

Impact of a severe flood on canopy composition, tree regeneration, and ground flora of the lower floodplain of gallery forests along the Red River, Canada

Abstract

The 1997 Red River flood afforded a valuable opportunity for studying the impact of an infrequent severe disturbance on gallery forests. In 1997 and 2002 we sampled two sites protected and two sites unprotected by a flood control structure near Winnipeg, Manitoba, Canada using three 150 m transects in the lower floodplain (n = 45 quadrats per site). The mature canopy of unprotected sites consisted of *Fraxinus pennsylvanica* Marsh. and *Ulmus americana* L. at low cover whereas protected sites contained five tree species. Regeneration data suggest *F. pennsylvanica* will continue to dominate in unprotected sites, with treefall providing opportunities for pioneer flood specialists like *Salix amygdaloides* Anderss. Fewer gap openings occurred in protected sites, in which *Acer negundo* L. and *F. pennsylvanica* will likely become co-dominants.

Understorey taxa normally able to survive the moderate disturbance associated with seasonal inundation of the lower floodplain of protected sites succumbed to the harsh conditions in the unprotected sites. Many were knocked back or eliminated by 2002, with greater reductions in richness and diversity in unprotected sites. Ruderals were promoted in unprotected sites but most were less prominent by 2002. Although several taxa, e.g., *Vitis riparia* Michx. and *Bidens frondosa* L. had significantly higher cover in protected sites by 2002, *Xanthium strumarium* L. and *Polygonum*

Isobel Waters¹, Erin Essery, Tracy Ruta, Jennifer Shay
Dept. of Biological Sciences, University of Manitoba, Winnipeg, Canada R3T 2N2

¹ email - waters@cc.umanitoba.ca

amphibium L. were the only understorey species with significantly higher cover in the unprotected sites. Correspondence analysis indicated flood protection generated differing trajectories, with site differences contributing to variable successional outcomes.

Introduction

Riverbottom gallery forests are a unique biological community within the North American prairie ecoregion (Keammerer et al., 1975). As linear landscape elements occurring on alluvial deposits along riverbanks, they are subject to periodic inundation. In drier western regions, gallery forests are dominated by *Salix* spp. (willow) and *Populus deltoides* Bart. ex Marsh. (eastern cottonwood) (Kindscher and Holah 1998). In North Dakota and Manitoba, these species are early successional dominants along exposed banks and new meanders, but are replaced by hardwoods of differing flood tolerance on upper terraces (Keammerer et al., 1975), coulees, and ox-bows cut-off from former channels. The higher precipitation and Riverdale silty clay soils of eastern prairie sites (Ehrlich et al., 1953) support gallery forests with floristic similarities to eastern deciduous forests (Essenberg, 1991).

The extent of gallery forests prior to European occupation is unclear (Kindscher and Holah, 1998). Fire suppression likely caused expansion in some regions whereas exploitation for fuel and construction depleted them in the immediate vicinity of human settlements. Agricultural and urban encroachments further threaten their persistence. The floristic composition of gallery forests along the Missouri River and its tributaries has been studied in North Dakota (Wikum and Wali, 1974; Keammerer et al., 1975; Johnson et al., 1976), South Dakota (Wilson, 1970), Illinois (Hosner and Minckler, 1963; Bell and del Moral, 1977) and Kansas (Abrams, 1986). Less is known about this ecosystem along the Red River in Canada, in spite of its declining status and importance of the Red River flyway for continental bird migration.

Floods are an integral part of the community's dynamics.

Their effects result from temporal variation in the flood cycle from frequent yearly events to 100+ y floods (Franceschi et al., 2000; Ward et al., 2002) and from varying flood intensity associated with depth, duration, and flow rate (Casanova and Brock, 2000; Kozlowski, 2002). Experimental studies in natural communities (Malecki et al., 1983) have documented long term effects of flooding cycles on community structure and succession (Greenwald and Brubaker, 2001), but there is less understanding of short term impacts. These are equally vital, particularly given the importance of post-flooding tree regeneration to succession (Jones et al., 1989; Turner et al., 1998).

Flooding tolerance includes physiological factors such as anoxia sensitivity (Bell, 1974; Blom, 1999), within-species genetically based ecotypic differences, and plastic differences during development (Jones et al., 1989). Progressively less tolerant woody (Keammerer et al., 1975; McLeod et al., 2000) and herbaceous (Menges, 1986) species increase in abundance with distance from the water's edge. Infrequent severe floods stress less tolerant species by inundating areas further from the bank and increase the mechanical stress and duration of inundation for more tolerant species. Reputedly

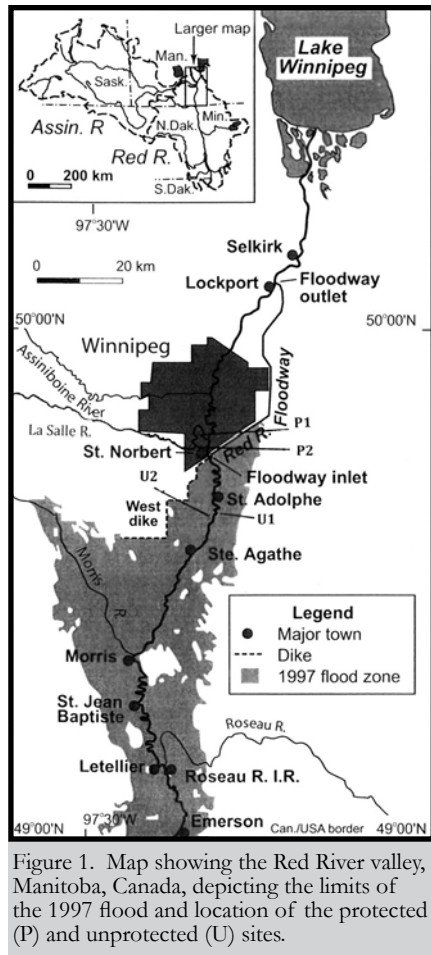


Figure 1. Map showing the Red River valley, Manitoba, Canada, depicting the limits of the 1997 flood and location of the protected (P) and unprotected (U) sites.

tolerant species can thus be vulnerable to damage during severe floods. The fate of understorey species varies from extirpation to opportunistic increases in relative abundance as a result of reduced competition. Succession models predict that this dynamic community response to flooding will have a powerful influence on the site's recovery trajectory (Turner et al., 1998).

