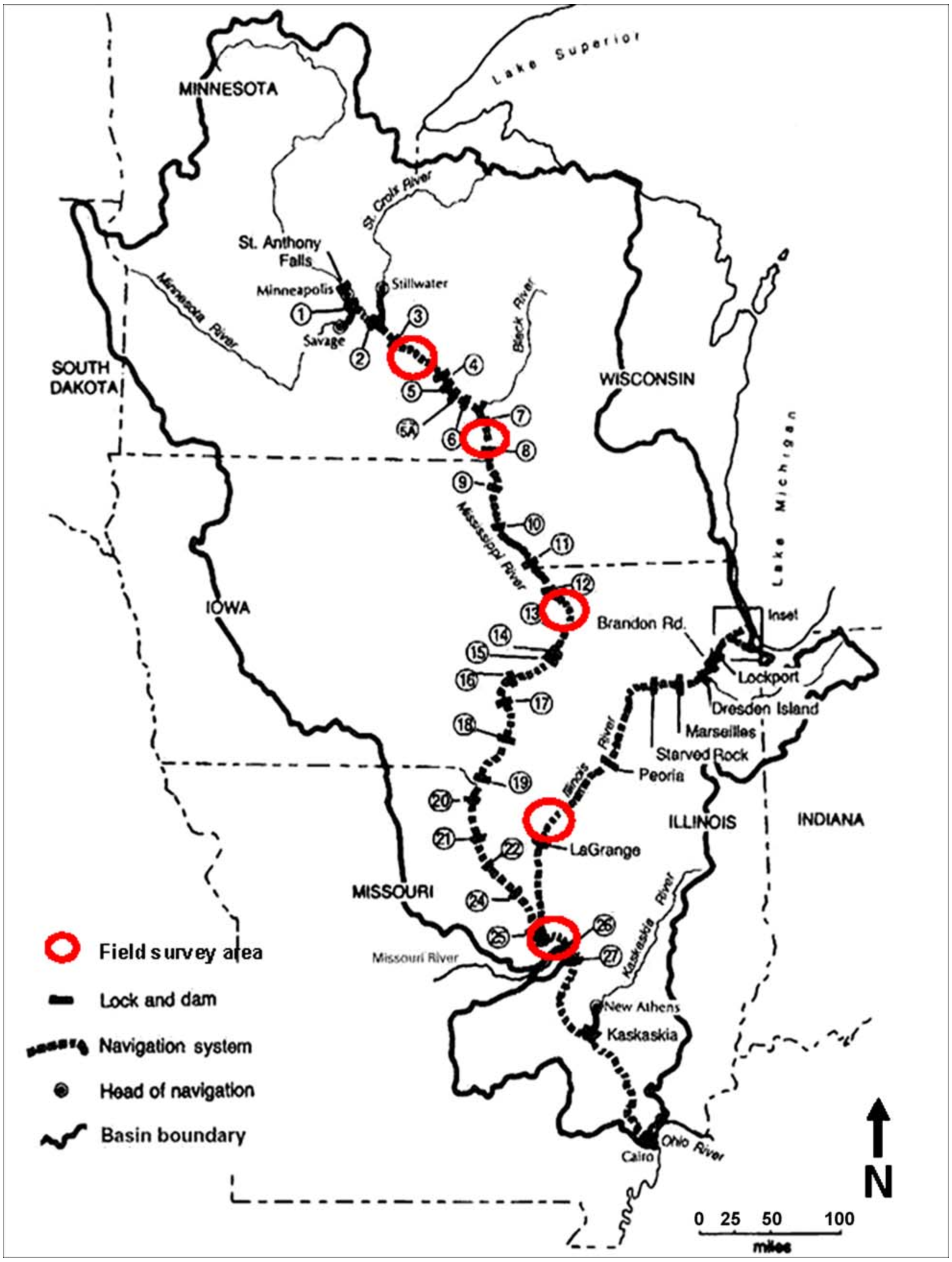

Fig. 1. Field survey areas in Navigation Pools 4, 8, 13, and 26 on Upper Mississippi River and the LaGrange Pool on Illinois River.

2.4. Results

Analyses of data from the adult tree survey suggested that the pre-1993 flood forest in the forested area of Pool 26 was dominated by *Acer* and *Quercus* with 27 and 14% of the total number of trees, and 36% and 28% of the total basal area, respectively (Fig. 2). *Fraxinus* was ~10% and Carya was ~2%, in terms of both the number of trees and the total basal area. *Ulmus* constituted 15% of the total number of trees and 5% of the total basal area. "Other" species, respectively, represented 36% and 18% of the number of trees and the total basal area (Fig. 2).

Examination of flood effects on individual species groups suggested that *Acer* lost 61% of its trees and 24% of its basal area, *Fraxinus* lost 29% and 21%, *Quercus* lost 49% and 36%, and *Carya* decreased by 31% and 28%, respectively (Fig. 3). *Ulmus* and Other species suffered a greater loss from the 1993 flood with 55% and

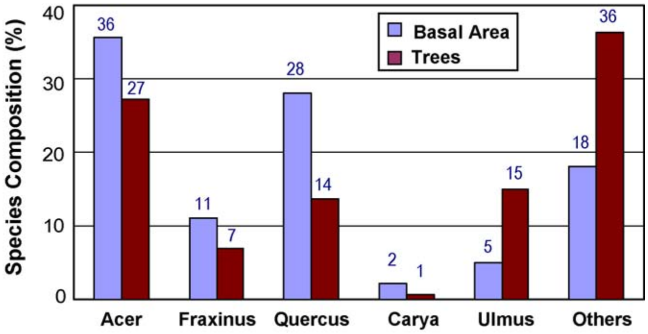

Fig. 2. The species composition (%) of each species in the Upper Mississippi River floodplain forests in terms of the basal area and the number of trees.

