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Floodplain Forest Response to Large-Scale Flood Disturbance

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ABSTRACT

Flood disturbance is the principal factor influencing species composition and distribution in floodplain forests. It has been widely assumed that these floodplain species have developed the ability to survive different magnitudes of flooding. However, research on the effects of large-scale flooding is lacking. Floodplain forests on Pool 26 of the Upper Mississippi River System, suffered high mortality following a 1993 flood disturbance. The degree of mortality was dependent upon tree species, forest community and tree size. Mixed forests suffered greater mortality in trees and saplings than did the maple-ash and oak forests studied. *Celtis occidentalis* and *Quercus palustris* were largely flood intolerant while *Fraxinus pennsylvanica* and *Acer saccharinum* were more tolerant. Larger diameter trees had better flood survivorship than did smaller diameter trees. Tree seedlings and lianos were intolerant of the flood event. Seedling regeneration was forest community and species dependent. Maple-ash forests had a seedling density of 365,700 seedlings/hectare while mixed and oak forests were significantly less (144,012 and 95,545 seedlings/hectare, respectively). *Acer saccharinum*, *F. pennsylvanica* and *Ulmus americana* were the dominant seedlings of the three forests communities. High canopy, overstory and understory covers reduced seedling density. Openings in the canopy and silt deposition initiated a tremendous response in the herbaceous strata. Annual forbs, grasses and grass-like plants responded favorably to the flood event, whereas, biennial and perennial forbs were largely lacking. *Bidens aritosa* was the dominant herbaceous plant occurring in over 75% of the quadrats sampled and having an average cover of 36%.

Key Words: flood disturbance; floodplain forest; seedling regeneration, Upper Mississippi River, LTRMP

INTRODUCTION

Periodic flooding is the most common disturbance event on floodplains and often determines the distribution of forest species and communities (Bedringer, 1978; Metzler and

Damman, 1985; Streng et al., 1989; Hughes, 1990; Oliveira-Filho et al., 1994). The degree of disturbance is dependent upon flooding frequency, duration, intensity, and timing as well as the stage of successional development in the forest community (Hosner and Boyce, 1962; Gill, 1970; Bell and Johnson, 1974; Bedringer, 1978). Most floodplain trees are adapted to survive moderate frequency, moderate intensity and short duration flooding when it occurs between late summer and early spring during plant dormancy (Johnson and Bell, 1976; Bedringer, 1978; Harms et al., 1980; Taylor et al., 1990). However, tree mortality increases with flood frequency, intensity, or duration and when flooding occurs during the growing season (Hosner and Boyce, 1962; Kozlowski, 1984; Yin et al., 1994; Yin, 1998). Infrequent, "large-scale" flooding is generally considered natural and may actually be a driving force of organism, community and landscape successional patterns (Hupp, 1983; Hupp and Osterkamp, 1985; Duncan, 1993; Michener et al., 1998). However, knowledge of forest community and individual tree species response to large-scale flooding is poorly understood due to the infrequency.

In 1993, a long duration, high intensity flood inundated floodplain forests along Reach 26 of the Upper Mississippi River System (UMRS) during much of the growing season (US Army Corps of Engineers, 1994) (Figure 1). This was the largest flood event on record in the vicinity of St. Louis, MO, and is considered to have exceeded the 100-year recurrence interval (Scientific Assessment and Strategy Team, 1994; Bhowmik et al., 1994). Our study 1) describes the impact of the 1993 flood on forest communities, community size classes, and individual species, 2) identifies tree seedling, herbaceous, and woody liano response to canopy gap openings caused by tree and sapling mortality, and 3) discusses changes in forest community composition as a result of the 1993 flood.

METHODS

Study Area

The UMRS includes the stretch of the Mississippi River from the confluence with the Ohio River near Cairo, Illinois, northward to the headwaters at Lake Itasca, Minnesota (Upper Mississippi River Basin Commission, 1981). It also includes the Illinois River, which merges with the Mississippi River approximately 218 miles upriver from the Mississippi-Ohio Rivers confluence. The Upper Mississippi and Illinois Rivers still retains approximately 50% (1,038,000 ha) of the original floodplain as unleveed (Delaney and Craig, 1997).

The study area included floodplain forests along the upper Mississippi River from Lock and Dam 25 to Lock and Dam 26 (Reach 26) and the lower Illinois River from the confluence to Illinois River mile 12 (Figure 2). There are four major floodplain forest communities on this reach of the UMRS: cottonwood-willow, maple-ash, mixed, and oak (Barclay, 1924; Hosner and Minckler, 1960, 1963; Eyre, 1980; Galatowitsch and McAdams, 1994; Yin et al., 1997). Cottonwood-willow forest communities occupy recent riverine sediment deposits and are subject to annual flooding. Maple-ash forest communities occupy areas subject to prolonged periods of anaerobic conditions and to annual flooding. Oak forest communities occupy the higher elevations (second bottoms) on the floodplain and are subject to flooding rarely or for short periods of time. These forest communities may be more dependent upon small gap creation from windfall or fire for community replacement than flood disturbance. Transition from a maple-ash to an oak forest community may occur with only a meter change in elevation. Mixed forests are an advanced successional stage that develops through lack of severe flood disturbance in maple-ash forest communities and tree-fall disturbance in oak forest communities.

Reach 26 of the Mississippi and Illinois Rivers is mostly unrestricted bordered by bluffs and the Missouri River floodplain. Low man-made and natural levees do occur along some stretches of the Mississippi and Illinois Rivers and along the tributaries. Natural levees and barrier bars along the Illinois River rise as much as 1.2 to 3.0 meters above the floodplain (Butzer, 1977). This approximates the crest elevations of the mean annual flood levels of the 1800's prior to impoundment. Sloughs and tributaries are scattered throughout the floodplain and numerous islands are present. The combination of barrier bars, levees, islands, and isolated water bodies has created a myriad of vegetative communities distributed according to slight changes in elevation and soil hydrology (Hupp and Osterkamp, 1985; Galatowitsch and McAdams, 1994). Forests occupy most of the lower elevation floodplains and islands with herbaceous wetland communities occupying a thin band near the waters edge. Although most of the higher elevation floodplain forest and wetlands have been converted to farmland, some of the higher elevation floodplain forests have been preserved in hunting clubs. The flood of 1993 inundated most of the floodplain resulting in almost continuous flooding from bluff to bluff along the Illinois, Mississippi and Missouri Rivers.

Sampling Methods

Experimental Design and Forest Community Delineation

Fourty-five sites were randomly selected using a geographic information system (GIS) (ArcView, ESRI, Inc., Redlands, CA), land coverage. An additional 15 sites were randomly selected from forest communities known to be oak. A global positioning system (GPS) was utilized to locate sites in the field during the summer of 1995. At each site a 314 m^2 (10 meter radius) circular plot was established. We recorded the taxonomic name (Mohlenbrock, 1986), measured the diameter at breast height (dbh) and identified the vigor of each tree (dbh greater than 10 cm) and sapling (dbh greater than 2.5 cm and less than 10 cm). We defined vigor as dead prior to 1993, dead after 1993, and currently living.