Control structures in the United States and Canada have reduced flooding incidence, duration, and depth. Dams and reservoirs in the U.S. have permanently flooded many gallery forests (Keammerer et al., 1975) while depriving downstream forests of the benefits of periodic inundation (Kozlowski, 2002). In the Canadian portion of the Red River valley, dikes provide some protection around larger towns, and Winnipeg is protected by a floodway (48 km long, 210-305 m wide, and 9.1 m deep) that diverts excess flows around the eastern side of the city (Figure 1; Burn and Goel, 2001). Flood flow rates and depths within the city have been substantially reduced (Manitoba Water Commission, 1998).

The 1997 Red River flood was classified as extreme with an estimated return time of 144 y (Burn and Goel, 2001). This event provided a rare opportunity to assess the response of the gallery forest to an infrequent severe disturbance (Turner et al., 1998). We compared the flood's short term impacts on the lower floodplain of unprotected upstream sites with protected sites downstream, both in the immediate aftermath of the flood in the fall of 1997, and five years later in 2002. We hypothesized that differences in flooding effects on survival and growth of woody and herbaceous species between protected and unprotected sites altered the forest's post-flooding successional trajectory.

Methods

Site history and description

The Red River (known in the U.S. as the Red River of the North) rises in Minnesota, drains an area of 270,000 km², and flows for 880 km over the relict bed of glacial Lake Agassiz to

Lake Winnipeg (Brooks and Nielsen, 2000). It frequently overflows its banks, fed by snowmelt and spring rains, with inundations lasting for several weeks and covering an extensive area (Brooks and Nielsen, 2000). There were extreme floods in 1826 and 1852, and the 1997 event (peak flow $4587 \text{ m}^3 \text{ s}^{-1}$) was the largest flood since 1852 (Burn and Goel, 2001), inundating 1836 km^2 and with a maximum width of 40 km (Haque, 2000) (Figure 1). Flood levels peaked at the Winnipeg floodway inlet on May 3-4, but because of the low mean valley gradient of 10 cm/km (Brooks and Nielsen, 2000), many areas in the basin were under 2-4.5 m of water for approximately three weeks (Rasid et al., 2000).

Southern Manitoba has a continental climate with long cold winters and short warm summers. The Winnipeg region has a mean annual temperature of 2.6° C and a mean annual precipitation of 513.7 mm (Environment Canada, 1994). The vegetation of the Red River forests is designated as “temporarily flooded cold-deciduous (alluvial bottomland hardwoods)” (Greenall, 1996). Mature forests are dominated by *Fraxinus pennsylvanica* (green ash), *Ulmus americana* (American elm), and *Acer negundo* (box elder) on lower reaches, with *Quercus macrocarpa* Michx. (burr oak) and *Populus tremuloides* Michx. (quaking aspen) on higher terraces. *Tilia americana* L. (American basswood) is a common associate in mid terrace regions.

Four sites were chosen: two upstream (U-unprotected) and two downstream (P-protected) of the floodway (Figure 1). Site U1 was on the east bank of the Red River near St. Adolphe; site U2 was on the west bank near the University of Manitoba’s Glenlea Research station. Although differing in microtopography, both unprotected sites had sparse forest canopies and large amounts of coarse woody debris including many dead trees and branches (Figure 2). Some of this debris was residual from a moderate flood ($3058 \text{ m}^3 \text{ s}^{-1}$) that occurred in 1996 (Burn and Goel, 2001).

The protected sites were on the east bank of the La Salle River, a small tributary flowing into the Red south of its junction



Image: Tracy Ruta

Figure 2. Both unprotected sites accumulated large amounts of woody debris (U1 1997). Photo taken in 1997.

with the Assiniboine. It has no independent control structure, but the La Salle's flow rates within the city are similarly reduced by the floodway. Both sites had closed canopies and little coarse woody debris. Protected sites on the Red River were unsuitable because the forest canopy has been substantially altered or eliminated within the floodway. Despite the floodway, the lower reaches of the protected sites experienced minor flooding albeit at lower flow rates and depth than the unprotected sites. At the 1997 flood peak, flow rates within the floodway were $2265 \text{ m}^3 \text{ s}^{-1}$, approximately 50% of unregulated levels (Haque, 2000). Depth was 752 feet geodetic compared with 773 feet geodetic upstream (Manitoba Water Commission, 1998) in the vicinity of the unprotected sites. Water levels also receded faster in protected sites, although we could not measure depth on the sites during the flood. Because even the highest terraces of the protected sites

were flooded in 1997, they could not serve as a nonflooded control. Thus, our comparison was not between flooded versus nonflooded sites, but rather between sites protected and unprotected from an extreme flooding event.