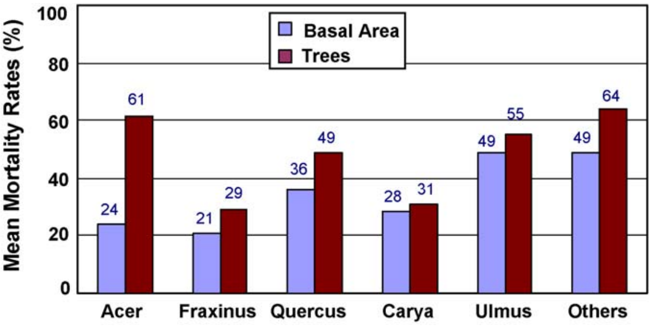

Fig. 3. Mean mortality rates for aggregated each species in both the number of trees and basal area.

Table 1
Post-flood 1995 mortality rates expressed as a function of DBH (cm), $f_m(d)$ for selected floodplain species in Pool 26 on the Upper Mississippi River floodplain (degrees of freedom $v = n - 1$).

Species	$f(d)$	Equations	r^2	v	t
Acer	$f_m(d)$	$1.413^{a}e^{-0.0407D}$	0.94	5	9.41^{b}
Fraxinus	$f_m(d)$	$0.671^{a}e^{-0.0329D}$	0.91	5	7.20^{b}
Quercus	$f_m(d)$	$1.009^{a}e^{-0.0173D}$	0.95	6	10.65^{b}
Carya	$f_m(d)$	No pattern	NA	NA	NA
Ulmus	$f_m(d)$	$0.616^{a}e^{-0.0161D}$	0.87	3	4.43^{a}
Others	$f_m(d)$	$0.806^{a}e^{-0.0099D}$	0.98	5	19.61^{b}
All combined	$f_m(d)$	$0.864^{a}e^{-0.0223D}$	0.98	7	16.58^{b}

[a] Statistically significant at $t_{0.05}$ level.
[b] Statistically significant at $t_{0.01}$ level.

64% of the number of trees, respectively. As for the loss of basal area caused by the 1993 flood, both *Ulmus* and Others lost as high as 49% (Fig. 3). Based on the survey data, the damage caused by the 1993 flood appeared to be more severe for *Acer*, *Ulmus* and Others than for *Quercus*, *Carya* and *Fraxinus*. The post-1993 flood tree survey analysis of forest community structure also suggested that the impacts of the flood resulted on average a mortality of 57% of the total number of trees and a decrease of 33% of the total basal area, which showed that fewer small trees survived the flood compared to the survival of larger trees.

Changes in DBH were analyzed as an aggregate measure of growth for the floodplain forest and its constituent species groups. The DBH values were classified into 10-cm intervals across all species to define an approximate "age-size" structure for the UMR floodplain forest. Based on this classification, analysis of the mortality data suggested that mortality rates decreased with increasing DBH classes for all species groups except Carya (Fig. 4). The relationships between mortality rates and DBH for each species were determined to be statistically significant at $t_{0.05}$ level and $t_{0.01}$ level (Table 1). The mortality function, $f_m(d)$ for all the species, except *Carya*, was expressed as a negative exponential function (Table 1; Fig. 4). This analysis suggests that the larger DBH classes were increasingly tolerant to flooding (Fig. 4).

Survival rates were calculated as the percent of DBH growth from one DBH class into another. The resulting survival rates for each species can be expressed as species-specific functions for pre-flood 1993, $f_s(d)$ and post-flood 1995–2006, $f_d(d)$ conditions (Table 2). All correlations were evaluated using *t*-tests. Statistic significance was defined as the $t_{0.05}$ level and $t_{0.01}$ level (Table 2). The survival rate for pre-flood *Acer* and *Quercus* can be described using a negative exponential function. A quadratic function best describes post-flood conditions (Table 2; Fig. 5). *Fraxinus* and *Carya* have quadratic functions for both pre- and post-flood circumstances. Survival rates for *Ulmus* and Other species are described by positive exponential functions for both pre- and post-flood conditions. Analyses of the combined data for all the species produced quadratic functions for pre- and post-flood succession patterns (Table 2; Fig. 5).

In addition to survival rates, the mean annual DBH growth was also determined for each species. From 1995 to 2006, the annual DBH growth after the 1993 flood was greatest for *Fraxinus* (648 cm/ha), followed by *Acer* (491 cm/ha) and Others (551 cm/ha). *Carya*

