Floodplain Forest Loss and Changes in Forest Community Composition and Structure in the Upper Mississippi River: A Wildlife Habitat at Risk

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Natural Areas Journal 18:138–150

ABSTRACT: Large floodplain forests represent a threatened and endangered type of ecosystem in the United States. Estimates of cumulative losses of floodplain forest range from 57% to 95% at different locations within the continental United States. Floodplain forests of the Upper Mississippi River (UMR) have significantly declined in extent due to agriculture, lock and dam construction, and urban development since European settlement. We collected data on shrubs, herbs, and trees from 56 floodplain forest plots in 1992 and compared our results with a previous analysis of historical tree data from the same area recorded by the General Land Office Survey in the 1840s. *Acer saccharinum* strongly dominates among mature trees and its relative dominance has increased over time. *Salix* spp. and *Betula nigra* have declined in relative dominance. Tree sizes are similar to those of presettlement forests, but present forests have fewer trees. The lack of early successional tree species and a trend toward an increasing monoculture of *A. saccharinum* in the mature stages indicate problems with regeneration. Because floodplain forests represent a rare habitat type, losses and changes in habitat quality could pose serious problems for wildlife that depend upon these habitats, especially birds.

Index terms: floodplain forest, wildlife habitat, Upper Mississippi River, historical forests, Driftless Area ecoregion.

INTRODUCTION

Large floodplain forests represent a threatened and endangered type of ecosystem in the United States. Estimates of cumulative floodplain forest losses range from over 95% of riparian forests in New Hampshire, West Virginia, and Missouri; 80% of bottomland hardwood forests in the lower Mississippi river alluvial plain and in Oklahoma; and 57% of forested wetlands in Ohio (Noss et al. 1995). The north-central United States has experienced the steepest losses of wetland forests anywhere in the United States: 47,650 ha were lost per year from 1940 to 1980, or 0.7% annually (Abernethy and Turner 1987). Nationwide, riparian areas are so degraded that 98% of U.S. streams do not meet federal criteria for designation as wild and scenic (Benke 1990). Floodplains have been used intensively by humans, even in prehistoric times, because of their abundance of food plants and wild game and their convenience as transportation routes (Theler 1991, Arzigian et al. 1994). Despite problems with flooding, many agricultural crops thrive in rich alluvial soils, and floodplains are prized for agriculture throughout the world (Malanson 1993, Mitsch and Gosselink 1993).

Major changes have occurred in the hydrology, geomorphology, and vegetation of the Upper Mississippi River (UMR) since European settlement (Wlosinski et al. 1995). Floodplain forests have been affected by these changes. Agriculture, lock and dam construction, and urban development on the Mississippi River have resulted in conversion of floodplain forests to nonforested habitats (Peck and Smart 1986). Early European settlers continuously harvested floodplain trees for firewood, railroad ties, and fuel for steamboats (Lapham 1854, Telford 1926). Later, large areas of floodplain forest were clearcut prior to impoundment for navigation purposes (Palas 1938, Fremling and Claflin 1984). Timber harvesting is now implemented to meet forest management objectives and to maintain wildlife habitat (Feavel 1986). Human influences on the river have resulted in changes in the annual hydrologic cycle of the UMR (Sparks 1995). Water elevations are now higher than they were historically and flooding is more severe (Belt 1975, Lubinski et al. 1991).

Geographic information system (GIS) maps derived from surveyor's maps from the late 1890s have been completed for selected areas of the UMR. A comparison of these maps with 1989 land cover data shows that, in some areas, up to 40% of UMR floodplain forested habitats have been destroyed since the late 1890s (M.R. Craig, landscape ecologist, River Studies Center, University of Wisconsin, La Crosse, unpubl. data). These estimates are conservative, since by the late 1890s some agricultural development had already occurred. Extrapolating from Peck and Smart (1986), Laustrup and Lowenberg (1994), and Yin and Nelson (1995), we estimate that before European settlement, floodplain forests of the UMR from St. Paul, Minnesota, to Alton, Illinois, occupied about 50%–70% of the floodplain; present day forests occupy only about 22%–25% of the floodplain. Other habitats in the floodplain include open water, submergent and emergent wetland vegetation, sedge meadow, and sand or mud. Despite evidence that UMR floodplain forests are threatened, little quantitative information on the plant community or successional processes is available. The UMR floodplain provides habitat for a wide range of vertebrates, including at least 57 mammal species, 37 species of reptiles and amphibians, and 292 species of birds (U.S. Fish and Wildlife Service, unpubl. data; Knutson et al. 1996). Recent declines in a number of these taxa indicate that the ecosystem health of the UMR could be at risk (Wiener et al. 1995). Without information on relationships between the plant community and habitat values of UMR floodplain forests, there is little to guide management efforts.

Besides providing habitat structure, floodplain forests contribute organic matter to the stream ecosystem. This material is a major source of energy for aquatic organisms (Vannote et al. 1980, Polit and Brown 1996). Flood pulses move this organic matter from the terrestrial to the aquatic system, providing a predictable annual boost in aquatic productivity (Junk et al. 1989).

The purpose of this paper is to synthesize the available information on UMR floodplain forests and to predict their future condition, particularly in terms of wildlife habitat. We present an analysis of the species composition and structure of floodplain forests of the Upper Mississippi River (Pools 6–10) in 1992. In addition, we discuss evidence that the present-day forests have changed in tree species composition compared with presettlement forests and present a prognosis for the future based on evidence of sapling abundance and potential for regeneration. We suggest that, without management, these forests are unlikely to regain their natural diversity due to abiotic conditions created by impoundment. We link the observed changes in floodplain forests with potential effects on wildlife species.

