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Effects of land use disturbance on seed banks of riparian forests in southern Manitoba¹

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Abstract: Riparian forests have been adversely affected by human land use and are threatened across North America. Seed banks play an important role in the maintenance and regeneration of forests, yet effects of land use and fragmentation on forest seed banks remain poorly understood. In 1998 and 1999, we assessed impacts of human disturbance on the diversity and species composition of seed banks in upland portions of riparian forests along an urban-rural gradient in southern Manitoba. Twenty-five forest fragments were categorized according to the following land-use: urban, suburban, high-intensity rural, low-intensity rural, and relatively undisturbed reference classes. Seeds of weedy and exotic species were positively associated with fragmentation, high levels of disturbance, and dry alkaline soils. Seed bank species diversity was lower in urban sites than in rural sites, and the similarity of urban to reference sites was significantly lower than that of rural to reference sites. In contrast, the proportion of exotic to native species richness was highest in seed banks of urban sites. Exotic species *Hackelia virginiana* and *Poa pratense* were associated with urban and suburban sites, respectively. Six exotic species were unique to urban sites; these included *Hesperis matronalis* and *Plantago major*. In contrast, many of the frequently encountered native species were absent from urban sites; these included *Anemone canadensis* and *Rubus idaeus*. These changes in seed bank may affect the ability of riparian forests to recover from adverse impacts associated with urban development and agriculture.

Keywords: disturbance, exotic, fragmentation, land use, riparian forest, seed bank.

Résumé : Les forêts riveraines ont été perturbées par l'utilisation anthropique du territoire et elles sont maintenant menacées en Amérique du Nord. Les réservoirs de graines jouent un rôle important dans le maintien et la régénération des forêts. Toutefois, on connaît encore peu de choses sur les effets de l'utilisation du territoire et de la fragmentation des habitats sur les réservoirs de graines. En 1998 et 1999, nous avons déterminé quels sont les impacts des perturbations humaines sur la diversité et la composition en espèces des réservoirs de graines des portions hautes de forêts riveraines le long d'un gradient allant de la ville à la campagne, dans le sud du Manitoba. Nous avons classé 25 fragments de forêts en fonction de l'utilisation du territoire : zone urbaine, banlieue, zone rurale intensément développée, zone rurale peu développée et zone peu ou pas perturbée (site témoin). Les graines des mauvaises herbes et des plantes exotiques sont positivement associées aux milieux fragmentés, fortement perturbés et avec sols secs et alcalins. La diversité en espèces des réservoirs de graines est plus faible dans les zones urbaines que dans les zones rurales. La similitude entre les sites urbains et les sites témoins est plus faible que celle qui existe entre les sites ruraux et les sites témoins. C'est d'ailleurs dans les réservoirs de graines des sites urbains que la proportion du nombre d'espèces de plantes exotiques par rapport au nombre d'espèces indigènes est la plus élevée. Les espèces exotiques *Hackelia virginiana* et *Poa pratense* sont associées respectivement aux sites urbains et aux banlieues. Il y a six espèces exotiques que l'on ne trouve que dans les sites urbains, notamment *Hesperis matronalis* et *Plantago major*. Par contre, plusieurs des espèces indigènes les plus fréquentes, comme *Anemone canadensis* et *Rubus idaeus*, sont absentes des mêmes sites. En conclusion, les changements observés au niveau des réservoirs de graines suite aux développements urbains et agricoles peuvent avoir un effet sur l'habileté des forêts riveraines à se régénérer.

Mots-clés : exotique, forêt riveraine, fragmentation, perturbation, réservoir de graines, utilisation du territoire.

Nomenclature: Looman & Best, 1987; Royer & Dickinson, 1999.

Introduction

Seed banks are important for the maintenance and regeneration of plant communities (Baskin & Baskin, 2001). Their relative size and life history characteristics often make them more important than the bud and propagule banks for plant community dynamics (Simpson, Leck & Parker, 1989). Information on seed banks can be used to describe past species composition and predict the composition, abundance, and distribution of species in the future, postrecruitment vegetation (Van der Valk & Pederson, 1989). Most seed bank studies have examined

arable or post-arable land, and few have examined the effects of human land use on forest seed bank diversity and composition (Poiani & Dixon, 1995).

Forest seed banks typically consist of small seeded (Pickett & McDonnell, 1989) and early successional species (Matlack & Good, 1990). As forest stands age, seed bank composition changes from short- to long-lived species, and seed bank species diversity and seed density both decrease (Roberts & Vankat, 1991). Forest seed banks are also influenced by environmental factors, in that seed density tends to increase with soil moisture (Leckie *et al.*, 2000) and decrease with pH (Pickett & McDonnell, 1989).

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Vegetation dynamics and seed banks are linked through disturbance (Jiménez & Armesto, 1992). Although most seed bank studies are conducted at the site level, human disturbance also can have important ramifications for seed banks at the landscape level. As landscapes become fragmented by intense use, distances among and the isolation of remnant patches tend to increase (Brothers & Spingarn, 1992), and seed dispersal is often adversely affected (Primack & Miao, 1992). Dispersal-restricted species, especially those that are ant-, gravity-, explosion-, and wind-dispersed with heavy seeds, may become extirpated as fragmentation increases (McLachlan & Bazely, 2001; Moffatt, 2002). In contrast, many early successional and exotic plant species with light and wind-dispersed or ingested seeds disperse effectively under these conditions (Stylinski & Allen, 1999).