Sampling and data analysis

At each site we established three parallel 150 m transects at 5 m, 15 m and 25 m from the channel. Along each transect we randomly placed fifteen 1 m \times 2 m quadrats with their long axis perpendicular to the river. In each quadrat percent cover of all understorey species and bare ground was estimated to the nearest 5% in 1997 and the nearest 1% in 2002. Nomenclature follows Kartesz (1994).

In 1997 mature tree cover was estimated on a rank scale of 0-3 for all species combined; in 2002 cover of mature trees with CBH (circumference at breast height) \geq 10 cm was estimated for each species. To facilitate comparison, the 1997 ranks were transformed by equating a rank of 3 to 100%; 2 to 67% and 1 to 33%. Mean cover was calculated for each understorey species at each site in both years. Analysis of variance ($P = 0.05$) was performed using Data Desk 4.1 (Data Descriptions, 1993) on the 2002 data. Protection from severe flooding was designated as the main treatment variable. Differences due to site and distance from the river's edge were also tested. Although this variable reflects elevation differences and hence flooding depth in locales with steep valley profiles, the Red River's shallow valley slope of 10 cm km⁻¹ (Brooks and Nielsen, 2000) makes distance from the river relatively uninformative, as Turner et al. (2004) observed along the Wisconsin river.

Species richness (S) was calculated as the number of species per site. Shannon's diversity index (H) (Hill, 1973) was calculated using mean relative cover; evenness (J) was derived as H/H_{\max} where $H_{\max} = \ln S$. Due to the influence of trace species on diversity measures (Hill, 1973), the proportion of trace species (P_{tr}) was calculated based on a mean cover $< 0.05\%$. We used correspondence analysis (CA) on species cover values to compare

Table 1. Mean cover of mature canopy trees (CBH > 10 cm) in 2002 and mean cover of seedlings and saplings (CBH < 10 cm) in protected (P) and unprotected (U) sites along the Red River in 1997 and 2002.

Tree species	Mature canopy 2002			Seedlings and saplings					
	P	U	P-value	1997			2002		
	P	U	P-value	P	U	P-value	P	U	P-value
<i>Acer negundo</i>	*3.6b	0a	0.03	1.6a	1.3a	0.82	0.4a	0.03a	0.24
<i>Fraxinus pennsylvanica</i>	2.7a	8.7b	0.03	11a	3.8a	0.59	1.8a	1.8a	0.98
<i>Quercus macrocarpa</i>	7.6b	0a		0.3a	0.01a	0.11	0.1a	0a	0.19
<i>Salix amygdaloides</i>	0.8a	0a	0.25	0	0	-	0a	0.2b	0.02
<i>Ulmus americana</i>	38.7b	6.3a		12.9a	1.1a	0.07	0.9b	0.04a	0.01
**Total tree cover (2002)	53.4	15.1		25.7	6.1		3.9	2	

*Results are shown for combined sites; means (n = 90 quadrats) followed by the same letter do not differ significantly at the P = 0.05 level (2002).
**Canopy cover of individual tree species was not recorded in 1997.

overall community response, with chord distance as the association measure (Podani, 1995). Similarity of understorey species composition between sites is indicated by their relative position in multivariate space. Distance between sites between years represents their successional trajectories.

Results

Canopy cover was substantially greater in the protected sites. Five species were present, with *Ulmus americana* dominant (Table 1). Total tree canopy cover was unchanged in protected sites between 1997 and 2002 (50% vs. 53.4%), but declined in unprotected sites from 26.7% to 15.1%. There were many dead fallen trees in the unprotected sites. *Fraxinus pennsylvanica* was the sole species in the U1 canopy by 2002, and it was the one tree species with significantly higher cover (P = 0.03) in unprotected (8.7%) than protected sites (2.7%) (Table 1).

In the regenerating tree stratum, *Ulmus americana* was the only species with significantly higher cover (P = 0.01) of seedlings

Table 2. Mean canopy cover (% +/- 1 S.D.) of selected understorey species in protected (P) and unprotected (U) sites in 1997 and 2002.

Life form	Species	1997		2002		P-value
		P	U	P	U	
Shrub	<i>Amelanchier alnifolia</i>	0.3	0.5	0	0	-
	<i>Corylus americana</i>	0.9	0	0	0	-
	<i>Crataegus chrysoarpa</i>	0.01	0.01	0.9b	0a	0.004
	<i>Lonicera</i> spp.	1.35	0	0	0	-
	<i>Rosa acicularis</i>	4.1	1.7	0.6b	0a	0.01
Woody vine	<i>Salix bebbiana</i>	0.6	5.5	0	0	-
	<i>Parthenocissus quinquefolia</i>	0.6	0.9	0.3a	0.01a	0.17
	<i>Toxicodendron radicans</i>	1	0.5	0.1a	0a	0.32
	<i>Vitis riparia</i>	0.5	0.5	13.1b	0.02a	-
		2.9	3.7	0	0	-
Perennial herb vine	<i>Amphicarpaea bracteata</i>	11.6	2.2	0	0	-
	<i>Menispermum canadense</i>	4.3	0.4	0.6b	0a	0.002
	<i>Smilax herbacea</i>	0	0.3	0	0	-
Annual vine	<i>Echinocystis lobata</i>	4.3	0.5	0.1b	0.05a	0.05
Perennial graminoid	<i>Elytrigia repens</i>	14.2	5.1	6.1a	5.3a	0.61
	<i>Carex</i> spp.	0.6	0.01	2.3b	0a	0.02
	<i>Elymus virginicus</i>	0.6	3	0	0	-
	<i>Phalaris arundinacea</i>	0.4	0	1.3a	0.4a	0.07
	<i>Poa</i> sp.	1.1	3	0	0	-
Annual graminoid	<i>Echinochloa crus-galii</i>	1.1	3	0	0	-
Perennial forb	<i>Anemone canadensis</i>	1.1	0.05	0.05a	0a	0.16

Means followed by the same letter did not differ significantly at the $p=0.001$ level in the specified year.