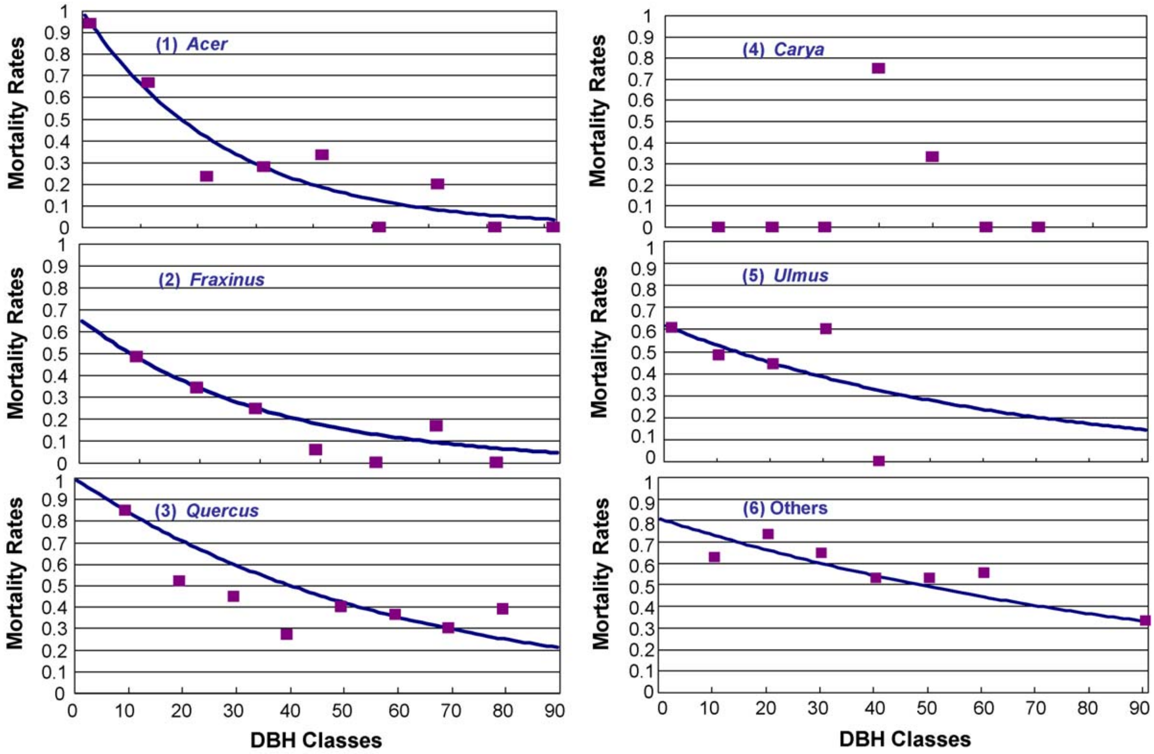

Fig. 4. Mortality rates caused by 1993 flood as a function of DBH class in the sampled floodplain areas of UMR Navigation Pool 26.

Table 2
Pre-$f_s(d)$ and post-flood survival rates $f_d(d)$ defined as growth from one BDH class (10-cm interval) into another and expressed as a function of DBH (cm) for floodplain species in Pool 26 on the Upper Mississippi River (degrees of freedom $\nu = n - 1$).

Species	$f(d)$	Equations	r^2	ν	T
Acer	$f_s(d)$	$0.759^a e^{-0.0067D}$	0.99	3	39.96^b
	$f_d(d)$	$-0.000237D^2+0.0281D+0.086$	0.98	7	24.83^b
Fraxinus	$f_s(d)$	$-0.000195D^2+0.0117D+0.562$	0.92	5	7.77^b
	$f_d(d)$	$-0.000195D^2+0.0117D+0.716$	0.91	6	8.03^b
Quercus	$f_s(d)$	$0.924^a e^{-0.0222D}$	0.94	7	11.35^b
	$f_d(d)$	$-0.000143D^2+0.0123D+0.352$	0.90	3	5.39^b
Carya	$f_s(d)$	$-0.000172D^2+0.0129D+0.001$	0.89	3	4.96^a
	$f_d(d)$	$-0.000318D^2+0.0254D+0.041$	0.95	4	8.71^b
Ulmus	$f_s(d)$	$0.871^a e^{-0.0527D}$	0.97	2	8.32^a
	$f_d(d)$	$0.822^a e^{-0.0527D}$	0.93	3	6.52^b
Others	$f_s(d)$	$0.075^a e^{0.0225D}$	0.88	6	6.53^b
	$f_d(d)$	$0.221^a e^{0.0167D}$	0.97	6	14.48^b
All Combined	$f_s(d)$	$-0.000309D^2+0.0277D+0.076$	0.96	4	10.05^b
	$f_d(d)$	$-0.000309D^2+0.0277D+0.196$	0.91	6	8.02^b

[a] Statistically significant at $t_{0.05}$ level.
[b] Statistically significant at $t_{0.01}$ level.