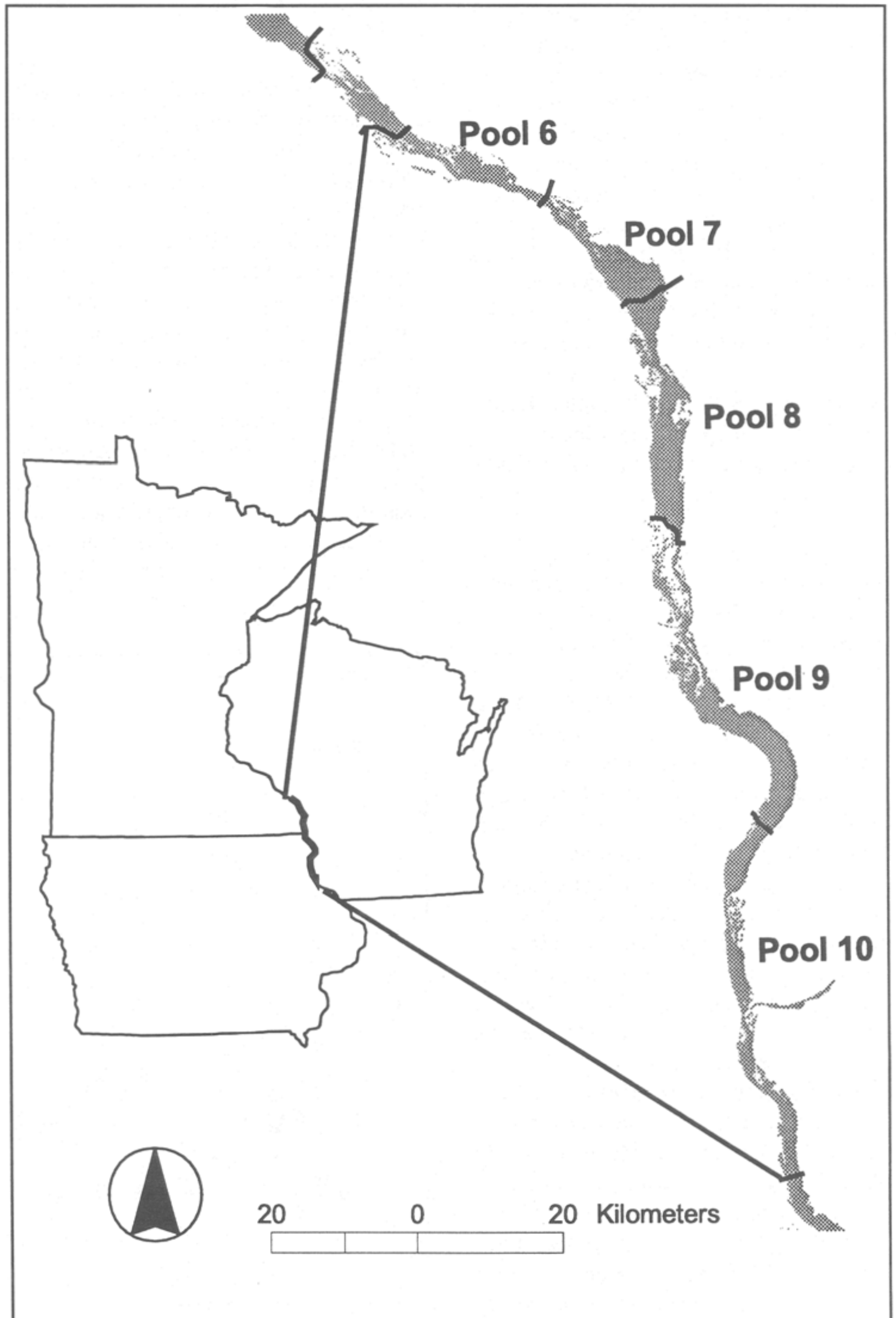

Figure 1. Location of the study area in Pools 6–10 of the Upper Mississippi River.

METHODS

We studied floodplain forests along the main channel of the Upper Mississippi River (Figure 1), from near Winona, Minnesota (Pool 6), to Guttenburg, Iowa (Pool 10), a distance of about 177 km. This section of the river flows through the Driftless Area ecoregion (Bailey 1994), a landscape of rolling hills and karst geology not covered by ice during the last (Wisconsin) glaciation. Here the UMR is unrestricted by levees and, during high water, the river floods some or all of its floodplain forests. Steep bluffs border the floodplain on both sides of the river. Large floodplain forest complexes of ≥100 ha are primarily found adjacent to the confluence of major tributaries such as the Black, Root, Upper Iowa, and Wisconsin Rivers. Elsewhere, forests are found along channel edges and on mid-channel islands. These forests are frequently flooded (every 2–5 years) and primarily publicly owned. We randomly selected 56 plots within the floodplain forests (> 70% tree canopy cover) using a 600-m x 600-m sampling grid overlaid on classified GIS land cover maps.

Within each plot, 3 to 10 sampling points were selected (mean = 5.4). Points were spaced at least 200 m apart and at least 50 m from an edge. None of the plots were flooded at the time of data collection. From May 20 through July 10, 1992, we collected data on trees, snags, and saplings at each point using the point-centered quarter method (Cottam and Curtis 1956, Mueller-Dombois and Ellenberg 1974). We collected data on shrubs, herbs, and trees at the focus sample point and three additional points 35 m from the focus point, 120 degrees apart. Herb and shrub cover were estimated using relevé classes (Mueller-Dombois and Ellenberg 1974). Means of herb and shrub cover were obtained by assigning the midpoint of the relevé class to each observation (Bonham 1989). Cover estimates overlapped so total cover could be > 100%. Trees were defined as woody plants > 8 cm dbh. Saplings were defined as single-stemmed woody plants < 8 cm dbh and > 1.5 m in height. Snags included dead standing wood > 12 cm dbh and > 1.5 m in height. Shrubs were defined as woody plants between 0.5 m and 1.4 m in height.

We calculated canopy cover as the mean of four densiometer readings, one reading at each cardinal direction. Plants were primarily identified in the field; herbarium specimens were collected for as many different species as time permitted. Herbarium specimens were identified to species wherever possible using standard herbarium techniques and the Ada Hayden Herbarium at Iowa State University. Species names follow Gleason and Cronquist (1991).

We calculated relative and absolute density, frequency, and dominance and importance values for trees and saplings (Cottam and Curtis 1956, Mueller-Dombois and Ellenberg 1974). Importance values for each species are the sum of relative density, relative dominance, and relative frequency. To determine tree and sapling size distributions, we grouped trees into 8-cm size classes, labeled with the midpoint of each class (8–16 cm = 12 cm class, 16–24 cm = 20 cm class, etc.). For the most dominant shrubs and herbs, we calculated the frequency (proportion of points in which a species was identified) and mean cover estimates. Vegetation size and cover estimates were calculated for each plot; mean values ± 1 SE for all plots are reported (Table 3).

To obtain a historical comparison, we compared our results with an analysis by Moore (1988). He studied floodplain forests in a portion of our study area using data from the 1840s. Moore analyzed General Land Office (GLO) Survey records of bottomland forest (1837–1854) from Houston County, Minnesota, and Allamakee County and Clayton County, Iowa. Our study area included these counties plus additional counties in Wisconsin. The floodplain in this portion of the UMR is bordered by steep bluffs on both sides of the river; the study areas were located between these bluffs.