<i>Arctium lappa</i>	0.7	0.2	0.4a	0a	0.15
<i>Artemisia biennis</i>	0.1	2.6	0a	0.8a	0.19
<i>Cirsium arvense</i>	0	0.2	1.6b	0.2a	0.001
<i>Galium triflorum</i>	2.3	0	0	0	-
<i>Laportea canadensis</i>	0.8	8.5	0	0	-
<i>Polygonum amphibium</i>	0.01	2.2	0a	4.4b	0.0002
<i>Argentina anserina</i>	2.1	0.01	0	0	-
<i>Rumex sp.</i>	1.9	2.2	1.6a	1.5a	0.88
<i>Scutellaria lateriflora</i>	0	2.2	0.2a	0.01a	0.06
<i>Maianthemum canadense</i>	1.3	0.8	0	0	-
<i>Sonchus arvensis</i>	1.4	0.7	0	0	-
<i>Stachys palustris</i>	1.7	4.4	0.6b	0a	0.02
<i>Taraxacum officinale</i>	0.4	2.9	0.01a	0a	0.16
<i>Thalictrum spp.</i>	1.8	2.9	1.3b	0a	-
<i>Urtica dioica</i>	0.7	0	0.05a	0a	0.09
<i>Bidens frondosa</i>	8	9.3	14.0b	2.2a	-
<i>Chenopodium album</i>	1.6	1.4	0.5b	0.01a	0.003
<i>Medicago lupulina</i>	3.9	0.1	0.01a	0.01a	0.86
<i>Oxalis stricta</i>	3.9	0.1	2.9b	0.01a	0.01
<i>Xanthium strumarium</i>	1.7	13	0.6a	3.9b	-
Bare ground	48.4	55.1	44.1a	78.6b	-

*Results are shown for combined sites; means ($n = 90$) followed by the same letter do not differ significantly at the $P = 0.05$ level (2002).

and saplings in protected sites in 2002 (Table 1). *Fraxinus* cover declined but by 2002 it was the only tree with regeneration cover greater than 1% (Table 1), with no differences between protected and unprotected sites. *Acer negundo* and *Q. macrocarpa* seedlings and saplings were a minor presence in protected sites. *Salix amygdaloides* (peach-leaved willow) regeneration was not apparent in 1997 but by 2002 it had low (0.2%) but significantly higher cover ($P = 0.02$) in unprotected sites (Table 1).

There was significantly more bare ground ($P < 0.0001$) in unprotected (78.6%) than protected sites (44.1%). By 2002, understorey cover was greater in protected sites including annual forbs, which had higher cover in unprotected sites in 1997 (Table 2). The predominance of bare ground led us to consider a species with a mean cover as low as 5-10% as a “high” cover species.

Shrubs were damaged in all sites but more so in unprotected sites. Several woody species e.g., *Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roemer (serviceberry) present in protected sites in 1997 were either absent or reduced in cover by 2002. *Rosa acicularis* Lindl. (prickly rose), *Crataegus chrysoarpa* Ashe (hawthorn) and *Vitis riparia* Michx. (riverbank grape) retained significantly higher cover in protected sites ($P = 0.01$, $P = 0.004$). Whereas *V. riparia* increased in cover in the protected sites in 2002, it declined sharply in unprotected sites. In contrast, several herbaceous perennial vines with moderate cover in 1997 in protected sites, e.g., *Menispermum canadense* L. (Canada moonseed) were reduced or eliminated at all sites in 2002. Only *Smilax herbacea* L. (carrion flower) persisted at low (0.6%) albeit significantly higher cover in protected sites ($P = 0.002$) (Table 2).

Perennial graminoids had higher cover in protected sites in 1997, but declined substantially by 2002. In 2002 cover of *Carex* spp., largely *C. atherodes* Spreng. (awned sedge), did not differ between protected and unprotected sites, whereas *Elytrigia repens* (L.) Desv. ex B. D. Jackson (quackgrass) was higher in protected sites ($P = 0.05$) (Table 2). Both *Elymus virginicus* L. (wild rye) and *Poa* spp. (bluegrass) increased in protected sites in 2002 (Table 2).

Table 3. Community measures of understorey vegetation in protected (P) and unprotected (U) sites in 1997 and 2002.

Measure	1997			1997		
	P1	P2	Mean	U1	U2	Mean
Richness (S)	57.0	49.0	53.0	51.0	49.0	50.0
*Shannon's diversity (H)	3.2	3.0	3.1	3.1	2.9	3.0
Shannon's evenness (J)	0.8	0.8	0.8	0.8	0.8	0.8
**PTr (%)	12.3	12.2	12.3	11.8	22.5	17.1
Measure	2002			2002		
	P1	P2	Mean	U1	U2	Mean
Richness (S)	25.0	26.0	25.5	18.0	16.0	17.0
*Shannon's diversity (H)	2.1	2.4	2.3	2.1	1.8	1.9
Shannon's evenness (J)	0.7	0.7	0.7	0.7	0.6	0.7
**PTr (%)	12.0	3.9	7.9	22.2	25.0	23.6
*Calculation based on mean relative cover values of species (n = 45 quadrats per site).						
**PTr is the number of species with a mean cover < 0.05% expressed as a percentage of all species found per site.						