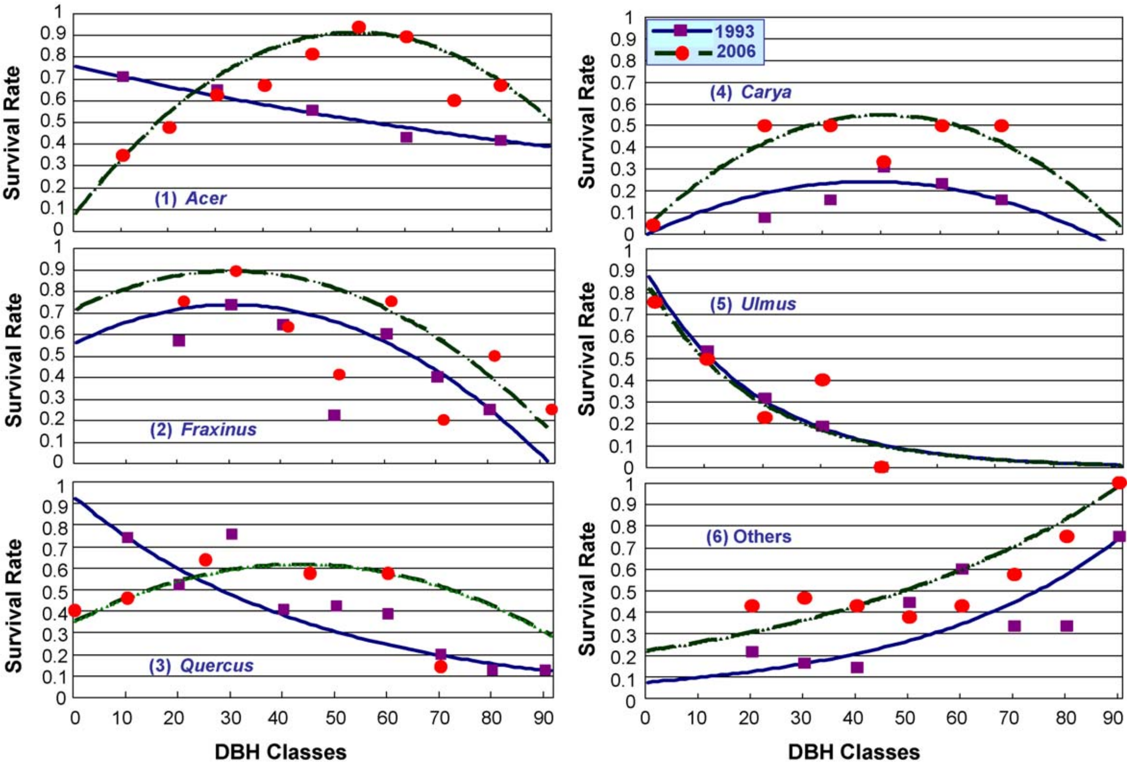

Fig. 5. The correlations between survival rates and DBH for pre-flood 1993 and post-flood 2006 patterns.

grew 261 cm/ha. *Quercus* and *Ulmus* had very low DBH growth of 55 and 32 cm/ha, respectively (Fig. 6).

Results of the seedling survey suggested that there was a great variability in average seedling density for each species and across the sampled plots (Table 3). The data indicate that *Acer* and *Fraxinus* seedlings accounted for ~82% of the total seedlings with 60,444 and 54,417 seedlings/ha. The combination of *Quercus* (7000 seedlings/ha) and *Carya* (2400 seedlings/ha) accounted for 6.5%, while *Ulmus* (5810 seedlings/ha) and "Others" (10,500 seedlings/ha) accounted for 11.5% (Table 3). The maximum number of seedlings of *Quercus* and *Carya* might have been as many as 13,333 and 3333 seedlings/ha, based on the variability encountered in the samples (Table 3).

Based on records of each individual seedling, the mean annual growth in height varied from as low as 6 cm/year for *Carya* to as high as 36 cm/year for *Ulmus* (Table 3). The maximum annual growth in height varied from 109 cm/year for *Quercus* to 400 cm/year for *Fraxinus*. However, the standard deviation (S.D.) in growth was high for all the species, especially for *Quercus* (mean = 28 cm/year and SD = 26) (Table 3). Further analysis suggested that growth in height was generally an increasing exponential function $f_{sg}(h)$ of individual seedling heights (Table 4; Fig. 7). The *t*-test for all the correlations r^2 was statistically significant at $t_{0.05}$ level and $t_{0.01}$ level (Table 4).

In contrast, seedling survival rates $f_{ss}(h)$ showed a decreasing exponential relationship with seedling heights (Table 4; Fig. 8). The *t*-test for all the correlations r^2 was also statistically significant at the $t_{0.05}$ level and $t_{0.01}$ level (Table 4). These results indicate that mortality rates increase with the growth in height and, as a result, only a small fraction of seedlings reach the forest canopy (Fig. 8). These data indicate that *Quercus* seedlings seldom grow and survive beyond 120 cm (Fig. 8). Therefore, it may become rare to find oak trees growing into canopy after the 1993 flood.

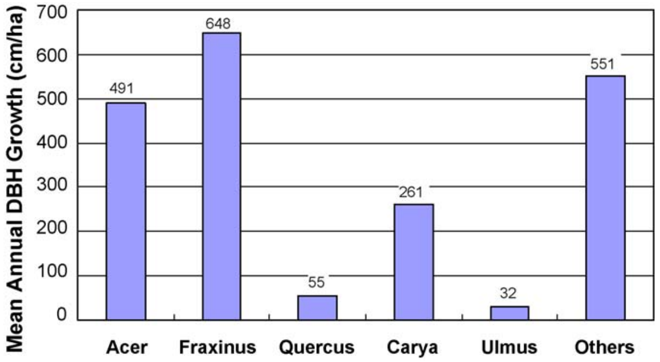

Fig. 6. Mean annual DBH growth (cm/ha) in the Upper Mississippi River floodplain forests.

Table 4
Correlations between seedling annual growth rates in height (cm/year) $f_{sg}(h)$ and seedling heights (H), and correlations between seedling annual survival rates $f_{ss}(h)$ and seedling heights (H) based on seedling data collected in Navigation Pools 4, 8, 13, and 26 on the Upper Mississippi River and the LaGrange Pool on the Illinois River (degrees of freedom $v = n - 1$).

Species	$f(h)$	Equations	r^2	v	t
Acer	$f_{sg}(h)$	$2.339^{a}e^{0.0319H}$	0.98	2	13.5[b]
	$F_{ss}(h)$	$e^{-0.0176H}$	0.95	7	11.6[b]
Fraxinus	$f_{sg}(h)$	$2.195^{a}e^{0.0255H}$	0.99	3	20.7[b]
	$f_{ss}(h)$	$e^{-0.0099H}$	0.99	8	33.8[b]
Quercus	$f_{sg}(h)$	$1.869^{a}e^{0.338H}$	0.98	4	15.3[b]
	$f_{ss}(h)$	$e^{-0.0397H}$	0.96	3	9.8[b]
Carya	$f_{sg}(h)$	$1.440^{a}e^{0.0244H}$	0.98	3	13.2[b]
	$f_{ss}(h)$	$e^{-0.0255H}$	0.96	4	10.9[b]
Ulmus	$f_{sg}(h)$	$17.624^{a}e^{0.0202H}$	0.94	2	5.7[a]
	$f_{ss}(h)$	$e^{-0.0135H}$	0.92	4	7.2[b]
Others	$f_{sg}(h)$	$2.605^{a}e^{0.0307H}$	0.99	4	49.0[b]
	$f_{ss}(h)$	$e^{-0.0264H}$	0.92	3	6.1[b]

[a] Statistically significant at $t_{0.05}$ level.
[b] Statistically significant at $t_{0.01}$ level.