RESULTS

We identified 138 plant taxa from the floodplain forests (Appendix A) and measured a total of 1,257 trees, 1,187 saplings, and 1,149 snags at 314 sampling points on 56 plots. *Acer saccharinum* was the dominant tree species, followed by *Ulmus* spp., *Fraxinus pennsylvanica*, and *Quercus bicolor* (Table 1). The sapling stratum was dominated by *Ulmus* spp. and *F. pennsylvanica*, followed by *A. saccharinum*, *Celtis occidentalis,* and *Q. bicolor* (Table 1). *Ulmus* spp. and *F. pennsylvanica* had a large cohort of saplings, whereas *A. saccharinum*

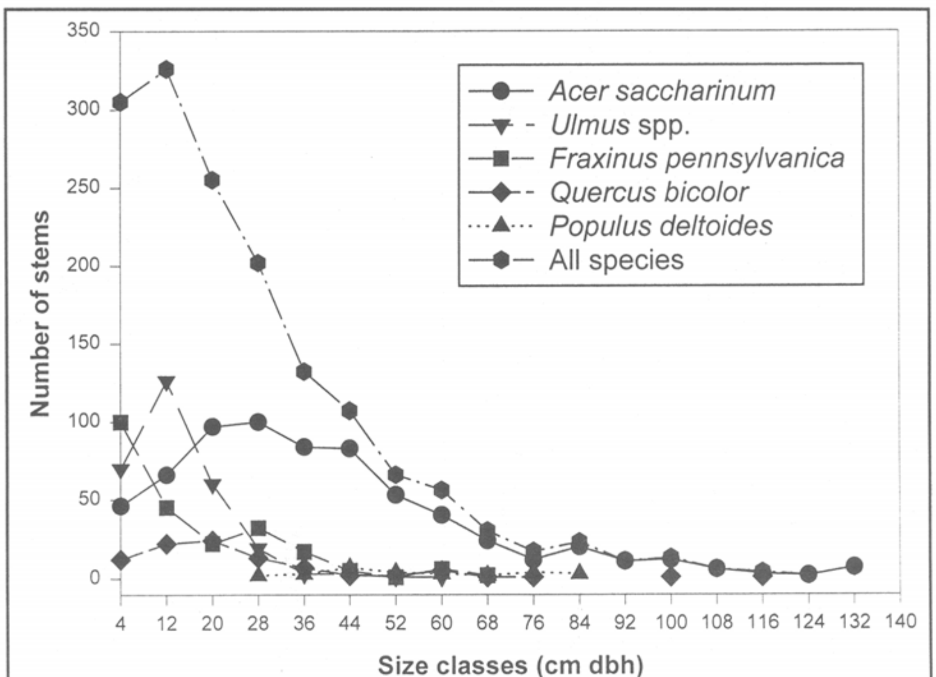

Figure 2. Size distribution of the most abundant floodplain forest tree species and the size distribution for all tree species.

Table 1. Tree and sapling species mean basal area; absolute and relative density, dominance, and frequency; and species importance value.

Scientific Name	Total Stems	Mean BA[a]	Abs. Dens.[b]	Rel. Dens.	Abs. Dom.	Rel. Dom.	Abs. Freq.	Rel. Freq.	IV[c]	IV Rank
TREES										
Acer saccharinum	620	1383.4	1.47	49.32	2029.39	74.06	0.77	37.46	160.84	1
Ulmus spp.	213	211.7	0.50	16.95	106.70	3.89	0.43	20.68	41.52	2
Fraxinus pennsylvanica	130	486.5	0.31	10.34	149.64	5.46	0.28	13.68	29.48	3
Quercus bicolor	79	603.6	0.19	6.28	112.83	4.12	0.12	6.03	16.43	4
Populus deltoides	28	2409.9	0.07	2.23	159.66	5.83	0.07	3.58	11.64	5
Celtis occidentalis	34	224.9	0.08	2.70	18.09	0.66	0.08	4.07	7.44	6
Betula nigra	28	681.2	0.07	2.23	45.13	1.65	0.06	2.93	6.81	7
Quercus rubra	32	470.7	0.08	2.55	35.64	1.30	0.05	2.61	6.45	8
Tilia americana	25	346.1	0.06	1.99	20.47	0.75	0.04	2.12	4.85	9
Carya cordiformis	24	245.9	0.06	1.91	13.97	0.51	0.05	2.28	4.70	10
Prunus serotina	14	438.0	0.03	1.11	14.51	0.53	0.03	1.30	2.95	11
Robinia pseudo-acacia	14	302.6	0.03	1.11	10.02	0.37	0.02	0.98	2.46	12
Acer negundo	7	443.8	0.02	0.56	7.35	0.27	0.02	0.98	1.80	13
Salix nigra	2	2307.2	0.00	0.16	10.92	0.40	0.01	0.33	0.88	14
Trees, unidentified	2	80.9	0.00	0.16	0.38	0.01	0.01	0.33	0.50	15
Morus spp.	2	77.0	0.00	0.16	0.36	0.01	0.00	0.16	0.34	16
Quercus alba	1	962.1	0.00	0.08	2.28	0.08	0.00	0.16	0.33	17
Pinus strobus	1	881.4	0.00	0.08	2.09	0.08	0.00	0.16	0.32	18
Betula papyrifera	1	475.3	0.00	0.08	1.12	0.04	0.00	0.16	0.28	19
Total	**1257**	**921.4**	**2.97**	**100.00**	**2740.54**	**100.01**	**2.07**	**100.00**	**300.01**	
SAPLINGS										
Ulmus spp.	271	23.7	0.17	22.83	4.13	46.80	0.47	22.96	92.59	1
Fraxinus pennsylvanica	387	5.3	0.25	32.60	1.32	14.92	0.58	28.45	75.97	2
Acer saccharinum	176	15.9	0.11	14.83	1.80	20.37	0.30	14.48	49.68	3
Celtis occidentalis	81	7.7	0.05	6.82	0.40	4.53	0.14	6.99	18.34	4
Quercus bicolor	46	11.4	0.03	3.88	0.34	3.83	0.10	4.66	12.37	5
Carya cordiformis	32	8.1	0.02	2.70	0.17	1.89	0.06	2.83	7.42	6
Robinia pseudo-acacia	32	9.5	0.02	2.70	0.20	2.21	0.04	2.16	7.07	7
Zanthoxylum americanum	32	1.3	0.02	2.70	0.03	0.29	0.06	3.00	5.98	8
Cornus spp.	18	2.9	0.01	1.52	0.03	0.38	0.04	2.00	3.90	9
Acer negundo	14	2.9	0.01	1.18	0.03	0.30	0.03	1.66	3.14	10
Tilia americana	11	10.3	0.01	0.93	0.07	0.82	0.03	1.33	3.08	11
Quercus rubra	11	8.5	0.01	0.93	0.06	0.68	0.03	1.33	2.93	12
Prunus serotina	14	3.8	0.01	1.18	0.03	0.39	0.02	1.16	2.73	13
Morus spp.	11	5.4	0.01	0.93	0.04	0.43	0.02	1.16	2.53	14
Trees, unidentified	14	3.3	0.01	1.18	0.03	0.34	0.02	1.00	2.52	15
Toxicodendron radicans	8	2.0	0.01	0.67	0.01	0.12	0.02	1.16	1.95	16
Viburnum lentago	8	2.6	0.01	0.67	0.01	0.15	0.02	1.00	1.82	17
Betula nigra	5	13.7	0.00	0.42	0.04	0.50	0.01	0.50	1.42	18
Rhamnus cathartica	5	11.9	0.00	0.42	0.04	0.43	0.01	0.50	1.36	19
Viburnum nudum	3	11.3	0.00	0.25	0.02	0.25	0.01	0.50	1.00	20
Shrubs, unidentified	2	14.9	0.00	0.17	0.02	0.22	0.01	0.33	0.72	21
Salix nigra	3	4.2	0.00	0.25	0.01	0.09	0.01	0.33	0.68	22
Sambucus canadensis	1	5.3	0.00	0.08	0.00	0.04	0.00	0.17	0.29	23
Amelanchier canadensis	1	2.0	0.00	0.08	0.00	0.01	0.00	0.17	0.27	24
Alnus serrulata	1	0.2	0.00	0.08	0.00	0.00	0.00	0.17	0.25	25
Total	**1187**	**11.6**	**0.76**	**100.00**	**8.83**	**100.00**	**2.05**	**100.00**	**300.00**	