Echinochloa crus-galli (L.) Beauv. (barnyard grass), the only annual graminoid with higher cover (3%) in unprotected sites in 1997, was absent from all sites in 2002.

As shown in Table 2, several perennial forbs, e.g., *Laportea canadensis* (L.) Weddell (wood nettle) and *Artemisia biennis* Willd. (biennial wormwood) were abundant in unprotected sites in 1997. However, *L. canadensis* was absent from all sites in 2002. Whereas several forbs had significantly higher cover in protected sites in 2002, *Polygonum amphibium* (water smartweed) was the only forb with significantly higher cover in unprotected sites. Amongst annual forbs, *Xanthium strumarium* (cocklebur) was significantly higher in 2002 in unprotected sites, although it had declined from 13% to 3.9%. *Bidens frondosa* cover was similar in all sites in 1997 but by 2002 it was significantly higher (14%) in protected sites, as was cover of *Oxalis stricta* L. (yellow wood sorrel) ($P = 0.01$) (Figure 3).



Figure 3. Top - An unprotected site (U1) shows strong presence of *Xanthium*. Below - A protected site (P1) shows high cover of *Laportea*. Photos taken in 1997.

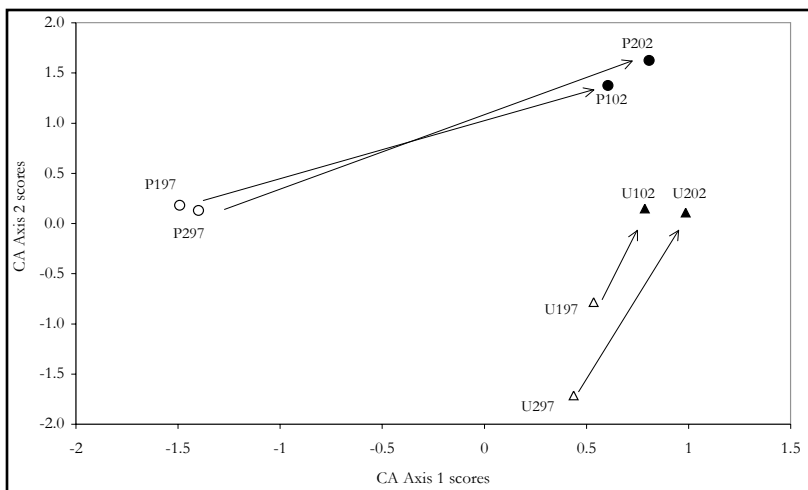


Figure 4. Ordination bi-plots generated by correspondence analysis (Podani, 1995) of understory species cover in protected (P) and unprotected (U) sites in 1997 and 2002

Community species richness (S) declined at all sites from 1997 to 2002. By 2002, evenness (J) was unchanged for protected and unprotected sites, but both richness (S) and diversity (H) were higher in protected than unprotected sites (Table 3). The proportion of trace species was higher in unprotected sites (23.6% vs. 7.9%) (Table 3). The first two axes of the correspondence analysis accounted for 50.4% of the variation in the understory data. Protected and unprotected sites were distinct from each other, with minor differences between sister sites (e.g., P1 and P2; Figure 4). The protected sites changed more between years, as indicated by their longer trajectories on the bi-plots. The direction of the trajectories suggests that some convergence of understory composition had occurred by 2002.

Discussion

As expected, the reduced flooding associated with the floodway greatly influenced both the canopy and the understory of the gallery forest along the Red River in the aftermath of a severe flood.

In the 5 y following the 1997 flood, many mature trees in un-

protected sites died, possibly exacerbated by the earlier, moderately severe flood of 1996. Mechanical as well as physiological impacts of prolonged submergence (Jones et al., 1989; Kozłowski, 2002) undoubtedly contributed to the low canopy cover in unprotected sites. Similar canopy reduction occurred after flooding along the Mississippi (Yin, 1998), the Paraná in Argentina (Franceschi et al., 2000) and the Rhine (Deiller et al., 2001). Total canopy coverage did not decrease in protected sites supporting our conclusion that no major alteration in canopy structure occurred in forests inside the floodway.

Flood tolerance differed between tree species. The absence of *Quercus macrocarpa* from unprotected sites reflects its well-known sensitivity to anoxia (Bell, 1974; Blom, 1999). Ward et al., (2002) suggested *Quercus* dominance can only occur after flood suppression for 200-300 y. Since even protected sites in the Red River valley experience minor seasonal flooding in most years, *Q. macrocarpa* will remain restricted to the upper terraces in all sites. This extreme sensitivity, as revealed by tree ring analysis, makes *Q. macrocarpa* a useful indicator of flooding history in the region (St. George and Nielsen, 2000). Less predictably, the absence of *A. negundo* from the canopy in unprotected sites suggests that although it has sufficient tolerance to cope with short term inundation in high water years in protected sites, it lacks the flood tolerance accorded it by Bell (1974). Its sensitivity may reflect mechanical rather than anoxic effects; Burns and Honkala (1990) report that its thin bark renders it susceptible to ice damage. Yin (1998) also reports high mortality of *A. negundo* after a severe flood.

Fraxinus pennsylvanica persisted in the canopy at all sites and showed extreme flood tolerance in unprotected sites, indicating that it may benefit from the absence of competitors in sites subject to prolonged submergence (Bell, 1974; Turner et al., 2004). However, Blom (1999) and Yin (1998) observed substantial *Fraxinus* mortality after severe flooding. The dominance of the canopy by *Ulmus americana* in protected sites suggests that it com-

petes well with *F. pennsylvanica* only in sites with less severe flooding. Our findings concur with Bell's 1974 report that *U. americana* tends to be absent from the lowest floodplain but dominates at middle elevations. Ward et al., (2002) also claim *U. americana* prefers less frequently inundated sites. Timing of inundation may be critical; Burns and Honkala (1990) report that *U. americana* withstands flooding while dormant but is damaged when flooding is prolonged into the season.