A successional pattern was constructed by comparing the DBH structure between 1995 (right after the 1993 flood) and 2006 (13 years after the flood). The pattern showed that, except for *Quercus*, all the species had continuously decreased abundance in successive DBH classes after the 1993 flood (Fig. 9). Although 7000 Quercus seedlings were produced following the flood, a value of zero in DBH class 10 suggests a disruption in oak development after the flood in 1993 (Fig. 9).

The analyses of the field survey data suggested that the recovery patterns through 2006 varied by species. The comparison

Table 3
Mean and standard deviation (SD) of seedling density (MD), maximum density, mean and SD of annual growth in height (MAHG), and maximum annual growth in height based on seedling data collected in Navigation Pools 4, 8, 13, and 26 on the Upper Mississippi River and the LaGrange Pool on the Illinois River.

Species	Mean density (seedlings/ha)	MD (S.D.)	Max density (seedlings/ha)	Mean annual height growth (cm)	MAHG (S.D.)	Max annual height growth (cm)
Acer	60444	(53549)	156667	21	(19)	107
Fraxinus	54417	(44488)	208000	28	(19)	400
Quercus	7000	(6333)	13333	28	(26)	109
Carya	2400	(998)	3333	6	(4)	27
Ulmus	5810	(5306)	14667	36	(29)	200
Others	10500	(10832)	42667	19	(12)	104

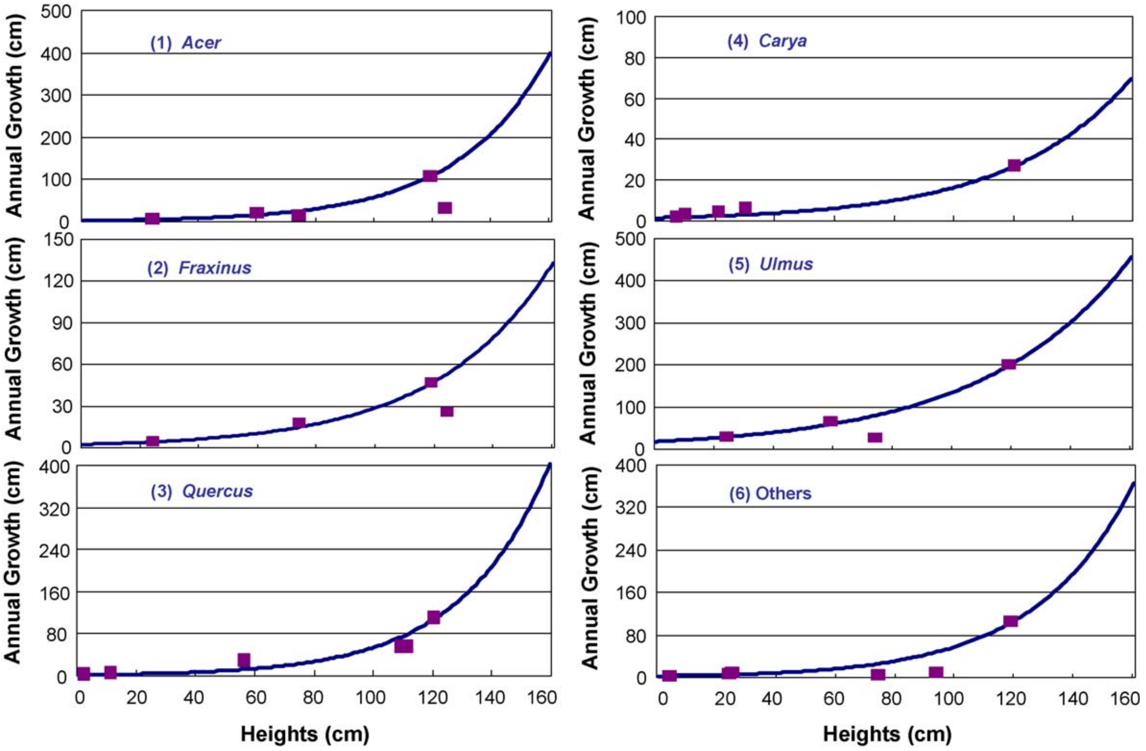

Fig. 7. The correlations between annual growth in height and seedling heights in the UMR floodplain forests.