Seed banks in human-dominated landscapes often have increased proportions of introduced weedy species that have adapted to these new conditions or originated from similar environments (Pickett & McDonnell, 1989). As disturbance increases, seed densities of forest seed banks may decline (Ingersoll & Wilson, 1990; Zabinski, Wojtowicz & Cole, 2000) and the similarity of seed banks to aboveground vegetation may decrease, due to an increased prevalence of early successional species (Qi & Scarratt, 1998). Indeed, particularly intense disturbance may exclude some species characteristic of seed banks in undisturbed forests (Zabinski, Wojtowicz & Cole, 2000).

Riparian forests are increasingly threatened by agriculture and urban development and are in decline across North America (Knutson & Klaas, 1998). Although they play an important role in river ecosystem structure and function (Gregory *et al.*, 1991; Tabacchi *et al.*, 1998; Brinson & Ver Hoeven, 1999), few studies have examined the effects of disturbance and fragmentation on these forests, and even fewer have examined the effects on their seed banks. The overall objective of our study was to characterize the seed banks of upland portions of riparian forests along an urban-rural gradient in southeastern Manitoba. We predicted that the proportion of short-lived and exotic species in the seed bank would increase with human disturbance, whereas species diversity and seed density would decrease. Moreover, disturbance effects would be greatest in urban and lowest in low-intensity, rural forest sites.

Methods

SITE DESCRIPTION

This study was conducted on 25 fragments of riparian forest along the Assiniboine River in southern Manitoba (Figure 1). The easternmost forest patch (49° 53' N, 97° 08' W) was located at the junction of the Assiniboine River with the Red River in downtown Winnipeg, while the westernmost forest patch (50° 02' N, 97° 50' W) was 50 km west. The study area was located at the southeast corner of the prairie ecozone, where agriculture currently represents 94% of the land base (Wiken, 1996). Remnant natural habitat in this region includes tall grass prairie and riparian forest.

Soil is from the Red River Association of the Blackearth soil zone and is well-to-poorly drained. These

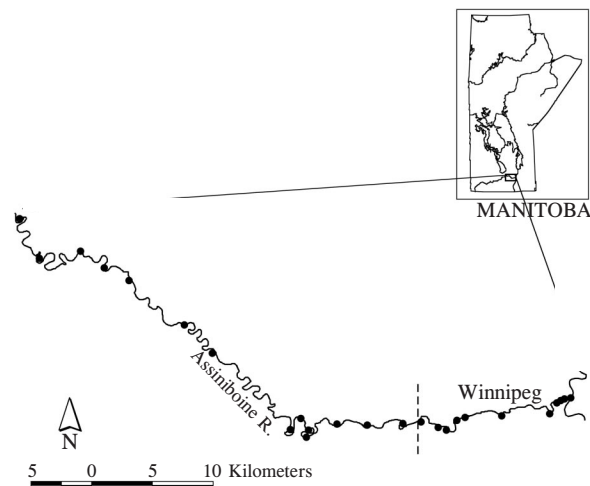


FIGURE 1. Location of the 25 study sites along the Assiniboine River in southern Manitoba (inset).

soils overlie lacustrine clay and alluvial deposits that make up the Red River Plain of the Lake Agassiz Basin (Ehrlich *et al.*, 1953). The climate of this region is continental, with an annual mean temperature of 2.4°C, ranging from a mean maximum of 26.1°C in July to a mean minimum of -23.6°C in January (Environment Canada, 2003). The mean annual precipitation is 504.4 mm; 404.4 mm falls as rain, which peaks in June.

SAMPLING DESIGN

SITE LEVEL

Potential forest sites were identified along an urban-rural land use gradient using aerial photos collected in August 1991 and 1994 (Linnet Geomatics International Inc., 1998). Sites were classified according to surrounding land use and include *i*) urban sites in the downtown core characterized by high rise office and apartment buildings; *ii*) suburban sites located outside the downtown core, but within the city perimeter, characterized by single family dwellings; *iii*) high-intensity rural sites surrounded by cash crops subject to regular pesticide and fertilizer use; *iv*) low-intensity rural sites surrounded by forage crops not subject to pesticide and fertilizer use; and *v*) high-quality reference sites that are generally recognized as being relatively undisturbed (C. Hemming, pers. comm.). Twenty-five sites, five in each land use class, were identified, and once selected, each site was visited to ensure that the remnant patch still existed as depicted in the aerial photos and to confirm classification.

Three line transects, each containing five sample points, were established at each site. Line transects were randomly located perpendicular to the river and at least 20 m apart and 50 m from any parallel forest edge. If the forest patch was greater than 250 m in width, it was divided into three subsections of equal width and one transect randomly located within each subsection. Along each transect, sample points were permanently marked at 0 m and 15 m from both the land and river edges of the forest patch. A fifth sample point was located 50 m from the land edge. The 0-m mark for the land edge in each

site was located at the point of edge maintenance or treated as a canopy drip line edge (Ranney, Bruner & Levenson, 1981). To eliminate the confounding effects of highly variable annual flooding, the 0-m mark on the river edge was located at the high-water line.