[a] Mean basal area per tree or sapling (cm^2).

[b] Density of trees or saplings per 100 m^2.

[c] Importance value = sum of relative density, relative dominance, and relative frequency.

had fewer saplings (Figure 2). No *Populus deltoides* trees smaller than 28 cm dbh were identified during sampling. Nut-bearing tree species, including all *Quercus* and *Carya* spp., were a minor component of the floodplain forests and were represented by few young trees (Figure 2).

Acer saccharinum strongly dominated the tree community (Figure 2), especially at size classes of 20 cm and larger. Its relative dominance increased over the 150-year period we examined (Table 2). However, *A. saccharinum* was not well-represented in the seedling stratum in 1992. Despite large numbers of young trees, *Ulmus* spp. and *Fraxinus* spp. were not well-represented as mature canopy trees. However, from the 1840s to 1992, the relative dominance of *Ulmus* spp. remained relatively stable, whereas *Fraxinus* spp. declined (Table 2). Although the relative dominances of the three floodplain forest co-dominants, *A. saccharinum*, *Fraxinus* spp., and *Ulmus* spp. have changed, their combined relative dominance in UMR floodplain forests has changed little in the last 150 years. Historically these three taxa comprised about 65% of relative dominance; today they make up about 75%. *Q. bicolor* maintained a minor presence across most size classes and had low relative dominance, even in the 1840s. Early successional species that declined in relative dominance in our study area are *Salix* spp. and *Betula nigra*; *P. deltoides* had low relative dominance in both time periods. Some *Quercus* species declined, whereas others increased, although none were ever dominant in the floodplain historically (Table 2). Tree sizes today are similar to those of the presettlement forests, but present forests have fewer trees. Mean tree dbh was similar in the two time periods (Table 2).

Herbs and shrubs were measured at 305 sampling points (Table 3). The shrub stratum was dominated by *F. pennsylvanica* seedlings, followed by *Toxicodendron radicans, A. saccharinum* seedlings, *Zanthoxylum americanum*, *Cornus* spp., *Q. bicolor* seedlings, and *C. occidentalis* seedlings. *Urtica dioica* was the dominant herb, followed by *Phalaris arundinacea*, *Impatiens* spp., and *T. radicans*. The understory of these forests varies in composition, depending upon soil type, light availability, and elevation. We found the understory of most plots to be quite open; shrubs were prevalent only at sites where they are not killed by frequent floods. Elevation data were not available for the floodplain, but sites with shrubs tended to be high-elevation sites (often islands 3–10 m above average water level; M. Knutson, pers. obs.). In the closed-canopy sites *U. dioica* dominated the herb stratum. *Toxicodendron radicans* thrived in more open sites, and *P. arundinacea* dominated the herbaceous stratum in canopy gaps.

DISCUSSION

Vegetation Changes

The major long-term changes we identified in our study of floodplain forests of the UMR include lower tree density, increased relative dominance of *Acer saccharinum,* and decreased representation of

Table 2. Comparison of presettlement and current floodplain forests of the Upper Mississippi.

	1840s[a]	1992[b]
Tree Variables		
Number of points	695	314
Trees per ha	511.9	297.4
Mean tree dbh (cm)	34.5	31.8
Mean basal area per tree (m^2)	0.093	0.092
Basal area per ha (m^2)	47.603	27.405
Species Importance Values (maximum value = 100)		
Fraxinus spp.	26.8	9.8
Acer saccharinum	20.4	53.6
Ulmus spp.	16.2	13.8
Salix spp.	10.1	0.3
Betula nigra	7.5	2.3
Quercus alba	4.7	0.1
Quercus spp., other than *alba* and *bicolor*	4.1	2.2
Populus spp.	2.1	3.9
Tilia americana	1.3	1.6
Juglans spp.	0.8	—
Acer saccharum	0.8	—
Carya spp.	0.5	1.6
Celtis occidentalis	0.4	2.5
Betula papyrifera	0.3	0.1
Quercus bicolor	0.2	5.5
Morus spp.	0.1	—
Prunus spp.	0.1	—
Robinia pseudoacacia	—	0.8
Acer negundo	—	0.6

[a] Based on Moore (1988). Presettlement data from surveyors' notes circa 1840s.
[b] Present study.

Table 3. Vegetation measurements for floodplain forests in the study area, 1992.