Species importance values (IV) were used to determine the forest community type at each site. IV's were calculated by summing species relative density and relative dominance (Whittaker, 1967; Bell, 1974). Sites were classified as either an oak or maple-ash forest community if the total IV for all *Quercus spp*. (oak) trees combined or *Acer saccharinum* (silver maple), *Acer negundo* (box elder) and *Fraxinus pennsylvanica* (green ash) trees combined was greater than 100. If the site could not be classified as an oak or maple-ash forest community, it was classified as a mixed forest (dominated by *Celtis occidentalis* and *Ulmus americana*). Sites with a combined IV greater than 100 for *Populus deltoides* (cottonwood) and *Salix nigra* (black willow) and were removed from the study because there were not enough of the cottonwood/willow forest types represented (dropped two sites). Mortality rates and changes in species importance values were used to describe forest community and species response to the 1993 flood event. Regression analysis (α=.05) was used to identify the significance of the relationship between tree dbh and percent mortality.

Canopy Gaps

Stratum cover was visually estimated at each subplot to determine canopy and subcanopy gaps. The strata included canopy (trees), subcanopy (saplings), overstory (combination of trees and saplings), understory (combination of seedling and herbaceous cover), and total (combination of all strata) cover estimates. Differences in strata cover between forest communities were determined using Tukey's W multiple comparison procedure (parametric, α=.05). We calculated the relationship between understory, overstory and seedling density by utilizing a General Linear Model (α=.05) by forest community.

Seedling and Herbaceous Measures

Within each plot, ten .25 m^2 (.5 m x .5 m) subplots were randomly established. Within each subplot, we identified each seedling (Mohlenbrock, 1986) and estimated its age. We defined a seedling as woody, non-vine, vegetation less than 2.5 cm in diameter. Herbaceous species were also identified (Mohlenbrock, 1986; Hitchcock, 1971) and ocular cover estimates were made. IV's were used to describe seedling composition among forest communities by combining relative frequency and relative density. We also used IV's to describe herbaceous composition (sum of relative cover and relative frequency). A General Linear Model (α=.05) was utilized to describe the relationship between seedling density and forest community.

RESULTS

Response of the Tree and Sapling Strata

Tree and sapling mortality, resulting from the 1993 flood, varied according to tree species, tree size and forest community. Prior to 1993, trees with the highest IV's in Pool 26 were *A. saccharinum*, *Q. palustris*, *F. pennsylvanica*, *U. americana*, and *Celtis occidentalis* (IV's of 58, 35, 25, 17, and 12 respectively) (Table 1). Following the flood of 1993 the IV's of *Celtis occidentalis*, *Q. palustris*, *P. deltoide*s, and *U. americana* trees decreased due to high mortality (91%, 57%, 57% and 49%, respectively). *Q. lyrata* and *F. pennsylvanica* trees had better survivorship (mortalities of 19% and 23%, respectively). *Acer saccharinum* trees also experienced high mortalities following the flood. However, relative to other species, the post-flood importance value of *A. saccharinum* increased due to high mortality in other tree species. Prior to flooding, the sapling cohort was dominated by *Celtis occidentalis*, *U. americana*, *A. saccharinum*, and *F. acuminata* (IV's of 42, 37, 37, and 36, respectively) (Table 1). *Acer negundo*, *A. saccharinum* and *Celtis occidentalis* saplings suffered high mortalities (100%, 96%, and 75%, respectively). Although, *F. acuminata*, *D. virginiana*, *Cornus spp*., *F. pennsylvanica*, and *U. americana* also suffered high mortalities (57%, 36%, 0%, 48%, and 66%, respectively), these species emerged as dominants in the post-flood sapling cohorts of Pool 26.

Across all forest communities, trees had lower mortality rates than did saplings (Table 2 and 3). Regression analysis utilizing tree dbh explained almost 66% of the variation (p = 0.0001, F = 3663.15) in percent mortality (Figure 3). Some outliers do appear to have high mortalities at large dbh's. These points represent large *P. deltoides* and indicate a species relationship.

The degree of tree and sapling mortality varied among forest communities. Mixed forests suffered greater tree mortality (60%) than maple-ash (41%) and oak (42%) forests due to high mortalities in all of the dominant tree species (Table 2). Oak forests had better sapling survivorship (mortality of 56%) than did maple-ash (80% mortality) and mixed (80% mortality) forests (Table 3). This may be related to the slightly higher elevation where these oak communities occurred, which decreased the length of flood disturbance.

Individual tree and sapling species mortality varied among forest communities. *Celtis occidentalis* and *Q. palustris* trees experienced very high mortalities in maple-ash forests (100 and 80%, respecitively) lower degrees of mortality in mixed (94 and 73%, respectively) and oak forests (74 and 54%, respectively) (Table 2). *Acer saccharinum*, *U. americana* and *F. pennsylvanica* trees experienced the greatest mortality in mixed forests (64, 60 and 36 % mortality, respectively) (Table 2). Other than *A. negundo*, all tree species experienced lower mortality in oak forests. Lower mortality rates on oak forests may be related to differences in elevation.

Canopy Gap Responses

The creation and size of gaps was highly variable (Table 4). Some forest communities showed little sign of flood disturbance while other similar communities were denuded of forest. Canopy (tree) cover was significantly different across forest communities (Table 4 and 5). Maple-ash forest communities had the largest mean canopy cover followed by oak and mixed forest. Oak forest communities had significantly greater subcanopy (sapling) coverage than the maple-ash and mixed forests (Table 5). This is related to the lower mortality rates in saplings exhibited by the oak forests. Overstory cover estimates were significantly different across all forest types (Table 5). Maple-ash forests had higher overstory cover than the oak or mixed forests. Mixed forest understory cover was significantly greater than that of oak and maple-ash forests (Table 5). This is the result of higher mortalities in both the trees and saplings in mixed forests. There was no significant difference in total cover between the three forest communities.

There was a relationship between the creation of gaps and response of the understory. The overstory explained 40% of the variation ($r^2 = 0.4$, $F = 106.55$, $p = 0.0001$) of understory cover for oak forests. Overstory explained significantly less of the variation in understory for maple-ash ($r^2 = 0.07$, $F = 19.80$, $p = 0.0001$) and mixed forests ($r^2 = 0.03$, $F = 4.27$, $p = 0.04$). This result may be related to the high cover of shade tolerant herbaceous vegetation and seedling germination. In many instances, a forest community may have had little disturbance and mortality in the tree cohort, but received several centimeters to several meters of newly deposited sediment. This initiated tremendous herbaceous and tree seedling germination.

Forest Regeneration and Woody Liano and Herbaceous Response

Following the flood of 1993, the floodplain seedling bank was essentially eliminated. Although care was taken to account for re-sprouts, none were identified and the mean age for all seedlings was between 1 and 2 years (Table 6). *Acer saccharinum* dominated the seedling bank of Pool 26 with a density of 146,502 seedlings/ha and occurred in 48% of the quadrats sampled. *Fraxinus pennsylvanica* and *U. americana* were codominant members of the post-flood seedling cohort (IVs of 30 and 21, respectively).

There was a significant relationship ($p = 0.0003$, $F = 9.65$) between seedling density and forest community. Maple-ash forests had a higher seedling density (365,700 seedlings/ha) than mixed and oak forests (144,012 seedlings/ha and 95,545 seedlings/ha, respectively).

Canopy, overstory, and understory cover were also significant predictors of seedling density ($p = 0.0001$, $F = 48.08$; $p = 0.0019$, $F = 9.71$; $p = 0.0001$, $F = 32.97$; respectively). Seedling density decreased as percent cover increased. However, with a low r^2 (0.14), other variables are more likely to influence seedling density.