At each sample point, the species composition of herbs, defined as any woody plants less than 0.5 m in height and all herbaceous species, was recorded as percent cover from July 1 to August 31, 1999. Early flowering species were later identified from May 15 to July 15, 2000. Two 2-m × 1-m quadrats per sample point were situated along each transect, and one of the three transects was randomly selected for an additional, third quadrat per sample point, resulting in 35 quadrats per site.

We measured forest canopy cover, topography, and aspect for all sample points in all transects. Canopy cover was calculated by averaging values visually assessed from the four corners of each 2-m × 1-m quadrat. Topography was classified on a scale that ranged from flat (1) to ridge and swale (4). Edaphic variables were measured at each sample point, but only along the two transects without the third quadrat. Percent soil moisture was calculated using soil cores (4 cm Ø × 20 cm) that were collected on September 9, 2000. These were immediately weighed for wet mass and subsequently oven-dried at 50°C for at least 24 hours, or until no further change in mass was observed, to determine gravimetric water content. Additional soil cores were collected, then air dried, ground, and sieved through a 2-mm screen in order to measure electrical conductivity (Ec), pH, and soil composition (*i.e.*, percent sand, silt, and clay). The Ec and pH were calculated using a 2:1 water:soil slurry. Soil texture was predicted using Near Infrared Reflectance Spectroscopy as described in Shenk and Westerhaus (1991), with a model derived from 75 of the 280 soil samples. These reference samples were selected from a principal component analysis of the reflectance spectra obtained from all soil samples (Stenberg, Nordkvist & Salomonsson, 1995). Soil composition of the reference samples was measured using the Bouyous Hydrometer Method (Kalra & Maynard, 1991).

Seed banks were sampled from July 15 to August 31, 1999. Sampling occurred in all 25 sites, and two cores were taken at each of the sample points. Along the two transects without the additional quadrat, we collected a (10 cm × 15 cm × 10 cm deep) soil sample. Although the soil depth distribution of seeds was unknown for the study area, most studies typically use cores only to a depth of 5 to 10 cm, as seed numbers tend to decrease at greater depths (Chambers, 1993). Samples were sifted using a 0.5-cm screen to remove coarse debris. As the soil often had a high clay content, 300 ml of each sifted sample was spread on 200 ml of sterile growth medium (Sunshine Mix 4, Fisons, Bellevue, Washington) to help prevent clumping. Samples were placed in 9.5-cm × 12-cm pots to an average depth of 4.5 cm, with 10 pots per flat representing each site, which were then randomly situated in the greenhouse. Control pots that contained only sterile growth medium were evenly distributed around the flats to detect potential greenhouse contaminants. Flats were exposed to a 16-hour photoperiod and alternating day-night temperatures of 10–25°C and were watered when needed.

We used seedling emergence to characterize seed banks. Though emergence requirements may not be met for all species, seedling emergence is generally recognized as the most accurate and efficient method to estimate seed bank composition (Gross, 1990; Brown, 1992; Baskin & Baskin, 2001). The number and identity of emergent seedlings was recorded using floras by Royer and Dickinson (1999) and Looman and Best (1987). Unidentified seedlings were transplanted and grown to maturity for identification. When seedlings no longer emerged, flats were stratified in a cold chamber at 2–3°C with a 12-hour photoperiod for 6 weeks. Flats were then returned to the greenhouse, where the soil was broken up and stirred to encourage germination of buried seeds. Cold stratification was conducted twice. After 14 months in the greenhouse, emergence had ceased and the project was terminated.

LANDSCAPE LEVEL

Land use around each site was classified using aerial photographs and determined as urban, suburban, high-intensity rural, and low-intensity rural land use. Healthy forest was defined as any portion of a patch having a minimum dimension greater than 30 m and without a manicured understory. Degraded forest was defined as any portion of a patch with a minimum dimension between 10 m and 30 m, without a manicured understory. Any forest patches with a manicured understory were classified according to contiguous land use. Our land use classification was cross-referenced against classified 30-m × 30-m Landsat imagery obtained from the Prairie Farm Rehabilitation Association (Agriculture & Agrifood Canada, unpubl. data).

Proportions of each land use surrounding forest sites were measured within a 1,000-m radius. A measure of connectivity, modified from Kenkel (1990), was calculated ($\text{Connectivity} = \sum A_i^2 (P_i D_i^2)^{-1}$, where A = patch area, P = perimeter, and D = centre to centre inter-patch distances) to assess the degree of isolation. Area:perimeter was calculated to assess shape in relation to fragmentation. Disturbance for each site ranged from no disturbance (0) to highly disturbed (9). This was calculated as an index, using the relative abundance of garbage (0–3), number and size of foot trails (0–3), presence of anthropogenic disturbance such as logging (0 or 1), and accessibility to both the entire site (0 or 1) and the interior of the site (0 or 1).