		Mean (SE)
VEGETATION VARIABLES		
Tree dbh (cm)		31.8 (1.2)
Sapling dbh (cm)		3.6 (0.1)
Snag dbh (cm)		31.5 (1.2)
Snags per ha		35.1
Basal area per snag (m^2)		0.081
Snag basal area per ha (m^2)		2.824
Canopy cover (%)		93.2 (0.7)
Shrub cover (%)		12.8 (2.4)
Herb cover (%)		66.9 (3.4)
	Frequency (% of plots)	Mean Cover [% (SE)]
SHRUB STRATUM		
Fraxinus pennsylvanica	43.3	1.5 (0.2)
Toxicodendron radicans	26.6	5.1 (0.8)
Acer saccharinum	12.1	0.1 (0.0)
Zanthoxylum americanum	11.8	1.0 (0.2)
Cornus spp.	11.1	0.8 (0.2)
Quercus bicolor	9.5	0.1 (0.0)
Celtis occidentalis	6.6	0.3 (0.1)
HERB STRATUM		
Urtica dioica	80.3	32.5 (1.8)
Phalaris arundinacea	69.8	11.7 (1.0)
Impatiens spp.	23.3	3.2 (0.6)
Toxicodendron radicans	17.7	3.4 (0.7)

some early successional species and some hardwoods in present-day forests. Nothing conclusive could be determined regarding trends in species richness because richness is highly dependent upon sample size. However, the diminished relative dominance of many species may be just as significant in changing the overall character and ecosystem processes of the forest community as actual species loss. Once a species becomes rare, it contributes little to nutrient cycling and wildlife habitat.

The changes we identified by comparing historical with contemporary data may be affected by minor differences in methodology that are difficult to determine from the GLO records. Different GLO surveyors may have recorded data, such as minimum diameter limits, in different ways. If GLO surveyors were biased against small-diameter trees (likely), that would only increase many of the differences we observed.

Researchers working in other sections of the UMR have also found that the floodplain forest tree community has changed since presettlement times. Nelson et al. (1994) analyzed GLO survey records (circa 1815 and 1817) and GIS maps for riverine forests in Pool 26 at the confluence of the Illinois and Mississippi Rivers. They also found that *A. saccharinum* had increased in relative dominance while other species had declined. Floodplain forests in Pool 26 were reduced from 56% to 35% of the landscape. Presettlement forests in the area studied by Nelson et al. (1994) were more open (86.8 stems ha^{-1}), whereas present-day forests are more dense (489 stems ha^{-1}). An increased dominance of *A. saccharinum* and decreased presence of *Salix* spp. since the time of settlement was also found by Barnes (1997) for a major tributary of the UMR, the lower Chippewa River in Wisconsin. Other large rivers such as the upper Missouri River have experienced major changes in forest composition associated with human-induced hydrologic changes (Johnson 1992, 1994). European rivers also have undergone major ecological change associated with human development activities (Decamps et al. 1988).

Intact riparian ecosystems should exhibit the full range of elevations from deep water habitats to terrace habitats. Tree species composition at any given latitude on the UMR varies predictably with elevation above the river channel because of species differences in flood tolerance and germination requirements (Dunn 1985, Galatowitsch and McAdams 1994). Low-elevation, frequently flooded forests are dominated by *A. saccharinum*, whereas high-elevation, infrequently flooded terraces allow germination and survival of *Quercus, Juglans, Carya,* and *Celtis* species, resulting in greater tree species diversity and more habitat diversity. Flood frequency, duration, and height affect the herbaceous species composition of floodplain forests (Menges 1986). Floodplain terrace has become a critically endangered ecosystem,because virtually all floodplain terraces (approximately 3–10 m above average water level) along the UMR have been converted to agriculture or urban development. Unfortunately, no quantitative analysis of losses for different elevation zones is available. When terrace habitats are lost, so are opportunities for establishment and survival of less flood-tolerant species, such as hardwoods.

The lack of early successional tree species and a trend toward an *A. saccharinum* monoculture in the mature stages indicate problems with regeneration of these floodplain forests. Regeneration problems result from the degradation of ecosystem processes. The changes we observed may be related to hydrologic changes that affect seed dispersal, seedling establishment, and both sapling and tree survival (Yeager 1949; Hosner 1958, 1960). Historic species composition and patterns of UMR floodplain forest succession were dependent upon the hydrology and fluvial dynamics that existed prior to lock and dam construction (Peck and Smart 1986, Yin and Nelson 1995). Under former natural conditions, the river channel migrated laterally back and forth over time within its floodplain (Everitt 1968). Primary succession occurred on exposed mud flats and sandbars where *Salix* spp., *P. deltoides*, and *A. saccharinum* forests became established. These were succeeded by *Q. bicolor*, *U. americana*, and *Carya cordiformis* on terraces (Galatowitsch and McAdams 1994). The specific factors contributing to the present extreme dominance of *A. saccharinum* are unknown, but they probably include a high water table, increased flood frequency and duration, reduced channel migration, replacement of diseased *U. americana*, favorable growing conditions on abandoned agricultural land, and cutting of the forest in the 1930s prior to lock and dam construction. We hypothesize that few species, aside from *A. saccharinum,* will be able to survive the high water tables and frequent flooding that predominate in most of the present-day floodplain forests. The high mortality among many species that occurred following the 1993 floods supports this hypothesis (Yin et al. 1994, Spink and Rogers 1996).

Present-day river hydrology is constrained except during flooding, and the river is not allowed to meander laterally. As a consequence, mean water levels and the height and duration of flooding have increased (Belt 1975; Grubaugh and Anderson 1988, 1989; Lubinski et al. 1991; Sparks 1995; Yin et al. 1997). These processes severely restrict development of new mud flats. Tree species richness has been negatively affected by these changes because few of the native tree species can tolerate frequent, prolonged flooding (Hosner 1958, 1960; Nelson et al. 1994). The hardwood species such as *Q. bicolor*, *Carya cordiformis*, and *Juglans nigra* have heavy seeds that are actively dispersed by vertebrates rather than passively dispersed via air or water. Some hardwoods that also grow in adjacent dry upland habitats, such as *Q. rubra,* may have ecotypes adapted to floodplain conditions. When most terrace forests were converted to agriculture and urban development, hardwood seed sources were fragmented or lost. Regeneration of hardwood forests in the floodplain is thwarted by problems with seed availability, seed dispersal across water barriers, and seedling and sapling survival under current hydrologic conditions.