There were 55 herbaceous and woody liano plant species identified in this study. Herbaceous and woody liano species composition following the 1993 flood was similar among forest communities (Table 9). However, there was variation in cover estimates by species (Table 7). This is the result of the heterogeneous flood disturbance and creation of canopy/subcanopy gaps. *Bidens aritosa* was the dominant species occurring in over 73% of the quadrats sampled and having an average cover of 36%. Percent cover of *B. aritosa* was considerably less on maple-ash forest communities, however this species still had a high frequency because of its ability to assume a dwarved physical stature in a low light environment. *Polygonum spp*., unknown forbs, *Leersia oryzoides*, *Carex spp*., unknown grasses, *Urtica dioica*, *Xanthium spp*., *Bidens cernua*, *Ipomoea pandurata*, *Campsis radicans*, and *Vitis spp*. were co-dominants (Table 7). Much of the herbaceous vegetation was represented by rosettes and seedlings resulting in the creation and dominance of unknown forbs and unknown grasses categories.

DISCUSSION

Forest Response

The perception that floodplain forests are resilient to flood disturbance may be erroneous and highly dependent upon the degree of disturbance. Results of this study indicate that the 1993 flood was a large-scale disturbance event that inflicted high mortality in all tree species. However, the rate of mortality was species, forest community and size specific. We identified *Celtis occidentalis*, *Q. palustris*, *P. deltoides*, and *U. americana* to be large-scale flood intolerant, while *Q. lyrata*, *F. pennsylvanica*, *Q. macrocarpa*, and *A. saccharinum* were more tolerant. These results are consistent with the findings of other studies of permanent inundation and large-scale flooding on the UMRS (Turner, 1930; Green, 1947; Yeager, 1949; Yin et al., 1994). Variations in species response to flooding are related to a species ability to avoid or tolerate a flood event (Kozlowski, 1984, 1997). With high mortality in species thought to be flood tolerant, the 1993 flood may be labeled as a rare disturbance event that compromised most means of flood avoidance and tolerance in tree species.

The relationship of tree mortality and forest community was one of ‘successional stage’ (disturbance gradient) and floodplain elevation. Mixed forests are an advanced stage in the successional pattern of floodplain forests of the UMRS (Hosner and Minckler, 1960; Galatowitsch and McAdams, 1994). Shade tolerant species abound in this forest community but appear to be moderately- to non-tolerant to a flood disturbance of this magnitude. Oak forests are also composed of species non-tolerant to large-scale flooding. However, the slightly higher elevation that these forests occupied may have lessened the effects of the 1993 flood. Maple-ash forests are composed of species that are considered flood tolerant. Nevertheless, the magnitude of the flood inflicted high mortality in even these species and eliminated the shade tolerant species that were present.

We found that tree mortality generally increased as diameter decreased. This supports the findings of previous studies (Harms *et al.*, 1980; Yin *et al.*, 1994). Harms *et al.* (1980) indicated that the relationship of higher survival of flooding with increased diameter as being related to tree vigor and root surface available to produce adventitious roots. Nonetheless, mortality was high in some species regardless of size (*Celtis occidentalis* and large *P. deltoides*) due to lack or compromise of physiological adaptations that promote flood survivorship.

The dominance of *U. americana* and *Celtis occidentalis* in the sapling cohort of maple-ash and oak forest communities, prior to the 1993 flood, indicate that these two forest communities on Reach 26 of the UMRS were experiencing a shift in species composition towards mixed forest communities. The dominance of *U. americana* and *Celtis occidentalis* in the sapling and tree cohorts of the mixed forests indicate that under the past hydric regime, a mixed forest community will persist for a considerable length of time until a disturbance event occurs. Large-scale flooding maybe that driving force increasing species diversity and landscape heterogeneity on the floodplain.

Seedling Response

Following a disturbance event, a suppressed seedling and seed bank often respond to canopy gap creation by germinating and or growing vigorously (Marshall,1927; Hosner and Minckler, 1960; Norton, 1983; Kohyama, 1984; Streng et al., 1989; Peterson and Pickett, 1995). This study determined that the pre-flood seedling bank was eliminated and that no seedlings greater than two years of age were found in 1995. This is consistent with the concept that seedlings are susceptible to high mortality if flooding occurs during the growing season over a prolonged period of time (McDermott, 1954; Hosner, 1958, 1959, 1960; Broadfoot and Williston, 1973; Peterson and Bazzaz, 1984; Jones et al., 1989). Nonetheless, there was astonishing seed germination and seedling development immediately following the flood disturbance (average density of 239,000 seedlings/ha and mean age of 1.8). Seedling densities identified by this study are 8 to 10 times greater than those reported for similar bottomland forests located near the confluence of the Mississippi and Ohio rivers in southern Illinois and central Ohio (Hosner and Minckler, 1960; Robertson et al., 1978; Boerner and Brinkman, 1996). The magnitude of the disturbance event and recentness of sampling following the 1993 flood would explain the vast differences between this study and that of Hosner and Minckler (1960), Robertson et al. (1978), and Boerner and Brinkman (1996). The increase in seedling densities following disturbance indicates the important role that these events play in forest reorganization, community succession and species composition.

Current knowledge of UMRS floodplain forest reorganization, would have predicted that *P. deltoides* and *Salix nigra* (pioneer species) would dominate the seedling cohort of all forests communities following the 1993 flood disturbance (Hupp, 1992; Galatowitsch and McAdams, 1994; Hodges, 1994; Yin et al., 1997; Rood et al., 1998). This widely accepted theory inclined Galatowitsch and McAdams (1994) to write, “After extreme flood episodes, as occurred in 1993, cottonwood-willow communities will increase in extent because they will form pioneer communities in the annual floodplain and on higher terrain as well”. However, these species played a minor role in the composition of the post-flood seedling bank of the most flood-impacted Reach of the UMRS. A factor influencing *P. deltoides* and *S. nigra* recruitment is an optimum seed-bed. Low litter depth, low herbaceous and overstory cover and dry soil conditions for part of the year are necessary for *P. deltoides* and *S. nigra* regeneration (Hosner and Minckler, 1960). High herbaceous cover following the 1993 flood event and an anthropogenically created and maintained high water table may have inhibited these two early pioneers species from regenerating.

Acer saccharinum, *F. pennsylvanica*, and *U. americana* (mid to late successional species) dominated the seedling bank of Reach 26 following the 1993 flood. The dominance of these three species is in agreement with other studies of floodplain forests of this region (Hosner and Minckler, 1960; Lindsey et al., 1961; Boerner and Brinkman; 1996). *Acer saccharinum*, *F. pennsylvanica*, and *U. americana* produce many seeds that are widely dispersed (wind and water) and capable of germinating in herbaceous cover and under anaerobic soil conditions (Hosner and Minckler, 1960; Young and Young, 1992). In addition to long dispersal distances, these species had high densities of surviving parent trees to facilitate regeneration. Early germination and establishment by these species will ensure a competitive advantage over seeds germinating later and may present little change in composition in the near future (Hibbs, 1983; Brokaw, 1985; Connel, 1989; Streng et al., 1989; Jones et al., 1994, 1997).