ANALYTICAL METHODS

We analyzed the seed bank of the riparian forest for landscape- and site-level responses to the urban-rural land use gradient. To characterize the seed bank at each site, Hill's (1973) diversity measures were used. These include N_0 , which describes the total number of species but is sensitive to rare species; N_2 , which is the reciprocal of Simpson's index and emphasizes dominance; and E_3 , an evenness measure calculated as N_2 divided by the total number of species. In addition, seed density (seedlings · m⁻² soil surface) and exotic:native ratios, based on N_0 and density, were calculated. Effects of land use disturbance on seed bank composition were further described by cal-

culating Soerenson's similarity (SS) among sample points within each site for each land use category and between sample points from each land use category and the reference land use sites [$SS = 2a \cdot (2a + b + c)^{-1}$, where a = species present in both samples, b = species present in only one sample, and c = species present in the other sample]. The effect of land use on diversity, SS, and seed density was analyzed using a one-way analysis of variance (ANOVA) (SAS Institute, 1985).

The effects of land use on the 15 most common species in the seed bank (those occurring in more than 5% of the pots) were analyzed using one-way ANOVA (SAS Institute, 1985). These species also were classified to functional groups, including origin (native or exotic); life form (annual or perennial grass; annual, biennial, or perennial forb; or woody); phenology (ephemeral, summer, or fall flowering between March-May, June-August, or September-November, respectively); and dispersal type (anemochore, barochore, autochore, epizoochore, endozoochore, or myrmecochore) (Ridley, 1930; Britton & Brown, 1970). Post-hoc Tukey's multi-comparison tests ($\alpha = 0.05$) were used to separate means when overall models were significant.

Canonical correspondence analysis (CCA) was conducted to determine relationships between species composition, site, and the constraining disturbance and environmental variables for the seed bank (Ter Braak, 1990). Land uses were classified as categorical variables and also used to constrain the analysis. CCA is a method of direct gradient analysis, which explains data through orthogonal axes of variation in decreasing order of importance. Rare species were down-weighted in importance.

Results

SEED BANK DESCRIPTION

In total, 1,565 seedlings belonging to 90 taxa emerged from the combined samples. Taxa were identified to species, except five that were only identified to genus and seven that remained unidentified. All *Carex* seedlings were grouped as *Carex* spp., as they rarely flower in greenhouses (B. Ford, pers. comm.), and were eliminated from subsequent analyses. The number of species per site ranged from six to 21, and mean species richness and dominance were 14.8 and 7.8, respectively. Density per site ranged from 142 to 907 seedlings \cdot m⁻², and mean density was 427.1 seedlings \cdot m⁻². The richness of exotic and native species was nearly equal, although the density of exotic species was 2.3 times that of native species.

The seed bank consisted mostly of herbaceous species; 67.9% and 28.9% of these were forb and graminoid species, respectively, and only 3.2% were woody (Figure 2). Moreover, 30.3% of the species were either annuals or biennials, and 59.6% were exotic to North America. Most (63.3%) flowered in the summer, and the two dominant dispersal mechanisms, wind- and animal-dispersed, each represented 39% of the seed bank. Ant-dispersed species were effectively absent, representing only 0.1% of the seed bank (Figure 2). In contrast to aboveground vegetation, the seed bank contained proportionately more

exotics and annual forbs and fewer ephemerals and endozoochores (Figure 2).

Of the 15 most common species, found in at least 5% of the pots, 13 were forbs, one was a graminoid (*Poa pratensis*), and one was woody (*Rubus idaeus*) (Table I). The most common species, *P. pratensis*, had a seed bank density of 61.6 seedlings m⁻², whereas the 15th most common species, *Hackelia virginiana*, had a seed bank density of 7.3 seedlings m⁻².

DISTURBANCE AND ENVIRONMENT

Species composition of the riparian forest seed bank was significantly related to disturbance and environmental variables (Figure 3). CCA axes 1 and 2 accounted for 18.2% and 15.0% of the variation, respectively, and, in total, accounted for 33.2% of the variation explained by the species correspondence analysis. When constrained, the species-environment correlations were 0.949 and 0.926 for axes 1 and 2, respectively. As the redundancy value was very high at 54.6%, correlations are meaningful (Økland, 1999).

Axis 1 was positively correlated with garbage and disturbance, and negatively correlated with area:perimeter, connectivity, and percent soil moisture (Figure 3a). Species positively associated with axis 1 were generally exotic or weedy (Figure 3b). Although many of these were rare and only found at one site, exotics *Arctium minus* and *Artemisia absinthie* were found in three and 10 sites, respectively, and the weedy native *H. virginiana* was found in eight sites. Species negatively associated with axis 1 were generally interior or hydrophilic species. These, again, were uncommon, with the exception of native *Phalaris arundinacea* and the exotic *Setaria viridis*, which occurred in three and six sites, respectively.

Axis 2 was positively correlated with canopy cover and negatively correlated with percent sand (Figure 3a). These correlations were not as strong as those of axis 1, and species associated with axis 2 were generally uncommon. More common, positively associated species included *Polygonum persicaria* and *Anemone canadensis*, whereas negatively associated species included natives *Epilobium glandulosum* and *Ranunculus abortivus* (Figure 3b).

LAND USE

Land use surrounding riparian forest had a substantial impact on the seed bank. Species richness was significantly ($P < 0.05$) lower for urban and higher for low-intensity rural sites, whereas the proportion of exotic to native diversity was significantly ($P < 0.05$) higher for urban sites (Table II). The similarity between urban and reference sites was significantly lower ($P < 0.01$) than that between rural and reference sites, and the seedling density of urban seed banks was approximately half that of low-intensity rural sites (Table II).