Assuming that the prevailing hydrologic and climatic conditions continue, the present mature, closed-canopy forests will probably be replaced by forests with smaller trees and more grass and shrub habitats. *Fraxinus pennsylvanica* and *Ulmus* spp. may increase in importance, based on flood tolerances and their abundance in the smaller size cohorts. *Fraxinus pennsylvanica* is a medium-sized tree with an average height at maturity of 15–18 m (Harlow et al. 1986, Burns and Honkala 1990). On good sites in our study area it may exceed average height (R. Urich, forester, U.S. Army Corps of Engineers, La Crescent, Minn., pers. com.). *Ulmus americana* achieves similar stature and now has a short life span due to Dutch elm disease. In contrast, other floodplain canopy trees attain much taller stature. *Acer saccharinum* grows to 20–27 m, *P. deltoides* to 27–33 m, and *Q. bicolor* to 20–23 m (Harlow et al. 1986, Preston 1989). Prior to Dutch elm disease, *U. americana* grew to heights of 25–34 m. Biotic competitive factors also affect floodplain forest successional patterns and species composition. *Phalaris arundinacea* is aggressive as a low-elevation terrestrial herb in the study area (Swanson and Sohmer 1978, Peck and Smart 1986, Galatowitsch and McAdams 1994). This grass invades the understory when the canopy opens and out-competes tree and shrub seedlings, thereby retarding forest succession in these openings. *Celtis occidentalis* ranked fourth in sapling importance value in our study, but this species does not tolerate flooding well. Yin et al. (1994) observed substantial mortality of *C. occidentalis* following the 1993 flood. It is unlikely that this species will ever attain dominance in the floodplain under current hydrologic conditions.

Plant diversity in the UMR floodplain is relatively high despite hydrologic conditions that potentially limit plant growth. Others researchers that have comprehensively surveyed herbaceous vegetation in several floodplain habitats have found even more species than we did. Swanson and Sohmer (1978) comprehensively studied vascular plants in Pool 8 of the UMR and found 482 species. Galatowitsch and McAdams (1994) listed 591 species compiled from published reports on UMR vegetation.

Potential Effects on Wildlife

Because floodplain forests differ greatly in plant species composition from adjacent upland forests, losses and degradation of habitat quality could pose serious problems for wildlife, especially birds, that depend upon these resources for survival. The uplands adjacent to our study area were historically oak–hickory forests. Due to fire suppression, the uplands are now dominated by *Acer saccharum*, *Quercus rubra,* and *Carya* spp. (Braun 1950) and thus constitute quite different habitats than the floodplain forests. Floodplains are highly productive habitats with abundant food resources, including aquatic invertebrates and fish.

Diversity in floodplain forest bird communities is high. In our study area, bird abundance in the floodplain is double that of adjacent upland forests (Knutson et al. 1996). In addition, floodplain forests in the Midwest provide habitat for some species at risk of population decline that are not found in other habitats (Knutson et al. 1996). The changes we identified in floodplain forests could have implications for forest-nesting birds because vertical vegetation structure and heterogeneity are important for some species, especially warblers (MacArthur 1958, 1964). Birds nesting in the upper canopy of UMR forests include herons and egrets (family Ardeidae), bald eagles (*Haliaeetus leucoceph-*

alus), red-shouldered hawks (*Buteo lineatus*), great horned owls (*Bubo virginianus*), flycatchers (family Tyrannidae), blue-gray gnatcatchers (*Polioptila caerulea*), yellow-throated vireos (*Vireo flavifrons*), warbling vireos (*V. gilvis*), red-eyed vireos (*V. olivaceus*), yellow-throated warblers (*Dendroica dominica*), cerulean warblers (*D. cerulea*), and Baltimore orioles (*Icterus galbula*) (Knutson 1995, Knutson and Klaas 1997). The cerulean warbler is a species of management concern (Office of Migratory Bird Management 1995) that is experiencing steep population declines both in the region and in North America (Hamel 1996, Robbins et al. 1992). One hypothesis that explains their decline on the UMR is the loss of mature *U. americana* trees that were taller and had stronger structure (larger limbs) at high canopy levels than *A. saccharinum* trees. We observed that cerulean warblers tend to perch in the tallest trees available in a forest patch. Detailed habitat studies elsewhere confirm their preference for tall, old-growth trees. They also prefer a well-developed subcanopy and understory (Robbins et al. 1992). Many members of the UMR bird community are heavily dependent on the presence of tall-canopied forests for breeding and feeding and will be adversely affected if a large-scale change toward a more open canopy and small-stature forest occurs.

Late-successional forests with many large snags are important to cavity-nesting birds, including wood ducks (*Aix sponsa*), hooded mergansers (*Lophodytes cucullatus*), barred owls (*Strix varia*), pileated woodpeckers (*Dryocopus pileatus*), great crested flycatchers (*Myiarchus crinitus*), and prothonotary warblers (*Protonotaria citrea*) (Knutson 1995). At least 23 species of cavity-nesters breed in the UMR forests (Knutson 1995). Understory shrubs and vines, abundant in floodplain forests that experience infrequent flooding, also provide important wildlife habitat. We found that American redstarts (*Setophaga ruticilla*) frequently nested in *T. radicans* and *Vitis riparia* entwined in mature trees, and yellow warblers (*Dendroica petechia*) and indigo buntings (*Passerina cyanea*) nested in *Salix* spp. thickets and other shrub habitats (M. Knutson, unpubl. data). This demonstrates the importance in the floodplain of higher elevation sites that support a rich shrub community (Knutson 1995).

While floodplains are naturally fragmented habitats, there is some evidence that corridor width is important in maintaining the full complement of floodplain bird species (Stauffer and Best 1980, Decamps et al. 1987, Knutson et al. 1996). Any restoration efforts should consider how to maximize not only the total area of floodplain forests, but how to create large, contiguous complexes of floodplain forest that are as wide as possible.

Birds are not the only wildlife that depend upon habitat provided by UMR floodplain forests. Remnant undeveloped terrace habitats along the UMR are rich in reptile and amphibian species (R. King, biologist, Necedah National Wildlife Refuge, Necedah, Wisconsin, pers. com.). Some species found in floodplain forest habitats, such as Blandings turtle (*Emydoidea blandingii*) and wood turtle (*Clemmys insculpta*), are of management concern (Coffin and Pfannmuller 1988). The eastern massasauga rattlesnake (*Sistrurus catenatus catenatus*) prefers floodplain forests in this region, and recent radio-telemetry studies indicate that adjacent dry, open habitats (similar to historic oak savannas) are important for reproductive activities of this species (R. King, pers. comm.). Many documented sightings of massasaugas in the region have been recorded near the mouths of major tributaries to the Upper Mississippi River (Oldfield and Moriarty 1994, Nordquist et al. 1994). This species is extremely rare and is listed as threatened, endangered, or of special concern in all states adjacent to the UMR. Floodplain forests of the UMR basin may constitute some of the last remaining refuges for this species in the region.