Future competitive relationships are likely to be more intense in protected than unprotected sites, where harsh conditions reduce the number of potential competitors (Casanova and Brock, 2002; Ward et al., 2002.) The complicating factor of Dutch elm disease may not alter these relationships in the short term due to juvenile resistance (Smalley and Guries, 1993). However as adult trees continue to succumb, particularly outside the city limits where programs designed to slow the spread of the disease have been curtailed, seed sources will inevitably decline. Thus, the main competitor of *F. pennsylvanica* in protected sites will become *A. negundo* when *Ulmus* is no longer being recruited into the canopy.

With the exception of *F. pennsylvanica*, seedlings and saplings all performed better in protected sites, suggesting that these sites will continue to support more canopy regeneration. Persistence of regenerating *F. pennsylvanica* in unprotected sites along with low amounts of *A. negundo* reinforces our view that *F. pennsylvanica* will increase in dominance in unprotected sites. Although *Q. macrocarpa* seedlings are more flood tolerant than mature trees (Burns and Honkala, 1990), their absence suggests that they will not be a factor in unprotected sites.

The presence of *Salix amygdaloides* seedlings in unprotected sites was notable. Given its high flood tolerance and ability to sprout after incurring mechanical damage (Blom, 1999), this riverbank specialist depends upon severe floods to persist in the gallery forest as part of a corridor of early succession specialists (Greenwald and Brubaker, 2001; Ward et al., 2002). Its flooding dependence is enhanced by seed dispersal by water and the ability

to germinate in waterlogged soils (Blom, 1999). We thus expect *S. amygdaloides* to find niche opportunities on the lowest reaches of unprotected sites, where it may provide limited competition to *F. pennsylvanica*. Despite the presence of mature specimens in the study area, the absence of regenerating *Populus deltoides*, another flood specialist, contrasted with its resurgence in Mississippi River floodplain forests following levee failure in a severe flood (Yin, 1998). Ironically, the greater success of diversions compared with levees means that sites protected by floodways are less likely to provide regeneration sites for flood specialists. We did not see significant *P. deltoides* regeneration in our unprotected sites, but the increased canopy opening from tree fall may provide opportunities for future colonization.

Increased bare ground and debris in unprotected sites is attributable to the higher flow rates upstream of the floodway (Haque, 2000). Greater physical disturbance removed vegetation and remaining debris impaired its re-establishment. Apart from such direct mechanical impacts, indirect effects of flooding on abiotic site conditions such as sediment deposition, nutrient loading, reducing levels and soil structure (Kozlowski, 2002) are likely to influence both tree and ground flora regeneration.

The vulnerability of woody taxa (Holmes et al., 2005) was evident in the damage to shrubs in all sites. Even minor seasonal flooding may harm particularly sensitive species such as *Amelanchier alnifolia*. Although such species have colonized the lower reaches of protected sites, their low abundance by 2002 indicates their susceptibility even when protected by control structures. *Vitis riparia* was a notable exception; although it too had higher cover in protected sites, it was more tolerant than other woody taxa. Lower cover of perennial graminoids in unprotected sites suggests they too suffer from prolonged submergence. The exception was *Carex* spp., but given its preference for waterlogged soils (Blom, 1999; Menges, 1986) its persistence in all sites is not surprising. The short term promotion of *Xanthium strumarium* and *Echinochloa crus-galli* in unprotected sites in 1997 is typical of

annual ruderals responding to a niche created by the flood, a response enhanced by hydrochory and higher light levels near the river's edge (Menges, 1986). Indeed, Gregory et al., (1991) suggested that floodplains are "one of the original habitats of weedy plants." In particular, because *X. strumarium* was one of only two understory species with significantly higher cover in unprotected sites by 2002, it clearly possesses high flood tolerance. However, its declining abundance by 2002 suggests that it depends on frequent flooding. *Bidens frondosa*, another flood tolerant annual, responds positively to flooding in both artificially flooded forests (Malecki et al., 1983) and experimental microcosms (Weiher et al., 1996). In contrast to *Xanthium*, the higher cover of *B. frondosa* in protected sites by 2002 suggests it occupies a generalist niche with no requirement or preference for severely flooded sites.

Opportunistic responses to flooding were not restricted to annuals. Herbaceous biennials and/or perennials such as *Laportea canadensis* and *Artemisia biennis* displayed a similar strategy in unprotected sites in 1997. Holmes et al. (2005) consider *L. canadensis* as characteristic of floodplain habitats in north central Ohio, although Menges (1986) reported that it occupied higher terraces. In contrast, the significantly higher cover of many weedy species such as *Oxalis stricta*, *Cirsium arvense* (L.) Scop. (Canada thistle), and *Arctium lappa* L. (greater burdock) in protected sites by 2002 suggests that extreme flooding in unprotected sites generates conditions too harsh for many ruderals. In particular the large amount of debris resulting from a severe flood—a feature not associated with other disturbances such as fire—reduces the suitability of the site for many ruderals. Menges (1986), Gregory et al., (1991) and Blom (1999) suggest that perennials will dominate the upper terraces and annuals the lower floodplains. No such distinction was evident in our study. Even five years after a severe flood our unprotected sites were occupied by a limited coterie of both annuals and perennials. Although weedy taxa occurred in all sites, protected sites appear more vulnerable to invasion, exacerbated by their urban location.