Land use was related to seed bank species composition. The 25 sites were grouped around their respective centroids when constrained by land use classification (Figure 4a). CCA axes 1 and 2 accounted for 36.3% and 29.1% of the variation, respectively, and, in total, accounted for 65.4% of the variation explained by the correspon-

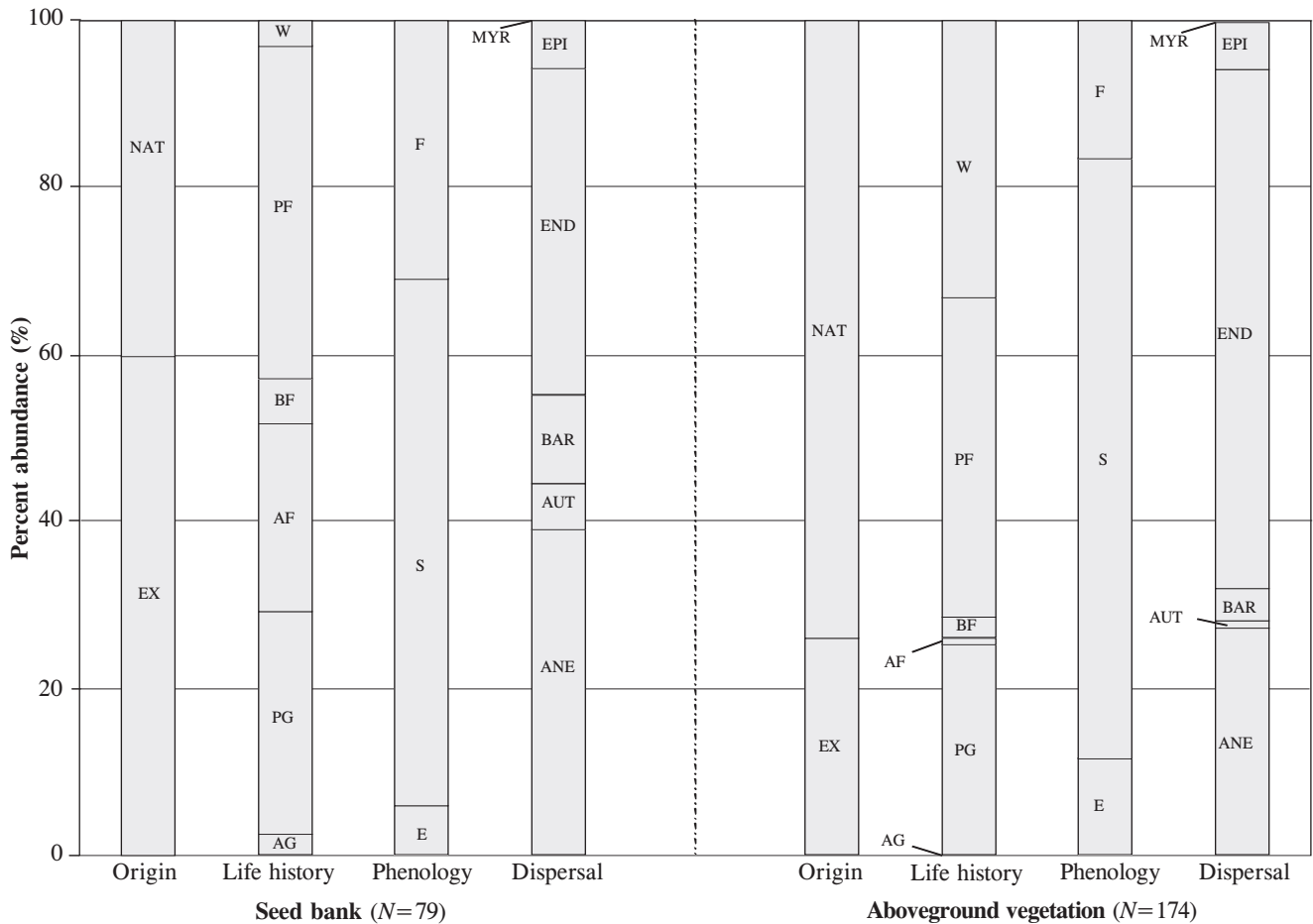


FIGURE 2. Comparison of aboveground vegetation and seed bank according to origin (native, Nat; exotic, Ex), life history (woody, W; perennial forb, PF; biennial forb, BF; annual forb, AF; perennial graminoid, PG; annual graminoid, AG), flowering phenology (fall, F; summer, S; ephemeral, E), and seed dispersal (anemochore, ANE; epizoochore, EPI; endozoochore, END; barochore, BAR; autochore, AUT; myrmecochore, MYR) guilds.

dence analysis. When constrained, species-environment correlations were 0.953 and 0.875 for axes 1 and 2, respectively. These correlations again were meaningful, although at 26.9% they exhibited a lower redundancy value.

In general, species unique to any category of land use occurred infrequently, and in many cases only occurred in one seed pot. Urban sites were clearly separated from the other land use types along axis 1 and were characterized by six unique exotic and three unique native species (Figure 4b). Of these, exotics *Hesperis matronalis* and *Plantago major* occurred in more than one pot. Sites from the four remaining land use categories separated less clearly along axis 2 (Figure 4a). Species unique to these four land uses that occurred in more than one pot were native *P. arundinacea*, which was associated with reference sites, and natives *Ambrosia artemisiifolia*, *Ribes americanum*, *Scutellaria lateriflora*, and *Veronica peregrina*, all of which were associated with low-intensity rural sites.