Celtis occidentalis and *Q. palustris* were poorly represented in the post-flood seedling bank, which we attribute to the relatively low number of seeds produced, short dispersal distances and low number of surviving adult trees. *Celtis occidentalis* is a slow growing, shade tolerant species and *Q. palustris* is a species that relies upon treefall or low intensity fire disturbance to release short-lived seedlings (Shelford, 1954; Minckler, 1957; Aust et al., 1985; Galatowitsch and McAdams, 1994). Both species rely upon gravity and frugivores for dispersal resulting in short dispersal distances and a large number of seedlings germinating under conspecific adults (Hoppes, 1988; Schupp, 1993; Steele et al., 1993; Steele and Smallwood, 1994). The requirement of a closed canopy to establish in, short dispersal distances, very slow growth, and high tree and sapling mortality, indicates that it may be several hundred years before *Celtis occidentalis* will re-establish at densities and sizes equal to that of pre-flood. *Quercus palustris* relies primarily upon gravity, small mammals (squirrels) and birds (blue jay) as dispersal agents. The larger seeds would indicate shorter dispersal distances than even *Celtis occidentalis*. However, lower tree mortality than *Celtis occidentalis* and establishment in gaps would indicate that the time frame for re-organization of *Q. palustris* would be substantially less.

Seedlings were more numerous in maple-ash than mixed or oak forest communities and in gaps than under canopy cover. The higher seedling densities identified in maple-ash forest communities is related to seed dispersal and location of conspecific adults. Although *A. saccharinum*, *F. pennsylvanica*, and *U. americana* produce light seeds that have high dispersal distances, a majority of the seedfall still occurs near the conspecific adults. An increase in seedling density with the formation of gaps is in agreement with other findings (Maguire and Forman, 1983; Boerner and Brinkman, 1996; Dunn, 1986; Molofsky and Augspurger, 1992). However, we found that it was a weak relationship. *Acer saccharinum*, *U. americana* and *F. pennsylvanica* had high germination and seedling densities in large gaps and in dense canopy cover. We observed that gaps were commonly over grown with herbaceous vegetation and vines attaining heights of approximately 2 meters. Sites with dense tree canopy also had high herbaceous and vine cover, although nowhere near that of the gaps. The light regime that these seedlings were exposed to in the summer of 1995 probably did not vary significantly from a densely forested site to a large gap due to the dense herbaceous cover. However, there may be an improved light environment in the long run for those seedlings in the gaps if they are able to capitalize on improved light conditions in the early spring or late fall when the herbaceous vegetation is less prevalent and if these seedlings can tolerate very low light levels and high root competition throughout the rest of the year. Also, reduced predation and fungal attack is likely to occur in gaps further increasing the chances of survival (Augspurger, 1984; Terborgh et al., 1993; Schupp, 1995; Wada et al., 2000; Wenny, 2000).

Herbaceous and Liano Vegetation Response

The creation of gaps in the forest canopy initiates a response from suppressed seedlings and herbaceous vegetation. Without continued disturbance, tree species eventually replace the herbaceous vegetation. However, the time frame involved is dependent upon the tree species ability to quickly grow above the herbaceous vegetation or survive extreme shading. Consequently, the herbaceous understory dictates what tree species are likely to regenerate into the immediate forest (Siccama et al., 1970; Maguire and Forman, 1983; Gilliam et al., 1995). Compared with other studies of the UMRS, species composition did change as a result of the 1993 flood event (Hus, 1908; Hosner and Minckler, 1960; Linsey et al., 1961; Eyre, 1980; Galatowitsch and McAdams, 1994). Annual plant species became more prevalent than grasses, grass-like plants and perennials. Annual life-forms are very well adapted to pulsed flood events (Hall et al., 1946; Lindsey et al., 1961; Menges and Waller, 1983; Galatowitsch and McAdams, 1994) by tolerating these extreme anaerobic conditions as a seed. In addition, the annual flood events disperse the seeds, deposit them with nutrient rich sediment and bury or inhibit competitors. The annual plant (such as *B. aritosa*) can then complete its life-cycle in a very short period of time before the next flood event occurs.

Creation of canopy gaps should allow for an increase in understory cover due to increased PAR and decreased competition for water and nutrients (Hosner and Minckler, 1960; Moore and Vankat, 1986; Perison et al., 1997). Consequently, many of the dominant understory species identified by this study have been classified as high-light specialists or light generalists (Menges and Waller, 1983; Galatowitsch and McAdams, 1994). However, our results were inconclusive in describing the relationship between overstory and understory cover. We believe that this is related to high herbaceous cover of shade tolerants (*Urtica dioica*) in low-impacted areas. We found that herbaceous cover was high in gaps and in the understory. This may be attributed to slightly increased levels of PAR with subcanopy gap formation and a rich sediment deposition.

The UMRS floodplain forest is characterized by a high abundance and diversity of woody vines (Hus, 1908; Shelford, 1954; Lindsey et al., 1961; Galatowitsch and McAdams, 1994). Following disturbance and gap creation in the forest canopy, vines commonly increase in biomass and abundance and may delay forest reorganization for an extended period of time (Shelford, 1954; Allen et al., 2005). Vines grow rapidly, survive moderate canopy, and through structural adaptations (tendrils) can grow up and on top of the herbaceous and seedling strata effectively shading competitors. However, for many species effective trellises must be available to facilitate this. Large-scale disturbances remove support structures (trellis) making it difficult for large woody vines to become established (Putz, 1984; Allen et al., 1997; Allen et al., 2005). Loss of hosts in large gaps may promote smaller statured vine species until larger trees can regenerate and act as effective trellis. We observed that woody vine abundance, biomass and diversity may have been reduced by the 1993 flood. *Vitis spp*., *Campsis radicans*, and *Toxicodendron radicans* were the only woody vines that were abundant and were restricted to the understory.

Implications

Floodplain forests provide valuable habitat for many species of wildlife (both residential and migratory) (Wiener et al., 1998; Knutson et al., 1999; Smith and Twedt, 1999), provide organic input into the aquatic system (Polit and Brown, 1996), and reduce bank erosion (Wiener et al., 1998). Over the past 200 years, floodplain forests have undergone significant anthropogenic modifications resulting in altered floodplain hydrology, altered river geomorphology, separation from the flood regime, and extensive forest clearing (Peck and Smart, 1986; Sparks, 1995; Wlosinski et al., 1995; Yin and Nelson, 1995; Yin et al. 1997; Sparks et al., 1998; Giedeman, 1999). These modifications have resulted in a change in the species composition of the floodplain forests with an increase in the dominance of *Acer spp*. and *Fraxinus spp*. and a decline in *Celtis occidentalis*, *Ulmus americana*, *Carya illinoensis*, *Quercus palustris*, *Populus deltoides*, and *Salix spp*. (Hus, 1908; Yeager, 1949; Everitt, 1968; Nelson *et al*., 1994; Yin and Nelson, 1995; Knutson and Klaas, 1998; Nelson and Sparks, 1998; Giedeman, 1999).

The 1993 flood event has further accentuated a shift towards a maple-ash dominated forest community. Interestingly, the trend of *Acer spp*. and *Fraxinus spp*. replacing *Quercus spp*. and *Carya spp*. has been reported for floodplain and upland forests worldwide and is generally related to river regulation (changes in the flooding regime) and lack of disturbance (Bragg and Tatschl, 1977; Lorimer, 1993; Chester et al., 1995; Neumeister et al., 1997; Abrams, 1998; Foster et al., 1998; Abrams et al., 1999; Huddle and Pallardy, 1999; Tinner, *et al*., 1999; Dey and Guyette, 2000; McCarthy and Evans, 2000).