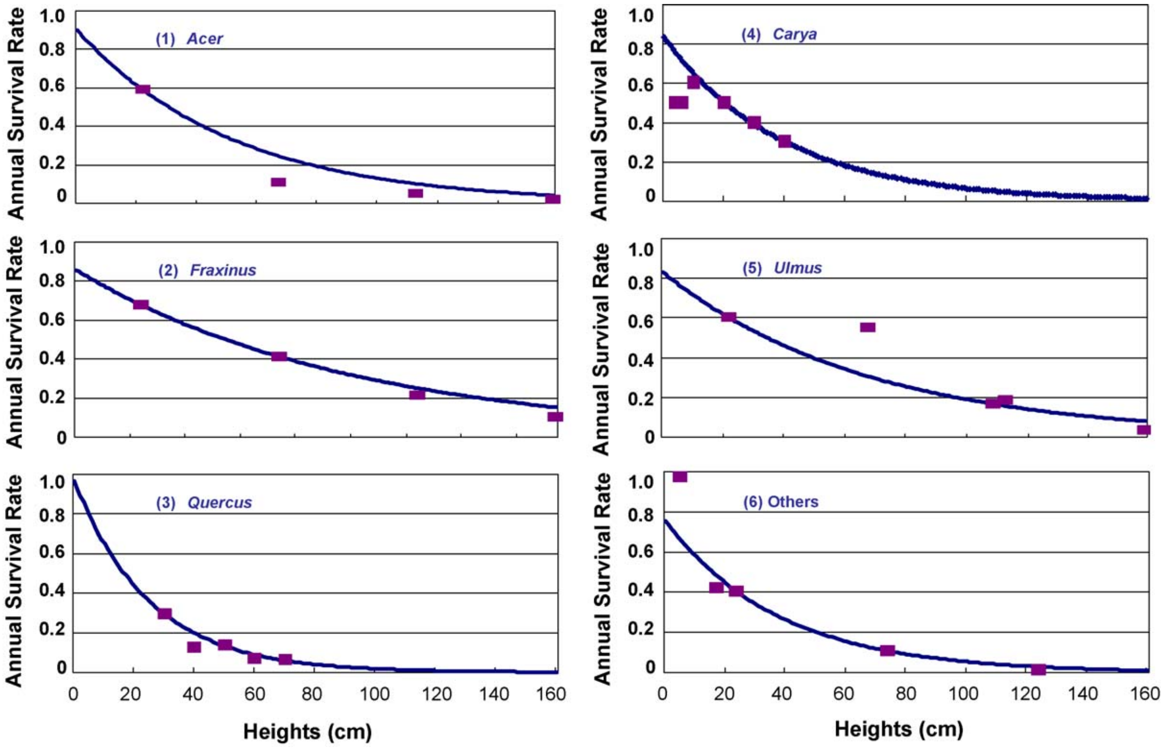

Fig. 8. Negative correlations between annual survival rates and seedling heights in the UMR floodplain forests.

of the number of trees and basal area for pre-flood 1993, post-flood 1995, and post-flood 2006 of each species shown in Fig. 10 suggested that the number of trees in 2006 was 1338 for *Acer*, 1170 for *Fraxinus*, 569 for *Carya*, and 1446 for ‘‘Others’’. These data suggest that the total number of trees in 2006 was greater than that in post-flood 1995 and also greater than that in pre-flood 1993 (Fig. 10a). *Ulmus* had 458 trees in 2006, which was close to the pre-flood 1993 number (490) and an increase from the post-flood 1995 value of 219 (Fig. 10a). However, *Quercus* had fewer trees (193) in 2006 compared to 1995 (230) and 1993 (449), which suggests a continuing decline after the 1993 flood (Fig. 10a). Similar declines of Quercus were also measured for basal area, which was 18 m^2/ha

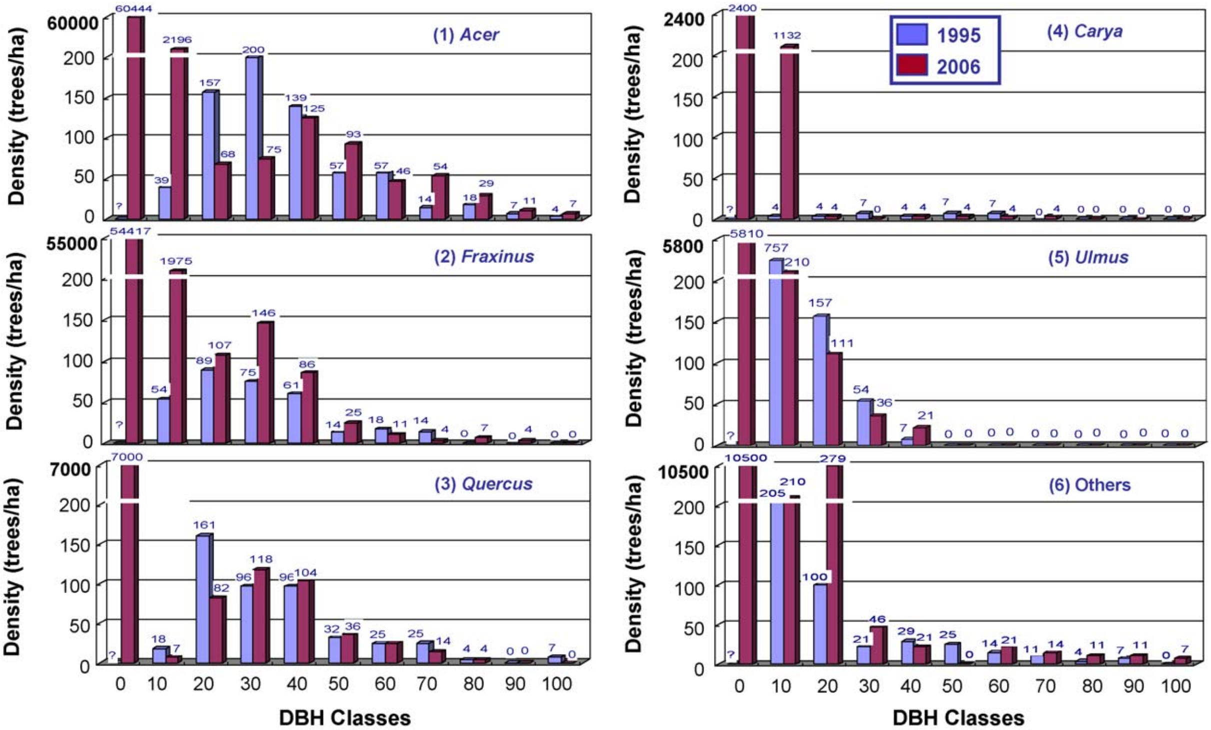

Fig. 9. The descending transition of the number of trees from seedlings (as DBH Class 0) to different DBH classes.