Effects of land use also were examined for 15 of the most common species (Table I). Exotic *H. virginiana* was significantly ($P=0.041$) associated with urban sites, exotic *P. pratense* significantly ($P < 0.0001$) associated with suburban sites, and exotic *Thlaspi arvense* significantly ($P=0.010$) associated with low-intensity rural sites. In contrast, many of the native species were absent ($P < 0.02$)

from the urban sites. These included *Anemone canadensis*, *Rubus idaeus*, and *Galium triflorum* (Table I).

Discussion

RIPARIAN FOREST SEED BANK

The mean density of the seed bank for the riparian forests in our study area was comparable to those found for temperate forests in Japan (Nakagoshi, 1985) and for riparian forests in northern Sweden (Grelsson & Nilsson, 1991), although the range exhibited in our study was much lower. Whereas others have found sites with no seed bank (Matlack & Good, 1990; Grelsson & Nilsson, 1991), all sites in our study area contained seeds, perhaps because of the high proportion of exotic species and their relatively persistent seed banks. The upper value of our seed bank density range was lower than many other studies, perhaps, in part, because all of our forest sites were somewhat degraded by surrounding land use. In turn, our seed banks were more diverse than most; they contained 50% more species than those of coastal plain forest in New Jersey (Matlack & Good, 1990) and Allegheny Plateau riparian forest in Pennsylvania (Hanlon, Williams & Moriarity, 1998). This may reflect the relatively great diversity of land use and forest types described in this landscape-level research.

TABLE I. Characterization of the 15 most common (occurring in > 5% of the pots) riparian forest seed bank species, with mean densities (N=5, seedlings m⁻²) for each land use type.

Species	Rank	Origin	Life Form	Phenology	Dispersal Type	Land use categories					ANOVA P
						Urban	Suburban	High rural	Low rural	Reference	
<i>Poa pratense</i>	1	Ex ^{1,2,3}	PG	S	END	6.7 ^b	168.0 ^a	85.3 ^{ab}	20.0 ^b	28.0 ^b	< 0.0001
<i>Sonchus arvensis</i>	2	Ex	PF	F	ANE	13.3	24.0	33.3	17.3	25.3	NS
<i>Cirsium arvense</i>	3	Ex	PF	F	ANE	21.7	12.0	33.3	36.0	28.0	NS
<i>Potentilla norvegica</i>	4	Nat	AF	F	END	31.7	6.7	4.0	36.0	8.0	NS
<i>Taraxacum officinale</i>	5	Ex	PF	E	ANE	11.7	12.0	5.3	21.3	2.7	NS
<i>Urtica dioica</i>	6	Ex	PF	F	END	33.3	4.0	70.7	50.7	1.3	NS
<i>Galium triflorum</i>	7	Nat	PF	S	END	0.0 ^b	0.0 ^b	13.3 ^{ab}	49.3 ^a	12.0 ^{ab}	0.025
<i>Rubus idaeus</i>	8	Nat	W	E	END	0.0 ^b	4.0 ^{ab}	17.3 ^{ab}	28.0 ^a	5.3 ^{ab}	0.031
<i>Plantago media</i>	9	Ex	PF	F	END	1.7	9.3	10.7	8.0	12.0	NS
<i>Thlaspi arvense</i>	10	Ex	AF	S	ANE	3.3 ^a	5.3 ^a	1.3 ^a	133.3 ^a	86.7 ^a	0.036
<i>Oxalis europaea</i>	11	Nat	PF	S	AUT	3.3	8.0	4.0	12.0	5.3	NS
<i>Anemone canadensis</i>	12	Nat	PF	S	ANE	0.0	4.0	1.3	65.3	1.3	NS
<i>Artemisia absinthae</i>	13	Ex	PF	F	ANE	48.3	1.3	1.3	5.3	10.7	NS
<i>Rorippa islandica</i>	14	Ex	PF	F	EPI	1.7	30.7	2.7	2.7	5.3	NS
<i>Hackelia virginiana</i>	15	Nat	BF	S	EPI	23.3	9.3	1.3	2.7	0.0	NS

¹ Codes as in caption of Figure 2.

² NS: non significant ($P > 0.05$).

³ Means within a row that have different superscript letters are significantly different from one another (Tukey's HSD) NS, not significant ($P > 0.05$).