The further decline in hard-mast and soft-mast tree species will likely result in a decrease in wildlife diversity, individual species density, and quality of habitat. Further research is necessary to understand the complex dynamics of seed production and dispersal and seedling germination and survivorship in floodplain forests of the UMRS. A more complete understanding of these processes will provide natural resource managers with the necessary information to improve and protect floodplain forests in the future.

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Figure 1. Mean annual post-dam (1940-1993) hydrograph and 1993 flood hydrograph at the confluence of the Upper Mississippi and Illinois Rivers (Mississippi River Mile 218, Grafton, IL).

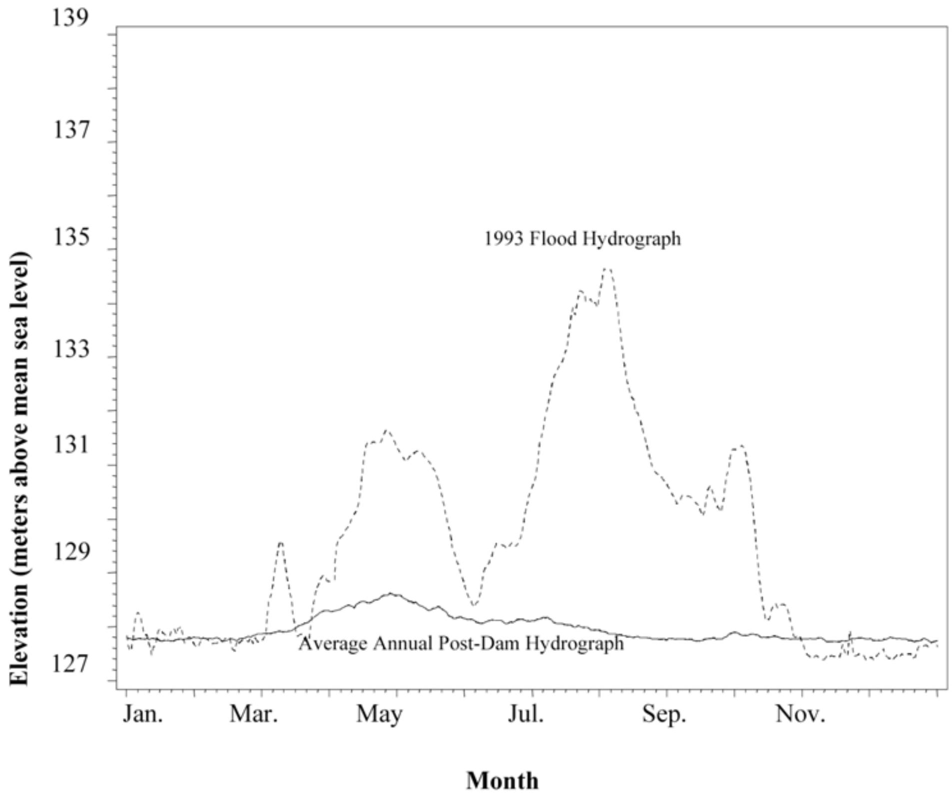

Figure 2.
Reach 26 study area showing the confluence of the Mississippi, Illinois, and Missouri Rivers.

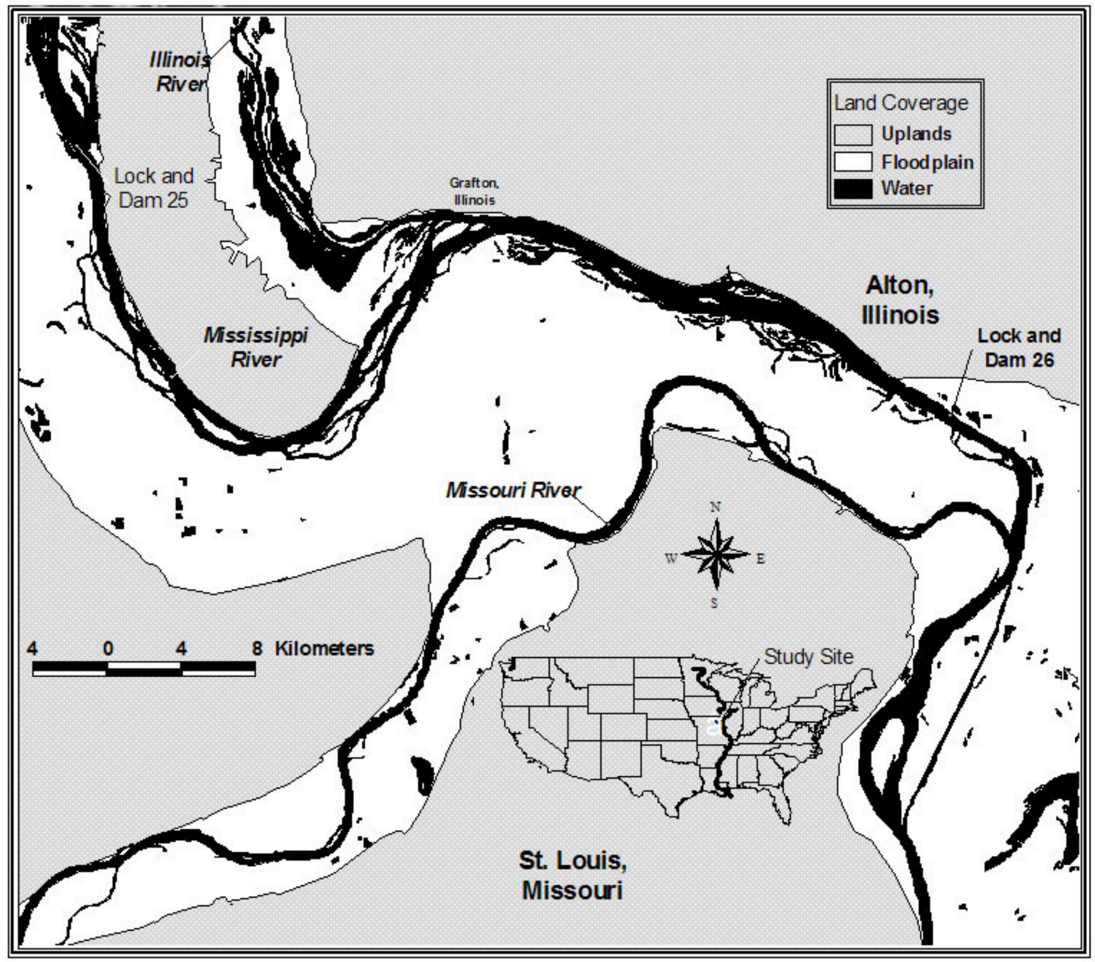

Figure 3. Percent mortality by diameter at breast height (dbh).