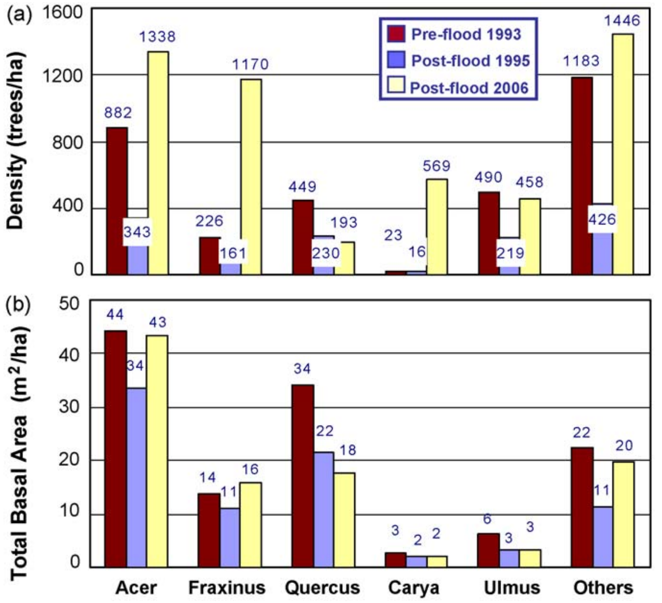

Fig. 10. Comparison of the number of trees and basal area for pre-flood 1993, post-flood 1995 and post-flood 2006.

in 2006, 22 m^2/ha in 1995 and 34 m^2/ha in 1993 (Fig. 10b). Unlike *Quercus*, all the Other species had higher basal area in 2006 than in 1995. Species such as *Fraxinus* even had higher basal area in 2006 than in pre-flood 1993 (Fig. 10b).

Differences between pre- and post-flood species composition were used to characterize rates of recovery from the 1993 flood. By 2006, *Acer* had almost recovered to the pre-flood condition. It did not change in its relative dominance in both the number of trees or basal area, with 36% in pre-flood 1993 versus 43% in post-flood 2006 for basal area composition (Fig. 11a) and 27% in pre-flood 1993 versus 26% in post-flood 2006 for tree composition (Fig. 11b). *Fraxinus* increased in terms of both basal area composition (from 11% to 16%, Fig. 11a) and tree composition (from 7% to 23%, Fig. 11b) with a higher growth in post-flood 2006 compared to pre-flood 1993. *Carya* increased dramatically in the number of trees from 1% before the 1993 flood to 11% in 2006, but the basal area maintained the same 2% after the flood. However, as of 2006, neither *Quercus* nor *Ulmus* had recovered in terms of basal area or tree compositions (Fig. 11). Other species also recovered well from the 1993 flood in both basal area (e.g., 18% in 1993 compared to 19% in 2006) and the number of trees (i.e., 36% in 1993 compared to 28% in 2006, Fig. 11).

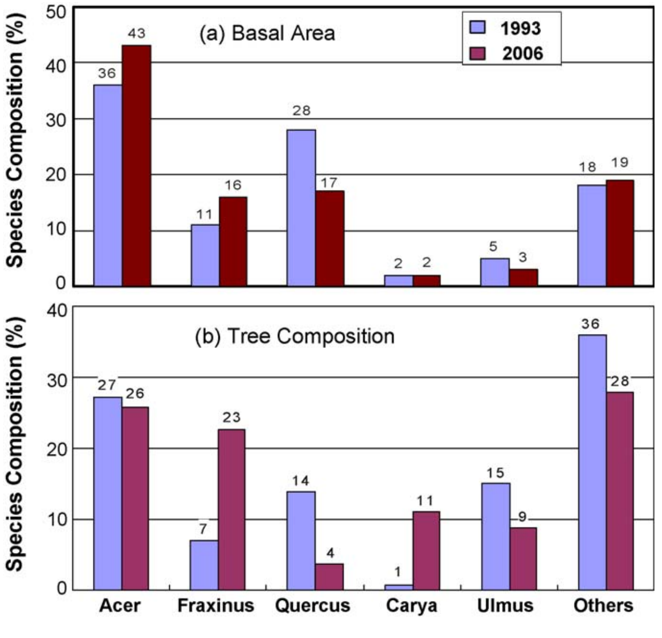

Fig. 11. The over all species composition (%) in terms of DBH and the number of trees with the comparison of pre-flood 1993 and post-flood 2006.

3. Discussion and conclusions

The results and analysis of the post-1993 flood tree and seedling surveys provide insights concerning the general response of the UMR floodplain forest to this dramatic event. The 1993 flood substantially reduced the number of trees for all the surveyed species compared to pre-flood conditions. The total loss may have been as high as 57% of the total number of trees. In general, mortality decreased with the increasing size (i.e., DBH) for all the species. Larger trees appeared more tolerant to flooding. These mortality rates can be described using negative exponential functions of DBH.

Analysis of the survey data also contribute to understanding of more species-specific responses to the 1993 flood. The data indicated that *Acer* and *Quercus* were dominant species in the 1993 pre-flood forest and constituted 27% and 14% of the total number of trees, and 36% and 28% of the total basal area, respectively (Fig. 2). In contrast to *Quercus*, *Acer* continued to dominate the 2006 post-flood forest (Fig. 11) and recovered in both the number of trees and basal area. *Quercus* continued to suffer following the 1993 flood in terms of losses in the number of trees and basal area as evidenced by the post-flood 2006 surveys. *Carya* increased in terms of the number of trees in post-flood 2006 compared to the pre-flood 1993 relative abundance.