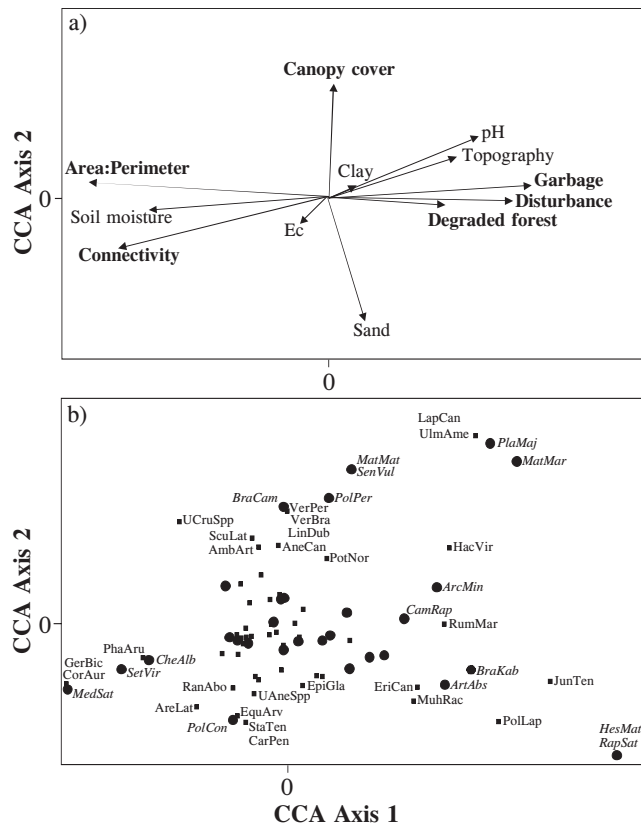


FIGURE 3. Results of Canonical Correspondence Analysis (CCA) of riparian forest seed bank composition, constrained by environment and disturbance (bold face) variables. a) N=84 species with selected exotic (open circle, italicized) and native (closed box) species depicted. b) N=12 constraining variables shown on 2x scale. First three letters refer to genus and second three to species. List of species available from corresponding author upon request.

Seed banks in our study were dominated by exotic species. Relative to other riparian forests (Hanlon, Williams & Moriarity, 1998), the proportions of herbaceous and exotic species were larger and those of woody and perennial species smaller (Moffatt, 2002). This, again,

is likely due to the degradation of these sites and the adverse effects of the surrounding land use. Ephemeral species were rare and were also largely absent from above-ground vegetation (Moffatt, 2002). This may be associated with the northern location of our study site, ostensibly at the edge of distribution for many of these species, but may also reflect decline in these forests associated with surrounding land use and the relative vulnerability of ephemerals to disturbance (McLachlan & Bazely, 2001).

Exotic species, including *Hesperis matronalis* and *Plantago major*, showed the greatest response to disturbance and environment variables. Sites that had low area:perimeter ratios and that were most isolated and disturbed had the greatest number of exotic and ruderal species. As human use increases and habitat becomes more open, forests become more susceptible to invasion, and seed banks may exhibit an increase in the proportion of exotics (Zabinski, Wojtowicz & Cole, 2000). Although our sites were often degraded and, as expected, characterized by shade-intolerant species, shade-tolerant forest species still remained in the seed bank (Pickett & McDonnell, 1989; Matlack & Good, 1990). In other studies, even those of relatively undisturbed sites, seed banks were similarly rich in both shade-tolerant and shade-intolerant species (Leckie *et al.*, 2000).

LAND USE

Human land use had a substantial impact on riparian forests in this study. Urban land use had the greatest effect on species composition, diversity, and density of the seed bank. Although effects of suburban land use were not as severe as those of urban use, they too altered seed bank species composition and diversity and seed density. Responses to use-associated disturbance were similarly and even more strongly reflected by aboveground herbaceous species (Moffatt, 2002). In urban sites, both seed banks and aboveground vegetation exhibited a higher ratio of exotics to native species, as these sites were much more disturbed, were dominated by edge habitat, had little if any interior habitat, and consisted of secondary forest. Urban seed banks were dominated by exotic and ruderal

TABLE II. Seed bank response to landuse ($N=5$) according to Hill's diversity measures [species richness (N_0) and dominant species (N_2), evenness (E_3)], density, exotic:native ratio, and Sorenson similarity (between seedbank and aboveground vegetation, within site seed bank composition, and between land use categories and reference sites).

		Land use category					ANOVA <i>P</i>
		Urban	Suburban	High rural	Low rural	Reference	
Seed Bank Diversity	$N_0^{1,2}$	11.0 ^b	13.0 ^{ab}	16.4 ^{ab}	18.2 ^a	15.4 ^{ab}	0.0471
	N_2	6.7	6.0	8.7	9.0	8.6	NS ²
	E_3	0.63	0.46	0.54	0.49	0.55	NS
Density (seedlings m ⁻²)		290.0	380.0	464.0	593.3	408.0	NS
Exotic:Native	Richness	1.7 ^a	0.9 ^b	0.9 ^b	1.0 ^{ab}	1.0 ^{ab}	0.0321
	Density	3.2	4.0	1.5	1.5	1.5	NS
Soerenson Similarity	Seedbank - Aboveground	24.2	17.9	23.4	26.6	20.8	NS
	Within site	15.8	22.4	21.7	30.0	23.4	NS
	Land use - Reference	25.4 ^b	39.8 ^{ab}	43.5 ^a	46.3 ^a	40.5 ^{ab}	0.0089

¹ Means within a row that have different superscript letters are significantly different from one another (Tukey's HSD).

² NS: non significant ($P > 0.05$).