For taxa with the requisite tolerance, regeneration opportunities will persist longer in severely flooded sites due to the prevalence of bare ground. Of these, *Polygonum amphibium*, which not only had higher cover in unprotected sites and was the only species to increase in cover in those sites, was the only perennial with indicator potential for severe flooding (Menges, 1986; Carter and Grace, 1990). Its semi-aquatic status suggests it is unlikely to persist unless severe flooding occurs with high frequency.

Lower richness and diversity in unprotected sites by 2002 indicate that the opportunities provided by flooding were offset by increased site harshness, a conclusion supported by the greater proportion of trace species in unprotected sites. Conditions fell outside the tolerance limits of many, leading to reduced diversity. Although some semi-aquatic specialists were promoted, this effect was counter-balanced by a larger number of species that were reduced or eliminated. These results concur with lower richness of flooded sites in Wisconsin (Menges, 1986) and the upper Rhine (Deiller et al., 2001), although in the latter study diversity was higher in flooded sites due to increased evenness. In contrast, Franceschi et al. (2000), reported stable levels of richness and diversity after prolonged flooding along the Paraná River. Ward et al. (2002), argue that the beneficial effects of flooding may skew the intermediate disturbance hypothesis (Connell, 1978), which predicts lower diversity in areas subject to high disturbance frequency. Although the lower diversity of our unprotected sites supports Connell's hypothesis, flooding effects on community parameters are complex, reflecting differences in the magnitude and extent of the disturbance and/or confounding factors. For example, many studies calculate diversity across all portions of riparian forests; whereas we restricted our analysis to the lower reaches.

The divergence evident in the bi-plots supports the view that protection from severe flooding alters understory species composition in gallery forests. The faster pace of succession in the protected sites reflects their less harsh post-flood conditions.

Although species composition is converging by 2002, stochastic changes in flood regimes and/or confounding site factors could disrupt or reinforce these successional trajectories, generating a multiplicity of potential community outcomes (Turner et al., 1998).

CONCLUSION

Gallery forests in the Red River valley incurred less damage from the extreme flood of 1997 to both their mature canopy and understorey strata in sites protected by the floodway. Tree regeneration data indicated that *Fraxinus pennsylvanica* was likely to dominate the canopy in the unprotected sites, whereas a greater number of tree species persisted in the protected sites. The understorey, with its greater variety of lifeforms, responded in a less clear-cut manner. Overall declines in richness and diversity in the unprotected sites were attributable to the harsher site conditions. Even five years after the event, cover values were lower for the majority of species. Although several flood specialists were promoted in the unprotected sites, it would appear that the floodway, which reduces but does not eliminate flooding, supports a less depauperate flora in gallery forests in the short term. However, weedy invasion is of concern in all sites, and most especially in the urban protected sites. Reduced exposure to the positive impacts of flooding, particularly in the event of lowered mid-continental precipitation as a result of global warming, may take its toll in the longer term. Continued monitoring of this vital ecosystem is essential.

Acknowledgements

We thank landowners and municipal authorities for permission to sample the sites. Dr. N. Kenkel assisted E. Essery with the correspondence analysis. Dr. B. Ford and L. Punter assisted with species identification. We thank Dr. G. Brooks for permission to use his map.

References

- Abrams, M.D. 1986. Historical development of gallery forests in northeast Kansas. *Vegetatio*, 65:29-37.
- Bell, D.T. 1974. Tree stratum composition and distribution in the streamside forest. *American Midland Naturalist*, 92:35-46.
- Bell, D.T. and del Moral, R. 1977. Vegetation gradients in the streamside forest of Hickory Creek, Will County, Illinois. *Bulletin of the Torrey Botanical Club*, 104:127-135.
- Blom, C.W.P.M. 1999. Adaptations to flooding stress: from plant community to molecule. *Plant Biology*. 1:261-273.
- Brooks, G.R. and Nielsen, E. 2000. Canadian landforms examples. *Canadian Geographer*, 44:306-311.
- Burn, D.H. and Goel, N.K. 2001. Flood frequency analysis for the Red River at Winnipeg. *Canadian Journal of Civil Engineering*, 28:355-362.
- Burns, R.M. and Honkala, B.H. 1990. *Silvics of North America*. Vol. 2. Hardwoods. Agricultural Handbook 654. Washington, DC: USDA Forest Service.
- Carter, M.F., and Grace, J.B. 1990. Relationships between flooding tolerance, life history, and short-term competitive performance in three species of *Polygonum*. *American Journal of Botany*, 77:381-387.
- Casanova, M.T., and Brock, M.A. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecology*, 147:237-250.
- Connell, J. 1978. Diversity in tropical rainforests and coral reefs. *Science*, 199:1302-1310.
- Data Descriptions. 1993. *Data Desk 4.1*. Ithaca, NY: Data Descriptions Inc.
- Deiller, A.F., Walter, J.M.N., and Tremolières et al. 2001. Effects of flood interruption on species richness, diversity and floristic composition of woody regeneration in the upper Rhine alluvial hardwood forest. *Regulated Rivers Research & Management*, 17:393-405.
- Ehrlich, W.A., Poyser, E.A., Pratt, L.E., and Ellis, J.H. 1953. Report of Reconnaissance Soil Survey of Winnipeg and Morris Map Sheet Areas. *Soils Report 5*. Winnipeg: Manitoba Department of Agriculture.
- Environment Canada. 1994. Canadian monthly climate data and 1961-1990 normals on CD-ROM. Downsview, ON: Environment Canada, Atmospheric Environment Service,
- Essenberg, C.B. 1991. Dutch elm disease and the vegetation composition of Manitoba's bottomland forests. M.Sc. thesis, Department of Botany, University of Manitoba, Winnipeg, MB.