Management and Research Implications

Primary management actions should focus on preventing additional losses of floodplain forests on the UMR and restoring diversity to the remaining forests. Forest management and research should focus on how to facilitate forest succession leading to a diversity of tree species composition, structure, and age, and how to minimize forest fragmentation and maximize corridor width. Models are needed for identifying the suitability of specific locations for different forest management options. These models could incorporate factors such as soil type, frequency and duration of flooding (elevation), and fragmentation. Detailed GIS maps of existing and historic land cover are already available for most reaches of the UMR. Better estimates of the extent of loss of floodplain forests are needed, not only along the Upper Mississippi River, but also on other riparian systems in the Midwest and elsewhere. We also need to know how important floodplain forests are for a range of plant and animal species.

Restoration of some floodplain forests in the elevation range of 3–10 m above average water level could promote a full complement of floodplain forest biotic communities in the UMR landscape. Such sites could support a more diverse tree community due to reduced flooding frequency and a lower water table. More diversity in the tree community means more diversity in the wildlife community. Lowering average water levels across large areas of the UMR long enough to allow trees to mature will be necessary to restore the existing forests. This will be difficult, given navigation and recreational boating demands. Another option is to restore forests on floodplain terraces currently used for agricultural production where those activities are subject to frequent flooding. However achieved, restoration efforts could increase the quantity and integrity of floodplain forests as wildlife habitats on the Upper Mississippi River.

ACKNOWLEDGMENTS

Funding for this study was provided by the U.S. Geological Survey Biological Resources Division (Patuxent Wildlife Research Center, Branch of Migratory Birds Research); Iowa State University; U.S. Fish and Wildlife Service (Region 3 Nongame Program); and the Minnesota Department of Natural Resources Nongame Program. Thanks to Louis Best, Brent Danielson, Kirk Moloney, Thomas Jurik, Yao Yin, Randy Urich, and Fred Meyer for reviewing earlier versions of the manuscript. Deborah Lewis assisted with the identification of herbarium specimens. Technical assistance was provided by R. Michael Erwin, Ingrid Moore, Brian Collins, Tom Pehowski, Vance Polton, Holly Dick, Pam Heidenreich, and Brenda VanBeek. This is Journal Paper No. J-16620 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Project No. 3137 and supported by Hatch Act and State of Iowa funds.

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Appendix A. Plants identified from Upper Mississippi River forests in 1992.

Common Name	Scientific Name[a]	Family
Boxelder	*Acer negundo* L.	Aceraceae
Silver maple	*Acer saccharinum* L.	Aceraceae
Common yarrow	*Achillea millefolium* L. @	Asteraceae
Red baneberry	*Actaea rubra* (Aiton) Willd.	Ranunculaceae
Purple giant hyssop	*Agastache scrophulariaefolia* (Willd.) Kuntze	Lamiaceae
Alder	*Alnus serrulata* (Aiton) Willd.	Betulaceae
Eastern serviceberry	*Amelanchier canadensis* (L.) Medikus	Rosaceae
False indigo	*Amorpha fruticosa* L.	Fabaceae
Hog-peanut	*Amphicarpaea bracteata* (L.) Fern. @	Fabaceae
Canadian anemone	*Anemone canadensis* L. @	Ranunculaceae
Rock-cress	*Arabis lyrata* L. @	Brassicaceae
Green dragon	*Arisaema dracontium* (L.) Schott. @	Araceae
Swamp-milkweed	*Asclepias incarnata* L.	Asclepiadaceae
Hoary alyssum	*Berteroa incana* (L.) DC @	Brassicaceae
River birch	*Betula nigra* L.	Betulaceae
Paper birch	*Betula papyrifera* var. *papyrifera* Marshall	Betulaceae
Birch	*Betula* spp.	Betulaceae
Beggar-ticks	*Bidens* spp.	Asteraceae
Bog-hemp (false nettle)	*Boehmeria cylindrica* (L.) Sw.	Urticaceae
Chinese mustard	*Brassica juncea* (L.) Czernj. @	Brassicaceae
Black mustard	*Brassica nigra* L.	Brassicaceae
Pennsylvania bitter-cress	*Cardamine pensylvanica* Muhl. @	Brassicaceae
Sedge	*Carex intumescens* Rudge. @	Cyperaceae
Bitternut-hickory	*Carya cordiformis* (Wang.) K.Koch.	Juglandaceae
Hackberry	*Celtis occidentalis* L. @	Ulmaceae
Buttonbush	*Cephalanthus occidentalis* L. @	Rubiaceae
Goosefoot (lamb's quarters)	*Chenopodium album* L. *	Chenopodiaceae
Spotted cowbane (water-hemlock)	*Cicuta maculata* L. @	Apiaceae
Knob-styled (silky) dogwood	*Cornus amomum* Mill. @	Cornaceae
Flowering dogwood	*Cornus florida* L.	Cornaceae
Northern swamp (gray) dogwood	*Cornus racemosa* Lam. @	Cornaceae
Round-leaved dogwood	*Cornus rugosa* Lam.	Cornaceae
Red osier-dogwood	*Cornus sericea* L.	Cornaceae
Honewort	*Cryptotaenia canadensis* (L.) DC. @	Apiaceae
Common dodder	*Cuscuta gronovii* Willd.	Cuscutaceae
Flatsedge	*Cyperus* spp.	Cyperaceae
Tick-trefoil	*Desmodium* spp.	Fabaceae
Wild cucumber	*Echinocystis lobata* (Michx.) T. & G.	Curcurbitaceae
Common horsetail	*Equisetum arvense* L. @	Equisetaceae
Common scouring rush	*Equisetum hyemale* L. @	Equisetaceae
Philadelphia daisy	*Erigeron philadelphicus* L.	Asteraceae
Wahoo	*Euonymus atropurpureus* Jacq. @	Celastraceae
Leafy spurge	*Euphorbia esula* L. *@	Euphorbiaceae
Wild strawberry	*Fragaria virginiana* Duchn.	Rosaceae
Green ash	*Fraxinus pennsylvanica* Marsh. @	Oleaceae
Bluntleaf-bedstraw	*Galium obtusum* Bigelow. @	Rubiaceae