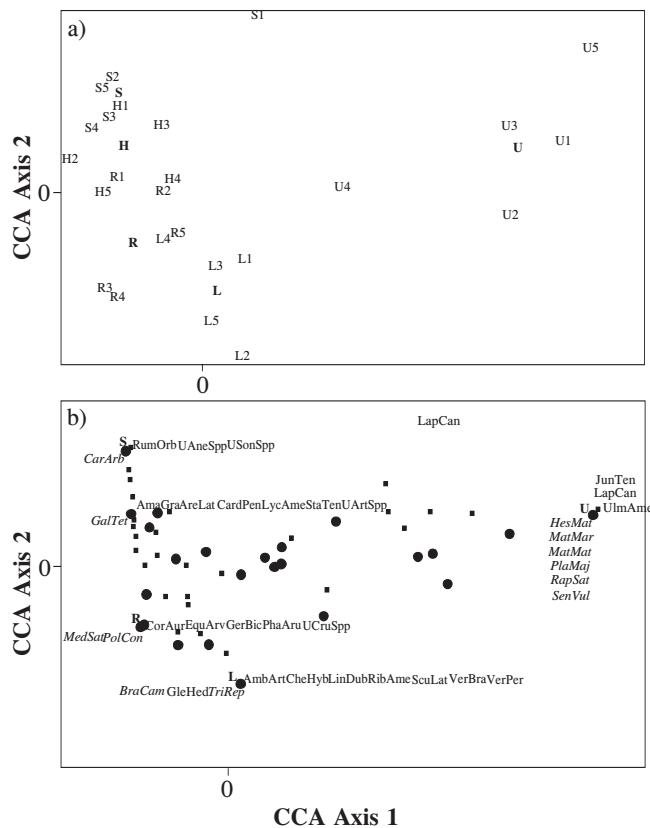


FIGURE 4. Results of Canonical Correspondence Analysis (CCA) of riparian forest seed bank composition, constrained by each land use class with the centroid (bold face) shown for (a) $N=25$ sites and (b) $N=84$ species with selected exotic (open circle, italicized) and native (closed box) species depicted. Land use classes are urban (U), suburban (S), high-intensity rural (H), low-intensity rural (L), and reference (R). First three letters refer to genus and second three to species. List of species available from corresponding author upon request.

species, and the lower diversity of urban and suburban seed banks also was a response to disturbance, as species richness generally declines with disturbance (Chambers, 1993). The lower seed density of urban sites may also be a response to the changes in site condition. The isolation and relatively small size of urban sites has likely

decreased the seed input from surrounding natural habitat (Moffatt, 2002). Moreover, it is likely that few seeds dispersing into urban sites become entrapped due to their typically compacted (Zabinski, Wojtowicz & Cole, 2000) and drier (Leckie *et al.*, 2000) soils.

Disturbance associated with urban land use was intense enough to eliminate broad groups of species from both the seed bank and aboveground vegetation. Indeed, four of the most dominant native species, including *Anemone canadensis* and *Carex* spp., were not present in urban seed banks. All were common in rural forests. Although moderate disturbance associated with suburban and rural land use also altered understory community composition, relatively rare species are likely to be replaced by more common species when disturbed (Wisheu & Keddy, 1991). If disturbance is great enough to alter the composition of the seed bank, it generally results in an increased number of exotic species (Zabinski, Wojtowicz & Cole, 2000). This is especially true in human-dominated landscapes, as many Eurasian exotics have evolved in response to human land use (Forcella & Harvey, 1983). The establishment of competitive or invasive species may, in turn, prevent the regeneration of native species (Stylinski & Allen, 1999).

Our study sites were selected across a wide range of edaphic conditions and land use types, which may have resulted in a widely varying seed bank. Site-level sample sizes also were relatively small, as practically required by landscape-level research. We attempted to compensate for this by increasing sample volume. These limitations may have obscured other important but less significant gradients that merit further interest, such as changes in species composition along the interior-to-edge of each site or differences between high- and low-intensity rural sites. Although corresponding to land use (Moffatt, 2002), potentially confounding downriver disturbance loading in the form of siltation and nutrient or pesticide concentration may have further contributed to variation among sites and may warrant future investigation. Seed banks in this study did show a substantial response to land use, but our approach was correlative and actual differences in seed dispersal among sites are now being investigated.

IMPLICATIONS

Seed bank studies have important implications for the management of riparian forests in human-dominated landscapes. Although effects of fragmentation on aboveground forest communities are well understood, landscape-level seed bank studies are rarely conducted. This may reflect inevitable logistical constraints and under-appreciation of the utility of seed banks by decisionmakers, as well as a relatively poor understanding of the mechanisms that underlie seed dispersal in degraded and fragmented forest systems. These kinds of data are important if seed banks are to be better understood and explicitly incorporated into management strategies.

Losses of some otherwise common native species and declines in seed density and species diversity in urban and suburban sites suggest that regeneration from the seed bank would lead to a shift in aboveground species composition. In particular, urban sites, with their very low diversity and density and high proportion of exotic species, cannot rely on the seed bank for future regeneration. The future persistence of these forests will likely depend on active restoration, including the removal of exotics and the planting of native species (McLachlan & Bazely, 2003). Although some urban forests in Manitoba are actively restored, this is almost entirely achieved by planting tree and shrub species. Given the paucity of the existing urban seed banks, the introduction of herbaceous species may also be necessary (Moffatt, 2002). Suburban seed banks were more diverse and similar to their rural and reference counterparts, suggesting that regeneration of suburban forests from existing seed banks may be more successful. It is, thus, important to understand how disturbance affects seed banks when planning conservation and restoration strategies for riparian forests in human-dominated landscapes.

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