Acer lost proportionately more on smaller trees, but fewer big trees following the 1993 flood (Fig. 3). *Acer* also responded to the flood with abundances of seedlings and rapid growth in height to enter the canopy and fill in the ‘‘gap’’ created by the flood (Figs. 7, 8 and 10). *Acer* appears highly adapted to flood disturbance in the UMR floodplain (Deiller et al., 2003; Peck and Smart, 1986).

Fraxinus constituted about 10% (Fig. 2) of the UMR floodplain forests. *Fraxinus* exhibited the lowest mortality rate (<30%) among all the measured species following the 1993 flood (Fig. 3). This species also produced an abundance of rapidly growing seedlings (Table 3). As a result, *Fraxinus* replaced *Quercus* and become the second dominant species in the UMR floodplain (Fig. 11). *Fraxinus* could be classified as a flood-stimulated species in the floodplain forests (Hook and Brown, 1973).

The mixed species group defined as ‘‘Others’’ included species with a successional pattern similar to *Acer*, although several of these species had much higher mortality rates (>60%) following the 1993 flood (Fig. 3). In 2006, constituents of this group recovered as much as 20 m^2/ha comparing to 22 m^2/ha in 1993 (Fig. 10) with 1446 trees/ha, which was much higher than that of 1183 trees/ha in pre-flood 1993. These species were the first to reach the canopy with more than 400 trees/ha in the 10 and 20 cm DBH classes by 2006 (Fig. 9). Members of this group appear characterized by high mortality rates associated with floods (Fig. 2), followed by a comparatively low seedling regeneration rate (Table 3). This mixed group sustains its contribution to the overall floodplain community by adding a proportion of fast-growing young trees to the canopy (Fig. 9).

The *Ulmus* group lost more than 50% of the trees and basal area following the 1993 flood (Fig. 3). However, by 2006, 458 elm trees per hectare had been established, compared to the 490 trees/ha for pre-flood 1993 and 219 in post-flood 1995. But the post-flood growth was comparatively slow (Fig. 10), which has delayed recovery of this group to pre-flood conditions.

Carya members proved to be tolerant to the 1993 flood and lost only about 30% in both basal area and density. However, *Carya* showed a slightly higher growth rate than *Quercus* and *Ulmus* in the post-flood years (Fig. 6). The seedling regeneration has been high, with more than 1000 trees/ha. The relative density of *Carya* was as low as 1% in pre-flood 1993, but increased to 11% in 2006. The results of the field surveys suggest that the 1993 flood was not the cause for the decline of *Carya* in the UMR floodplain. The observed widespread mortality of hickory could be attributed to outbreaks of hickory bark beetle, *Scolytus quadrispinosus* suggested by Flickinger (2006).

The 1993 flood resulted in <50% in mortality for *Qurecus* (Fig. 3). The failure of Quercus to recover from the flood damage appears to result from both a lack of seedlings and poor seedling growth after the flood (Table 3; Fig. 8). Young *Quercus* trees in the post-flood years grow much slower than that in pre-flood 1993. The average DBH growth in post-flood years is only 55 cm/ha compared to 261 for *Carya*, 491 for *Acer* and 648 for *Fraxinus* (Fig. 6). As a result, *Quercus* contributes only 4% of the relative density in post-flood 2006 (Fig. 11). Oaks might fail to regenerate in sufficient numbers to persist in the future forest (Yin and Nelson, 1995; Nelson, 1997; Bodaly et al., 2004; Leake and Johnson, 2006).

Analysis of the responses to the 1993 flood permits a simple classification of these species in terms of their susceptibility to and ability to recover from severe floods. As suggested by Küßner (2003), those species-specific mortality and successional patterns can be explained by different sensitivities to floods and differing abilities to recover. Defining the sensitivity to flooding (SN) as high, moderate and low, and the recovery rates (RR) as fast, moderate and slow, the successional characteristics for the six "super-species" can be classified for *Fraxinus* as low-SN, fast-RR, for *Acer* as moderate-SN, fast-RR, for *Carya* as low-SN, moderate-RR for Others as high-SN, moderate-RR, for *Ulmus* as high-SN, slow-RR, and for *Quercus* as moderate-SN, slow-RR. Based on this classification, *Fraxinus* appears to be a flood-stimulated species. *Acer*, *Carya* and Others could be termed flood-tolerant species, while *Ulmus* and *Quercus* might be defined as flood intolerant species.

This classification and its underlying quantitative characterization of UMR floodplain forest dynamics might assist in effective management and restoration. The comparatively low relative density of mature oak trees and sparse oak seedlings likely results from a combination of low growth rate, sensitivity to flooding, and low rates of acorn production and germination (Dey et al., 2000; Nelson, 1997; Yin and Nelson, 1995). These characteristics suggest that planting of oak seedlings and better flood management may be necessary to increase the abundance of oaks in the floodplain forests of the Upper Mississippi River.

In conclusion, different species might respond to the 1993 flood with different tolerance and successional strategies. The integrated approach and quantitative method proposed in this research could provide a unique way to understand forest succession patterns and predict long-term impacts of flood on forest dynamics in the UMR floodplain ecosystem. A simulation model could be the way to synthesize and integrate the information and functions from this research for a better understanding of impacts of different flood intensity and frequency on forest dynamics (Ebenhöh et al., 2009; Campagne et al., 2009) and for the evaluation of different alternatives in the UMR ecosystem restoration (Yin et al., in this issue).

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