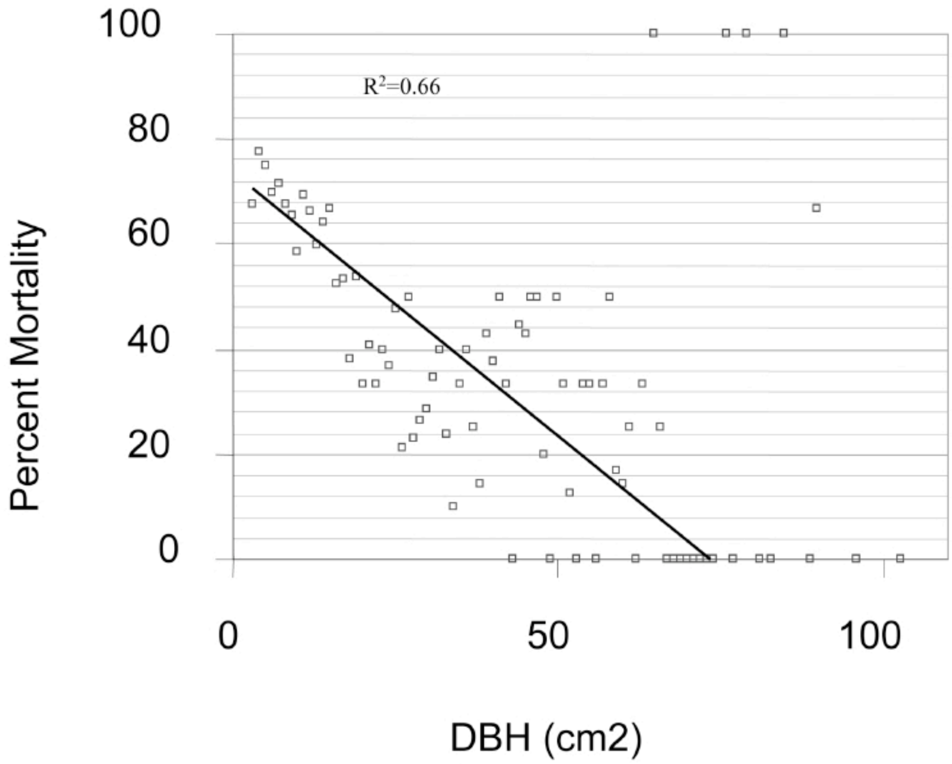

Table 1. Response of trees and saplings to the 1993 flood.

	Pool 26 Pre-1993 Flood		Pool 26 Post-1993 Flood			
Species (n)	Density/ Hectare	Importance Value	Mortality (%)	Density/ Hectare	Importance Value	**Change in Importance Value**
Tree						
Acer negundo (50)	27.9	10.4	42.0	16.2	10.9	**0.5**
Acer saccharinum (283)	158.1	58.3	42.4	91.1	63.8	**5.5**
Celtis occidentalis (84)	46.9	11.6	90.5	4.5	2.2	**-9.4**
Fraxinus pennsylvanica (123)	68.7	25.3	22.8	53.1	33.0	**7.7**
Populus deltoides (23)	12.9	10.0	56.5	5.6	8.0	**-2.0**
Quercus lyrata (62)	34.6	10.7	19.3	28.0	15.5	**4.8**
Quercus macrocarpa (13)	7.3	4.3	30.8	5.0	5.9	**1.6**
Quercus palustris (145)	81.0	34.8	57.3	34.6	26.9	**-7.9**
Ulmus americana (122)	68.2	16.7	49.2	34.6	14.7	**-2.0**
Other (95)	53.1	18.0	41.1	31.3	18.9	**0.9**
Total (1000)	**558.7**	**200.0**	**45.6**	**303.9**	**200.0**	**-------**
Sapling						
Acer negundo (40)	22.4	8.9	100.0	0.0	0.0	**-8.9**
Acer saccharinum (162)	90.5	36.6	96.3	3.4	6.3	**-30.4**
Celtis occidentalis (199)	111.2	42.2	74.9	27.9	31.1	**-11.1**
Cornus spp. (13)	7.3	1.7	0.0	7.3	7.0	**5.2**
Crataegus spp. (26)	14.5	6.6	50.0	7.3	11.0	**4.4**
Diospyros virginiana (33)	18.4	7.4	36.4	11.7	14.0	**6.6**
Forestiera acuminata (202)	112.9	35.7	56.9	48.6	51.2	**15.5**
Fraxinus pennsylvanica (31)	17.3	7.2	48.4	8.9	12.1	**4.9**
Ulmus americana (148)	82.7	36.6	66.2	28.0	41.1	**4.5**
Other (61)	34.1	17.7	91.7	3.4	26.3	**8.6**
Total (915)	**511.3**	**200.7**	**72.1**	**146.4**	**200.0**	**-------**

Table 2. Tree response by forest community response to the 1993 flood.

Tree Species (n)	Pool 26 Pre-1993 Flood Density/ Hectare	Importance Value	Pool 26 Post-1993 Flood Mortality (%)	Density/ Hectare	Importance Value	**Change in Importance Value**
Maple-Ash						
Acer negundo (22)	25.0	10.0	31.8	17.1	11.2	**1.2**
Acer saccharinum (249)	283.2	103.8	41.8	164.8	103.1	**-0.7**
Celtis occidentalis (25)	28.4	6.6	100.0	0.0	0.0	**-6.6**
Fraxinus pennsylvanica (83)	94.4	37.1	20.5	75.1	44.0	**6.8**
Populus deltoides (8)	9.1	7.5	37.5	5.7	8.2	**0.7**
Quercus lyrata (5)	5.7	1.7	20.0	4.6	2.3	**0.5**
Quercus macrocarpa (0)	-------	-------	-------	-------	-------	**-------**
Quercus palustris (10)	81.0	3.7	80.0	2.3	1.8	**-1.9**
Ulmus americana (46)	68.2	12.7	41.3	30.7	12.2	**-0.5**
*Other (39)	53.1	16.8	38.4	27.3	17.3	**0.4**
Total (487)	**558.7**	**200.0**	**41.1**	**327.5**	**200.0**	**-------**
Mixed						
Acer negundo (23)	56.3	20.9	47.8	29.4	25.5	**4.7**
Acer saccharinum (22)	53.9	19.9	63.6	19.6	25.3	**5.4**
Celtis occidentalis (36)	88.2	24.5	94.4	4.9	4.8	**-19.7**
Fraxinus pennsylvanica (22)	53.9	19.3	36.4	34.3	31.5	**12.3**
Populus deltoides (15)	36.8	27.4	66.7	12.2	19.9	**-7.4**
Quercus lyrata (0)	-------	-------	-------	-------	-------	**-------**
Quercus macrocarpa (2)	4.9	2.3	0.0	4.9	5.0	**2.7**
Quercus palustris (11)	27.0	24.8	72.7	7.4	20.6	**-4.2**
Ulmus americana (50)	122.5	32.3	60.0	49.0	29.3	**-3.1**
*Other (37)	90.7	28.8	43.3	51.4	38.0	**9.2**
Total (218)	**534.1**	**200.0**	**60.1**	**213.2**	**199.9**	**-------**
Oak						
Acer negundo (5)	10.0	2.4	60.0	4.0	1.6	-0.8
Acer saccharinum (12)	23.9	5.9	16.7	19.9	7.4	1.5
Celtis occidentalis (23)	45.8	10.0	73.9	12.0	4.7	-5.4
Fraxinus pennsylvanica (18)	35.8	8.2	16.7	29.9	11.7	3.4
Populus deltoides (0)	-------	-------	-------	-------	-------	**-------**
Quercus lyrata (57)	113.5	35.7	19.3	91.6	50.3	14.6
Quercus macrocarpa (11)	21.9	14.3	36.4	13.9	19.4	5.2
Quercus palustris (124)	246.8	100.7	54.0	113.5	81.8	-18.9
Ulmus americana (26)	51.8	11.4	42.3	29.9	11.5	0.1
*Other (19)	37.8	11.5	36.8	23.9	11.8	1.3
Total (295)	**587.2**	**200.1**	**42.4**	**338.4**	**200.0**	**-------**

*Other includes: *Carya illinoensis*, *Carya spp.*, *Cercis canadensis*, *Crataegus spp.*, *Diospyros virginiana*, *Forestiera acuminata*, *Gleditsia aquatica*, *Gleditsia triacanthos*, *Morus spp.*, and *Salix nigra*.