Common Name	Scientific Name[a]	Family
Wild geranium	*Geranium maculatum* L.	Geraniaceae
Ground ivy	*Glechoma hederacea* L. *	Lamiaceae
Hedge-hyssop	*Gratiola virginiana* L. @	Scrophulariaceae
Sunflower-everlasting	*Heliopsis helianthoides* (L.) Sweet @	Asteraceae
Eastern waterleaf	*Hydrophyllum virginianum* L.	Hydrophyllaceae
Winterberry	*Ilex verticillata* var. *padifolia* (Willd.) T. & G. @	Aquifoliaceae
Touch-me-not (jewel-weed)	*Impatiens* spp.	Balsaminaceae
Southern blue flag	*Iris virginica* L. var. *shrevei* (Small) E. Anderson @	Iridaceae
Juniper	*Juniper* spp.	Cupressaceae
Wood nettle	*Laportea canadensis* (L.) Wedd.	Urticaceae
Motherwort	*Leonurus cardiaca* L. @	Lamiaceae
Annual toadflax	*Linaria canadensis* (L.) Dum.-Cours. @	Scrophulariaceae
Honeysuckle	*Lonicera* spp.	Caprifoliaceae
Bugle-weed (horehound)	*Lycopus* spp.	Lamiaceae
Fringed loosestrife	*Lysimachia ciliata* L. @	Primulaceae
Moneywort	*Lysimachia nummularia* L. *@	Primulaceae
Swamp-loosestrife	*Lysimachia thyrsiflora* L.	Primulaceae
Field-mint	*Mentha arvensis* L.	Lamiaceae
Allegheny monkey-flower	*Mimulus ringens* L. @	Scrophulariaceae
Heart-leaved umbrella-wort	*Mirabilis nyctaginea* (Michx.) MacMillan @	Nyctaginaceae
White mulberry	*Morus alba* L. @	Moraceae
Water scorpion-grass (forget-me-not)	*Myosotis scorpioides* L. @	Boraginaceae
Sensitive fern	*Onoclea sensibilis* L.	Onocleaceae
Royal fern	*Osmunda regalis* L. @	Osmundaceae
Wood-sorrel	*Oxalis stricta* L.	Oxalidaceae
Pellitory	*Parietaria pensylvanica* Muhl. @	Urticaceae
Grape-woodbine	*Parthenocissus vitacea* (Knerr) A. Hitchc. @	Vitaceae
Reed canary-grass	*Phalaris arundinacea* L.	Poaceae
Phlox	*Phlox* spp.	Polemoniaceae
Sycamore	*Platanus occidentalis* L.	Plantanaceae
Lady's thumb	*Polygonum persicaria* L.	Polygonaceae
Smartweed	*Polygonum* spp.	Polygonaceae
Cottonwood	*Populus deltoides* Marsh.	Salicaceae
Old-field five-fingers	*Potentilla simplex* Michx. @	Rosaceae
Black cherry	*Prunus serotina* Ehrh. @	Rosaceae
White oak	*Quercus alba* L.	Fagaceae
Swamp white oak	*Quercus bicolor* Willd.	Fagaceae
Pin oak	*Quercus palustris* Muench.	Fagaceae
Northern red oak	*Quercus rubra* L.	Fagaceae
Common buckthorn	*Rhamnus cathartica* L. *@	Rhamnaceae
European alder-buckthorn	*Rhamnus frangula* L. @	Rhamnaceae
Sumac	*Rhus* spp.	Anacardiaceae
Gooseberry	*Ribes* spp.	Grossulariaceae
Black locust	*Robinia pseudo-acacia* L. *	Fabaceae
Smooth rose	*Rosa blanda* Aiton. @	Rosaceae
Raspberry	*Rubus* spp.	Rosaceae
Cutleaf coneflower	*Rudbeckia laciniata* L. @	Asteraceae

Common Name	Scientific Name[a]	Family
Red sorrel	*Rumex acetosella* L. @	Polygonaceae
Swamp-dock	*Rumex verticillatus* L. @	Polygonaceae
Arrow-head	*Sagittaria* spp.	Alismataceae
Sandbar willow	*Salix exigua* Nutt. @	Salicaceae
Black willow	*Salix nigra* Marsh.	Salicaceae
Common elder	*Sambucus canadensis* L. @	Caprifoliaceae
Heart-leaved groundsel	*Senecio aureus* L. @	Asteraceae
Single-stemmed groundsel	*Senecio integerrimus* Nutt. @	Asteraceae
White campion	*Silene latifolia* Poiret. @	Caryophyllaceae
Catbrier	*Smilax herbacea* L. var. *lasioneura* (Small) Rydb. @	Smilacaceae
Bristly greenbrier	*Smilax hispida* Muhl.	Smilacaceae
Bittersweet (nightshade)	*Solanum dulcamara* L.	Solanaceae
Goldenrod	*Solidago* spp.	Asteraceae
Hedge-nettle	*Stachys palustris* L. @	Lamiaceae
Smooth hedge-nettle	*Stachys tenuifolia* Willd. @	Lamiaceae
Chickweed	*Stellaria* spp.	Caryophyllaceae
Dandelion	*Taraxacum officinale* Weber.	Asteraceae
Purple meadow-rue	*Thalictrum dasycarpum* Fischer & Ave'-Lall. @	Ranunculaceae
Basswood	*Tilia americana* L.	Tiliaceae
Common poison-ivy	*Toxicodendron radicans* var. *negundo* (Greene) Reveal	Anacardiaceae
Smooth spiderwort	*Tradescantia ohiensis* Raf. @	Commelinaceae
Spiderwort	*Tradescantia virginiana* L.	Commelinaceae
Fistulous goat's beard	*Tragopogon dubius* Scop. @	Asteraceae
Trillium	*Trillium* spp.	Liliaceae
Cat-tail	*Typha* spp.	Typhaceae
Elm	*Ulmus* spp.	Ulmacae
Tall nettle	*Urtica dioica* L. var *procera* (Muhl.) Wedd. @	Urticaceae
Bellwort	*Uvularia grandiflora* J. E. Smith	Liliaceae
Hoary vervain	*Verbena stricta* Vent. @	Verbenaceae
Nannyberry	*Viburnum lentago* L. @	Caprifoliaceae
Withe-rod (wild raisin)	*Viburnum nudum* L. var. *cassinoides* (L.) T. & G.	Caprifoliaceae
Viburnum, other	*Viburnum* spp.	Caprifoliaceae
Dooryard-violet	*Viola sororia* Willd. @	Violaceae
River-bank grape	*Vitis riparia* Michx.	Vitaceae
Common prickly ash	*Zanthoxylum americanum* Mill. @	Rutaceae

[a] Names follow Gleason and Cronquist 1991.

* species not indigenous to North America

@ voucher specimen deposited in the Ada Hayden Herbarium (ISC), Department of Botany, Iowa State University.