- Franceschi, E.A., Torres, P.S., Prado, D.E., and Lewis, J.P. 2000. Disturbance, succession and stability: a ten year study of temporal variation of species composition after a catastrophic flood in the river Parana, Argentina. *Community Ecology*, 1:205-214.
- Greenall, J. 1996. Manitoba's terrestrial plant communities. Manitoba Conservation Data Centre, MS Report No. 96-02. Winnipeg, MB.
- Greenwald, D.N., and Brubaker, L.B. 2001. A 5000-year record of disturbance and vegetation change in riparian forest of the Queets River, Washington, U.S.A. *Canadian Journal of Forest Research*, 31:1375-1385.
- Gregory, S.V., Swanson, F.J., McKee, W.A., and Cummins, K.W. 1991. An ecosystem perspective of riparian zones. *Bioscience*, 41:540-550.
- Haque, C.E. 2000. Risk assessment, emergency preparedness and response to hazards: the case of the 1997 Red River Valley Flood, Canada. *Natural Hazards*, 21:225-245.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54:427-432.
- Holmes, K.L., Goebel, P.C., Hix, D.M., Dygert C.E., and Semko-Duncan M.E. 2005. Ground-flora composition and structure of floodplain and upland landforms of an old-growth headwater forest in north-central Ohio. *Journal of the Torrey Botanical Society*, 132:62-71.
- Hosner, J., and Minckler, L.S. 1963. Bottomland hardwood forests of southern Illinois – regeneration and succession. *Ecology*, 44:29-41.
- Johnson, W.C., Burgess, R.L., and Keammerer, W.R. 1976. Forest overstory vegetation and environment on the Missouri River floodplain in North Dakota. *Ecological Monographs*, 46:59-84.
- Jones, R.H., Sharitz, R.R., and Mcleod, K.W. 1989. Effects of flooding and root competition on growth of shaded bottomland hardwood seedlings. *American Midland Naturalist*, 121:165-175.
- Kartesz, J.T. 1994. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland (2nd ed.) Volume. 2. Portland OR: Timber Press.
- Keammerer, W.R., Johnson, W.C., and Burgess, R.L. 1975. Floristic analysis of the Missouri River bottomland forest in North Dakota. *Canadian Field Naturalist*, 89:5-19.
- Kindscher, K., and Holah, J. 1998. An old-growth definition for western hardwood gallery forests. General Technical Report SRS-22. Asheville, NC. USDA, Forest Service, Southern Research Station.
- Kozłowski, T.T. 2002. Physiological-ecological impacts of flooding on riparian forest ecosystems. *Wetlands*, 22:550-561.
- Malecki, E.S., Lassoie, J.R., Rieger, E., and Seamans, T. 1983. Effects of long-term artificial flooding on northern bottomland hardwood forest com-

- munity. *Forest Science*, 29:535-544.
- Manitoba Water Commission. 1998. An independent review of the 1997 Red River flood: interim report. Manitoba Water Commission, Winnipeg, MB.
- McLeod, K.W., Reed, M.R., and Wike, L.D. 2000. Elevation, competition control, and species affect bottomland forest restoration. *Wetlands* 20:162-168.
- Menges, E. . 1986. Environmental correlates of herb species composition in five southern Wisconsin floodplain forests. *American Midland Naturalist*, 115:106-117.
- Podani, J. 1995. SYN-TAX 5.02.Mac. Computer programs for multivariate data analysis on the Macintosh system. Budapest: Scientia.
- Rasid, H., Haider, W., and Hunt, L. 2000. Post-flood assessment of emergency evacuation policies in the Red River basin, Southern Manitoba. *Canadian Geographer* 44:369-386.
- St. George, S., and Nielsen, e. 2000. Signatures of high magnitude 19th-century floods in *Quercus macrocarpa* tree rings along the Red River, Manitoba. *Geology* 28:899-902.
- Smalley, E.B., and Guries, R.P. 1993. Breeding elms for resistance to Dutch elm disease. *Annual Review of Phytopathology*, 31:325-354.
- Turner, M.G., Baker, W.L., Peterson C.J., and Peet, R.K. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems*, 1:511-523.
- Turner M.G., Gerbel, S.G., Dixon M.D., and Miller, J.R. 2004. Distribution and abundance of trees in floodplain forests of the Wisconsin River: Environmental influences at different scales. *Journal of Vegetation Science*, 15:729-738.
- Ward, J.V., Tockner, K., Arscott, D.B., and Claret, C. 2002. Riverine landscape diversity. *Freshwater Biology*, 47:517-539.
- Weiher, E., Wisheu, I.C., Keddy, P.A., and Moore, D.R.J. 1996. Establishment, persistence and management implications of experimental wetland plant communities. *Wetlands*, 16:208-218.
- Wikum, D.A., and Wali M.K. 1974. Analysis of a North Dakota gallery forest: vegetation in relation to topographic and soil gradients. *Ecological Monographs*, 44:441-464.
- Wilson, R.E. 1970. Succession in stands of *Populus deltoides* along the Missouri River in Southeastern South Dakota. *American Midland Naturalist*, 83:330-342.
- Yin, Y. 1998. Flooding and forest succession in a modified stretch along the upper Mississippi River. *Regulated Rivers Research & Management*, 14:217-225.