Table 3. Sampling response by forest community to the 1993 flood event.

SaplingSpecies (n)	Pool 26 Pre-1993 Flood Density/ Hectare	Pool 26 Pre-1993 Flood Importance Value	Mortality (%)	Pool 26 Post-1993 Flood Density/ Hectare	Pool 26 Post-1993 Flood Importance Value	**Change in Importance Value**
Maple-Ash						
Acer negundo (8)	9.1	4.2	100.0	0.0	0.0	**-4.2**
Acer saccharinum (132)	150.1	77.5	97.7	3.5	8.8	**-68.8**
Celtis occidentalis (44)	50.1	23.3	95.5	2.3	7.2	**-16.0**
Cornus spp. (0)	-------	-------	-------	-------	-------	**-------**
Crataegus spp. (12)	13.7	8.3	58.3	5.7	20.3	**12.0**
Diospyros virginiana (9)	10.2	5.5	55.6	4.6	14.5	**9.0**
Forestiera acuminata (68)	77.3	32.1	52.9	36.4	72.5	**40.4**
Fraxinus pennsylvanica (8)	5.7	4.3	40.0	3.4	13.0	**8.7**
Ulmus americana (60)	68.2	35.8	66.7	22.7	63.7	**27.9**
*Other (12)	13.7	8.3	99.9	0.0	0.0	**-8.3**
Total (350)	**398.1**	**199.3**	**80.3**	**78.5**	**200.0**	**-------**
Mixed						
Acer negundo (27)	66.1	23.7	100.0	0.0	0.0	**-23.7**
Acer saccharinum (12)	29.4	10.1	100.0	0.0	0.0	**-10.1**
Celtis occidentalis (52)	127.4	43.0	100.0	0.0	0.0	**-43.0**
Cornus spp. (0)	-------	-------	-------	-------	-------	**-------**
Crataegus spp. (4)	9.8	4.2	50.0	4.9	10.0	**5.9**
Diospyros virginiana (2)	4.9	3.6	50.0	2.5	7.8	**4.1**
Forestiera acuminata (62)	151.9	46.1	5.1	63.6	99.4	**53.4**
Fraxinus pennsylvanica (8)	19.6	7.3	75.0	4.9	10.0	**2.7**
Ulmus americana (44)	107.8	48.1	72.7	29.4	60.0	**12.0**
*Other (15)	36.8	14.3	92.9	4.9	12.8	**-1.5**
Total (226)	**553.7**	**200.3**	**80.1**	**110.2**	**200.0**	**-------**
Oak						
Acer negundo (5)	10.0	2.6	100.0	0.0	0.0	**-2.6**
Acer saccharinum (182)	35.8	9.9	83.3	6.0	7.2	**-2.7**
Celtis occidentalis (103)	205.0	58.8	53.4	95.5	57.9	**-0.9**
Cornus spp. (13)	25.9	6.1	0.0	25.9	13.9	**7.7**
Crataegus spp. (10)	19.9	6.4	40.0	11.9	9.2	**2.8**
Diospyros virginiana (22)	43.8	12.2	27.3	31.8	18.4	**6.3**
Forestiera acuminata (72)	143.3	33.7	59.7	57.8	34.9	**1.1**
Fraxinus pennsylvanica (18)	35.8	13.3	38.9	21.9	17.6	**4.4**
Ulmus americana (44)	87.6	31.2	59.1	35.8	30.0	**-1.1**
*Other (34)	67.7	25.9	85.3	10.0	11.0	**-14.9**
Total (339)	**674.8**	**200.0**	**56.3**	**296.6**	**200.0**	**-------**

*Other includes: *Carya spp.*, *Cephalanthus occidentalis*, *Cercis canadensis*, *Gleditsia triacanthos*, *Maclura pomifera*, *Morus spp.*, *Quercus lyrata, Quercus macrocarpa*, and *Quercus palustris*.

Table 4. Cover response to the 1993 flood event.

Stratified Cover (n)	Mean % cover	Standard Deviation	Minimum	Maximum
Maple-Ash				
Canopy (279)	54.4	33.1	5.0	100.0
Subcanopy (279)	18.1	24.9	5.0	95.0
Overstory (279)	60.5	32.3	5.0	100.0
Understory (279)	65.5	31.0	0.0	100.0
Total (279)	87.9	14.8	25.0	100.0
Mixed				
Canopy (130)	28.7	27.8	5.0	95.0
Subcanopy (130)	21.9	26.3	5.0	95.0
Overstory (130)	40.7	31.0	5.0	95.0
Understory (130)	74.0	31.3	0.0	100.0
Total (130)	88.2	19.8	25.0	100.0
Oak				
Canopy (160)	39.4	32.3	0.0	95.0
Subcanopy (160)	25.0	30.5	0.0	95.0
Overstory (160)	51.7	36.1	0.0	100.0

Table 5. Stratified cover differences by forest community. Forest types with Similar codes do not differ statistically (p>0.05) using Tukey's HSD (Honestly Significant Difference).

Forest Community	Canopy	Subcanopy	Overstory	Understory	Total
Maple-Ash	A	A	A	A	A
Mixed	B	AB	B	B	A
Oak	C	B	C	A	A

Table 6. Tree seedling response to the 1993 flood event.

Species (n)	Frequency	Relative Frequency	Density/ Hectare	Relative Density	Importance Value	Mean Percent Cover	Mean Age
Maple-Ash							
Acer negundo (155)	14.7	7.2	22219.4	6.1	13.3	2.5	1.9
Acer saccharinum (1804)	113.6	55.9	258599.3	70.7	126.6	2.8	1.7
Celtis occidentalis (13)	3.9	1.9	1860.9	0.5	2.5	8.7	1.9
Cephalanthus occidentalis (10)	3.6	1.8	1433.7	0.4	2.2	8.5	2.0
Diospyros virginiana (4)	1.1	0.5	572.0	0.2	0.7	0.8	1.0
Fraxinus pennsylvanica (171)	25.8	12.7	24567.7	6.7	19.4	5.0	1.9
Quercus palustris (7)	1.4	0.7	1003.6	0.3	1.0	3.0	2.0
Ulmus americana (299)	27.6	13.6	42833.0	11.7	25.3	1.8	1.9
Other (88)	11.5	5.6	12610.8	3.5	9.1	3.3	2.0
Total (2551)	**203.2**	**100.0**	**365700.4**	**100.0**	**200.0**	**2.9**	**1.8**
Mixed							
Acer negundo (10)	3.1	2.3	3076.9	2.1	4.5	1.3	1.3
Acer saccharinum (143)	70.0	53.2	74760.0	51.9	105.1	8.6	1.9
Celtis occidentalis (4)	3.1	2.3	1230.8	0.9	3.2	3.0	1.8
Cephalanthus occidentalis (9)	3.8	2.9	2769.2	1.9	4.9	12.2	1.8
Diospyros virginiana (2)	1.5	1.2	615.4	0.4	1.6	1.0	1.5
Fraxinus pennsylvanica (119)	16.9	12.9	36621.5	25.4	38.3	1.9	1.7
Quercus palustris (8)	2.3	1.8	2464.6	1.7	3.5	1.5	1.7
Ulmus americana (68)	27.7	21.1	20935.4	14.5	35.6	1.7	1.8
Other (5)	3.1	3.0	1538.5	1.1	4.1	0.8	1.5
Total (368)	**131.5**	**100.7**	**144012.3**	**100.0**	**200.7**	**4.7**	**1.8**
Oak							
Acer negundo (1)	0.6	0.6	250.0	0.3	0.8	1.0	1.0
Acer saccharinum (37)	18.1	16.9	9280.0	9.7	26.6	2.6	2.0
Celtis occidentalis (29)	9.4	8.7	7237.5	7.6	16.3	1.2	1.6
Cephalanthus occidentalis (71)	13.8	12.8	17765.0	18.6	31.4	7.6	2.0
Diospyros virginiana (26)	5.6	5.2	6502.5	6.8	12.0	1.0	1.3
Fraxinus pennsylvanica (23)	11.3	10.5	5760.0	6.0	16.5	4.1	1.9
Quercus palustris (41)	12.5	11.6	10250.0	10.7	22.4	3.0	2.0
Ulmus americana (102)	19.4	18.0	25497.5	26.7	44.7	1.6	1.8
Other (52)	16.9	16.9	13002.5	13.6	30.5	1.8	2.1
Total (382)	**107.5**	**101.2**	**95545.0**	**100.0**	**201.2**	**3.1**	**1.9**

Table 7. Herbaceous and liano response to the 1993 flood event.

Species	Cover	Std. Dev.	Minimum	Maximum	Relative Cover	n	Frequency	Relative Frequency	IV
Maple-Ash									
Bidens aritosa (191)	23.1	25.8	1.0	100.0	12.2	191.0	68.5	25.8	38.0
Bidens cernua (14)	5.0	4.6	1.0	15.0	2.6	14.0	5.0	1.9	4.5
Campsis radicans (22)	21.9	21.5	1.0	70.0	11.6	22.0	7.9	3.0	14.5
Carex spp. (47)	8.2	15.0	1.0	80.0	4.3	47.0	16.8	6.4	10.7
Ipomoea pandurata (56)	14.8	16.9	1.0	80.0	7.8	56.0	20.1	7.6	15.4
Leersia oryzoides (32)	15.0	25.4	1.0	90.0	7.9	32.0	11.5	4.3	12.3
Polygonum spp. (25)	30.3	29.8	1.0	88.0	16.0	25.0	9.0	3.4	19.4
Toxicodendron radicans (26)	15.9	19.0	1.0	70.0	8.4	26.0	9.3	3.5	11.9
Unknow n Forbs (104)	9.1	16.0	1.0	75.0	4.8	104.0	37.3	14.1	18.9
Unknow n Grasses (56)	4.0	6.7	1.0	45.0	2.1	56.0	20.1	7.6	9.7
Urtica dioica (88)	5.6	12.5	1.0	65.0	2.9	88.0	31.5	11.9	14.8
Vitis spp. (47)	15.0	21.4	1.0	100.0	7.9	47.0	16.8	6.4	14.3
Xanthium spp. (22)	13.7	17.7	1.0	73.0	7.2	22.0	7.9	3.0	10.2
Other (10)	8.0	***	***	***	4.2	9.8	3.5	1.3	5.6
Total	**189.5**	***	***	***	**100.0**	**739.8**	**265.1**	**100.0**	**200.0**
Mixed									
Bidens aritosa (106)	50.1	37.8	1.0	100.0	22.1	106.0	81.5	33.1	55.1
Bidens cernua (11)	19.0	17.2	5.0	63.0	8.4	11.0	8.5	3.4	11.8
Campsis radicans (9)	17.9	13.8	1.0	45.0	7.9	9.0	6.9	2.8	10.7
Carex spp. (17)	10.2	19.4	1.0	70.0	4.5	17.0	13.1	5.3	9.8
Ipomoea pandurata (16)	11.1	13.9	1.0	45.0	4.9	16.0	12.3	5.0	9.9
Leersia oryzoides (8)	3.5	2.1	1.0	5.0	1.5	8.0	6.2	2.5	4.0
Polygonum spp. (16)	23.4	27.3	1.0	90.0	10.3	16.0	12.3	5.0	15.3
Toxicodendron radicans (9)	11.3	8.3	1.0	25.0	5.0	9.0	6.9	2.8	7.8
Unknow n Forbs (47)	7.8	11.0	1.0	70.0	3.4	47.0	36.2	14.7	18.1
Unknow n Grasses (24)	15.5	23.8	1.0	95.0	6.9	24.0	18.5	7.5	14.3
Urtica dioica (32)	6.2	11.5	1.0	63.0	2.7	32.0	24.6	10.0	12.7
Vitis spp. (14)	15.7	24.1	1.0	80.0	6.9	14.0	10.8	4.4	11.3
Xanthium spp. (7)	22.6	15.2	5.0	45.0	9.9	7.0	5.4	2.2	12.1
Other (5)	12.4	***	***	***	5.5	4.6	3.6	1.4	6.9
Total	**226.8**	***	***	***	**100.0**	**320.6**	**246.6**	**100.0**	**200.0**
Oak									
Bidens aritosa (118)	42.7	36.3	1.0	100.0	22.3	118.0	73.8	25.1	47.4
Bidens cernua (25)	5.6	4.8	1.0	21.0	2.9	25.0	15.6	5.3	8.3
Campsis radicans (9)	8.2	5.9	1.0	20.0	4.3	9.0	5.6	1.9	6.2
Carex spp. (38)	16.0	20.2	1.0	80.0	8.3	38.0	23.8	8.1	16.4
Ipomoea pandurata (23)	9.5	16.6	1.0	80.0	4.9	23.0	14.4	4.9	9.8
Leersia oryzoides (45)	15.7	20.0	1.0	90.0	8.2	45.0	28.1	9.6	17.7
Polygonum spp. (33)	31.8	35.3	1.0	100.0	16.6	33.0	20.6	7.0	23.6
Toxicodendron radicans (21)	16.5	24.4	1.0	90.0	8.6	21.0	13.1	4.5	13.1
Unknow n Forbs (49)	3.9	4.9	1.0	23.0	2.0	49.0	30.6	10.4	12.5
Unknow n Grasses (25)	8.8	13.0	1.0	40.0	4.6	25.0	15.6	5.3	9.9
Urtica dioica (35)	3.9	10.7	1.0	63.0	2.0	35.0	21.9	7.4	9.5
Vitis spp. (25)	3.2	3.5	1.0	15.0	1.7	25.0	15.6	5.3	7.0
Xanthium spp. (18)	21.8	29.0	1.0	98.0	11.4	18.0	11.3	3.8	15.2
Other (6)	4.2	***	***	***	2.2	6.3	3.9	1.3	3.5
Total	**191.8**	***	***	***	**100.0**	**470.3**	**293.9**	**100.0**	**200.0**